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MONOGRAPH OF THE  
VOLES & LEMMINGS





# MONOGRAPH OF THE VOLES & LEMMINGS (MICROTINÆ)

LIVING AND EXTINCT

BY

MARTIN A. C. HINTON

VOL. I

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## PREFACE

THE Voles and Lemmings form a group that presents many difficulties to the systematist; they are also of special interest in relation to the dental evolution of the Simplicidentate Rodents. Mr. Hinton's monograph is the result of an intensive study that began more than twenty-five years ago; his work on the fossil species has led him to certain conclusions as to the sequence of Pliocene and Pleistocene deposits and the date of the Glacial Period, which were put forward at the 1925 meeting of the British Association, and will be published in the next number of the Proceedings of the Yorkshire Geological Society. This first volume includes a general account of the Microtinæ and a systematic revision of 14 of the 31 genera; the second, the preparation of which is well advanced, will conclude the work. Attention may be called to Mr. Hinton's views as to the importance of habits and environment in specific differentiation; when ideas of this kind are derived from a profound and intimate study of a group they should be worthy of serious consideration.

The author wishes to acknowledge his indebtedness to Mr. A. C. Savin of Cromer for the loan, without restriction of time, of a very large collection of Microtine remains from the Cromerian Beds; also to Mr. W. J. Lewis Abbott, Miss D. M. A. Bate, Dr. H. P. Blackmore, Dr. Frank Corner, Mr. J. Wilfrid Jackson, Mr. A. S. Kennard, Dr. H. C. Male, the late Dr. C. I. Forsyth Major, Dr. L. S. Palmer, Prof. S. H. Reynolds, Dr. R. F. Scharff, Dr. O. Wettstein, and Mr. Gilbert White for gifts or loans of fossil material. Thanks are also due to the Geological Survey of England and Wales, the Irish National Museum, the Royal Scottish Museum, the Museums of Cambridge University, Bristol, Norwich, Ipswich, Taunton, and Wells, the Bristol University Spelæological Society and the Vienna Museum, for the loan of material.

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the Hon. Ivor Montagu, who made a special examination of the great collections in Leningrad, and collected important material in the Caucasus.

The drawings of skulls have been made by Mr. Terzi; those of the teeth are by the author. The index has been prepared by Miss N. S. Kaye.

C. TATE REGAN  
(Keeper of Zoology).

*British Museum (Natural History),*  
*June, 1926.*

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# MONOGRAPH OF THE MICROTINÆ

## I. STRUCTURE AND CLASSIFICATION

### a. INTRODUCTION.

THE Voles and Lemmings are Simplicidentate Rodents belonging to the great family Muridæ, of which they constitute a subfamily, the Microtinæ. They are very widely distributed, ranging throughout the Holarctic region from the limits of terrestrial mammalian life in the high north southwards to the Alpine meadows of the mountains of Guatemala (just within the Neotropical region) and to those of Yunnan and Burma (in the Oriental region). They are not, however, known to live in Northern Africa, although a species of the fossorial genus *Ellobius* has left its remains in the Pleistocene deposits of Tunis and Algeria, and members of less highly specialized genera inhabit or have inhabited some of the islands of the Mediterranean. The vertical range of the subfamily is also wide, extending from the sea-beach up to the limits of mammalian life, at altitudes of about 20,000 feet in the Himalayas.

The oldest forms yet discovered are found in the later Pliocene deposits in Europe, and are already fully developed voles. Not improbably the Microtinæ originated in early Tertiary times in Northern and Central Asia, and it is to future palæontological work in that continent and perhaps in the high north that we must look for information about the forms which once connected the Microtinæ with the other subfamilies of Muridæ.

Having regard to the sedentary habits of these rodents and to their wide distribution, it is not surprising to find that the subfamily is a large one, comprising thirty-one genera and several hundred species. Within rather narrow limits the species show considerable plasticity, developing numerous more or less well-marked geographical or purely local races to meet the exigencies of the environment. They have therefore attracted a great deal of attention from systematists, and a very large number of generic, subgeneric, specific and subspecific names have been bestowed upon them in an extensive and widely scattered literature. In consequence the group has become one of the most difficult to deal with from a systematic point of view. Quite apart from this, however, many of the most important and most

widely ranging species are extraordinarily perplexing animals. Although they attain sexual maturity and an adult appearance at a very early age, their growth continues for an unusually long period, during which colour, form of the skull and structure of the teeth may change to such an extent that in old age they may present characters widely different from those shown in the earlier "adult" stages of growth. To work out the life-histories of such mammals thoroughly requires a large amount of material and more time than is at the disposal of a systematist busied with the task of determining collections as they arrive in the Museum. One general result of my work has been to reduce the number of genera and species considerably.

The Microtinæ are of great general interest and merit careful attention. Their structure is highly modified in relation to subsistence upon a diet despised by most other Muridæ, and to their burrowing habits, but it retains certain primitive features which seem to throw light upon the problems connected with the ancestry of the Simplicidentate Rodents and with the evolution of their molars. The close adaptation of form and structure to the needs of special functions shown by the skulls, teeth, and other organs of the Microtinæ deserve close study; in one genus (*Mimomys*) at least, where we can trace a single phylum forward in time, we find a good example of recapitulation. Owing to the short range in time of the individual species the group is of great importance to the geologist who has to correlate scattered deposits like those of the Pleistocene period in Britain.

The Microtinæ become of considerable economic importance in certain circumstances, as in "mouse years," when, favoured by lenient weather and often by unwitting human intervention, voles and lemmings swarm and inflict great losses upon agrarian industries. In such years, too, riparian species occasionally do serious damage to the banks of streams and canals by their burrowing operations. When present in reasonable numbers these rodents, like most other creatures, play their part in maintaining the general balance of Nature, and in uncultivated lands their fossorial activities endow many tracts, which would otherwise be completely barren, with comparative fertility.

Some species are apparently concerned in the dissemination of disease, as, for example, the Japanese *Microtus montebelloi*, which is believed to be one of the natural reservoirs of Infectious Jaundice and Japanese River Fever.

The North American genus *Ondatra* is of much value as a fur-bearer. During the open season the flesh of this animal is extensively used as food in the large towns of eastern North America.

Much remains to be done before a really satisfactory account of the subfamily can be written. The present work is intended to summarize existing knowledge and to direct attention to some points of more general interest that require further investigation.



## b. PREVIOUS WORK AND PRESENT TREATMENT.

Modern knowledge of the Microtinæ is based upon Miller's "Genera and Subgenera of Voles and Lemmings," published in 1896.<sup>1</sup> In that fine work Miller gave an admirable review of the earlier classifications and established a natural classification which swept away the more or less artificial systems of his predecessors (de Selys-Longchamps 1836-1862, Blasius 1857, Baird 1857, Fatio 1867, Coues 1874, Blanford 1881, Lataste 1887). Subsequent research has tended only to extend and to correct in detail the results at which Miller arrived.

Miller confined his attention chiefly to the living members of the subfamily, of which he recognized seven genera, namely, *Synaptomys*, *Lemmus*, *Dicrostonyx*, *Phenacomys*, *Evotomys*, *Microtus* and *Fiber* [= *Ondatra*]. *Synaptomys* included two subgenera, *Synaptomys* and *Mictomys*, as in the present work; whereas *Microtus* included eleven subgenera, namely, *Eothenomys*, *Antelomys*, *Lagurus*, *Alticola*, *Hyperacrius*, *Pedomys*, *Phaiomys*, *Pitymys*, *Chilotus*, *Microtus*, *Arvicola*, and *Neofiber*, all of which are now accorded full generic rank. *Ellobius*, here included in the Microtinæ, was not regarded as a member of the subfamily.

Miller's work both stimulated and facilitated further research, so that in current literature more than fifty genera and subgenera (including fossil forms) are recognized. But some of these are not valid, and here only thirty-one genera and subgenera are described.

The most important recent addition to our knowledge concerns the remarkable genus *Prometheomys* described in 1901 by Satunin. Vinogradov has prepared a valuable and beautifully illustrated account of some material now in Leningrad; that paper, to which I am greatly indebted, will be published elsewhere. My knowledge of the genus rests, however, upon an even more solid foundation, thanks to the Hon. Ivor Montagu, who visited the Caucasus in the interests of the British Museum last autumn. There he obtained a magnificent series of specimens representing all the stages of growth of this rare animal; this material has enabled me to reach a definite conclusion as to the relationship of the genus and substantially to confirm Vinogradov's results.

As regards living species my work has been greatly lessened by the labours of Miller and Thomas in the Old World; and by those of Bailey, Hollister and many others in America. The collection of North American Microtinæ in the British Museum, although sufficient to enable one to appreciate generic characters and those of some of the leading species, is far too small and incomplete to warrant any attempt being made to give an independent and new account of American species and subspecies. But revisions of the North American species of *Evotomys* and

<sup>1</sup> North American Fauna, No. 12, 1896.

*Microtus* (in the wide sense understood by Miller in 1896) by Vernon Bailey<sup>1</sup> and of *Ondatra* by Hollister<sup>2</sup> have been published by the United States Biological Survey; in order to make the present book as compendious as possible free use has been made of this admirable work.

Knowledge of fossil Microtinæ has grown slowly since the days of Buckland and Cuvier, who seem to have been the first to pay attention to this part of the subject. In this country palæontological work on the group has been done chiefly by Owen, Sanford, Blackmore and Alston, E. T. Newton, Forsyth Major and the present writer; on the Continent we are indebted chiefly to Pomel, Hensel, Forsyth Major, Nehring, Woldrich, and Méhely. In America fossil remains have attracted less attention: Cope and Hollister are the chief writers who have dealt with them hitherto.

Mention must be made of the work of Forsyth Major and Winge, two distinguished men who paid much attention to the Microtinæ; their respective contributions to the special literature of the group are among the most valuable we possess. In the writings of Forsyth Major we find the one theory that, in my opinion, fits all the facts and accounts satisfactorily for the evolution of rodent molars. In those of Winge is a masterly review of all the mammalian orders, together with a lucid exposition of the principles which should be used as a guide when investigating the relationships of mammals. One may differ from Winge on almost every point of detail and yet find inspiration and guidance in his work.

Every mammal is the product of two distinct and sometimes conflicting forces; a compound of relatively essential characters, fixed for the time being in each group by inheritance, and of more or less plastic characters which yield like potter's clay to the thumb of stern necessity. It is the special use that a mammal makes of its various organs that results eventually in a more or less perfect adaptation of form and structure to particular functions, no matter whether the special use is called into being by tempting opportunity or by the compelling stress of circumstances. Use and habit, all that goes to make environment in the widest sense, have thus made species what they are; no character is absolutely beyond the reach of external influences, although in practice some may never be reached. That characters so acquired become in the course of generations intensified, customary, and at last the normal heritable attributes of a species is the lesson taught by every scrap of philosophical palæontological work upon the Mammalia that has been done since the day when Kowalevsky published the celebrated introduction to his memoir on *Anthra-*

<sup>1</sup> BAILEY, "Revision of the American Voles of the genus *Evotomys*," Proc. Biol. Soc. Washington, 11, pp. 113-138, 1897.

BAILEY, "Revision of American Voles of the genus *Microtus*," N. Amer. Fauna, No. 17, 1900.

<sup>2</sup> HOLLISTER, "A Systematic Synopsis of the Musk Rats," N. Amer. Fauna, No. 32, 1911.

*cotherium*; it is the lesson turned to practical use by Winge in systematic work. If the more or less substantial mask of specialization be stripped off from each species one finds the primitive core of each animal underneath; if the primitive characters so found be used as the bases of comparison there is no difficulty either in arranging species, genera, and families in natural order, or in conceiving what the essential characters of the ancestor common to any given group must have been. That is what I have attempted to do in this book. The stripping process is, however, by no means easy, and it reveals many a disconcerting gap in our knowledge.

### C. GENERAL CHARACTERS OF THE MICROTINÆ.

#### *External Characters.*

In general outward form the Microtinæ differ but little from ordinary rats and mice. All are more or less evidently modified for burrowing, and a few, in addition to their fossorial peculiarities, show conspicuous adaptation for aquatic habits. The members of the subfamily thus display a somewhat striking uniformity in outward appearance, and lack that variety of shape which is so characteristic of the Cricetinae and Murinae.

*In relation to their size* voles and lemmings are robust, thickset animals with broad, more or less flattened heads and short, bluntly rounded muzzles. The eyes and ears are small and in some genera are very greatly reduced. The limbs are moderately long, muscular and powerful; but they are hidden to a great extent in the general integument of the trunk, a circumstance which gives the Microtinæ a characteristic short-legged appearance.

The hands and feet have each five digits armed with claws which differ considerably in size and form, according to the habits, in different genera; the thumb is always greatly reduced and bears either a small claw or else a flattened nail. When least modified the palms bear five, the soles six well-developed pads; but in the more highly specialized forms some or all of these pads may lose their functional importance and tend to disappear. Typically the palms and soles are naked between the pads, or but scantily and incompletely clothed with hair; but in the more specialized forms they may become either completely naked, as in the aquatic genus *Ondatra*, or densely covered with hair, as in the boreal genus *Dicrostonyx*; in both these genera the modification is accompanied by reduction of the palmar and plantar tubercles. The upper surfaces of the hands and feet are always well clothed, but the lower surfaces of the digits are usually naked, with the skin thrown into scaly annulations by transverse folds.

The tail is never very long, but may reach a length about two-thirds that of the head and body; in several genera it is quite short and in some is reduced to a mere vestige considerably shorter

than the hind-foot. The skin of the tail is scaly, the scales usually forming rather well-marked annulations; it is more or less well clothed with stiff hairs, which may or may not conceal the scales; frequently a distinct terminal pencil of variable length and thickness is developed.

The fur tends to be soft and dense in all the Microtinæ; in those most highly specialized for fossorial life it is very short, fine, uniform, silky, and mole-like in texture; whereas in the aquatic forms the contrast between the silky, dense under fur and the longer, stiffer, and more lustrous contour-hair is intensified.

The normal mammary formula in the group is  $2 - 2 = 8$ , there being two pectoral and two inguinal pairs of mammæ in the females. In many genera one or both pairs of pectoral mammæ become functionless and disappear, the formula being reduced to  $1 - 2 = 6$  or  $0 - 2 = 4$ ; exceptionally the inguinal mammæ suffer reduction, so that the formulæ  $2 - 0 = 4$ ,  $2 - 1 = 6$ , and  $1 - 1 = 4$  are not unknown within the subfamily.

In many genera specially developed glands are present upon the flanks or hips in adult males and sometimes in both sexes. Special perineal glands, secreting a powerful musk, occur in the genus *Ondatra*.

#### Skull.

The skull of the Microtinæ is always of firm and often of relatively massive construction, the sagittal sutures between the paired frontal, premaxillary, maxillary, and palatine bones generally fusing and disappearing either before or shortly after birth. Normally the skull is characterized by the shortness of the rostrum (in dorsal view), and by the forward position of the orbit, which is always anterior to a vertical plane touching the front edges of the anterior molars. The form of the outer wall of the infraorbital canal is also characteristic; it is a stout, more or less vertical plate of bone (the "masseteric plate" or "descending ramus of the maxillary root of the zygoma"), which is always placed more or less transversely or obliquely to the long axis of the skull; the front edge is slightly emarginate or undercut and never projects in advance of the front border of the superior ramus of the maxillary root of the zygoma.

The infraorbital canal itself is formed essentially as in other Muridæ, its upper portion being widened for the transmission of a slip from the *masseter medialis* muscle, its lower portion, narrow and slit-like, serving for the passage of the facial or infraorbital branch of the superior maxillary or second division of the fifth nerve and the accompanying vessels; in *Ellobius*, however, the lower part of the canal is reduced and closed, but the upper portion, in compensation, is somewhat more spacious than usual.

The zygomatic arches are strongly built and more or less widely bowed laterally; each is greatly strengthened by the oblique position and peculiar shape of its lower maxillary root

(the "masseteric plate" described above), which forms a great flying buttress for the support of the fore-part of the arch; the superior maxillary root, forming the roof of the infraorbital canal, is very short. The distal end of each maxillary zygomatic process is expanded into a broad fork which receives the anterior end and much of the lower border of the jugal; this bone is always very short and is confined to the central portion of the arch, bridging the small interval between the maxillary and squamosal zygomatic processes. The squamosal root of the zygoma is relatively weak.

The nasals are relatively short, often ending anteriorly well behind the front faces of the incisors, and never conspicuously in advance of them; posteriorly they terminate usually either a little in front of or on a level with the anterior margin of the orbit.

The interorbital region is always clearly defined, but in its degree of constriction it differs considerably in different genera and species, as well as in different stages of growth in one and the same individual, tending as a rule to become narrower with age. In many forms the temporal ridges, which always extend far forwards, approach each other and in adults fuse to form a median crest in the interorbital region; in other forms the ridges though salient remain more or less widely separated by a median sulcus; in many genera the ridges are feeble and both the interorbital region and the interval between the ridges in that region remain wide and flat even in old age.

On the roof of the braincase the temporal ridges usually diverge from the hinder part of the interorbital region to points above and nearly in the same transverse plane as the glenoid articulations; thence the ridges converge slowly to the hinder part of the parietal region and then again curve outwards, passing the extremities of the interparietal to join the front face of the occipital crest. Throughout their course, after leaving the frontals, these ridges tend to follow the upper edge of each squamosal, but they impinge upon the parietals anteriorly and cross the lateral wing of each parietal in the post-glenoid region. In some genera (*Ondatra*, *Prometheomys*, and *Ellobius*) the temporal ridges are closely approximated throughout in the later stages of growth; and in *Prometheomys* they form a salient sagittal crest which, in old age, extends from the interorbital region to the occiput.

The squamosals are always largely developed, forming a great deal of the sides of the braincase. In this subfamily no post-orbital processes are ever formed by the frontals; but very characteristic post-orbital crests are developed upon the squamosals for the attachment of a tendinous portion of the anterior part of the temporal muscle on each side; in some genera these crests are represented by prominent peg-like processes. In genera in which the temporal ridges form an interorbital crest, the squamosals frequently show a tendency to approach each other anteriorly,

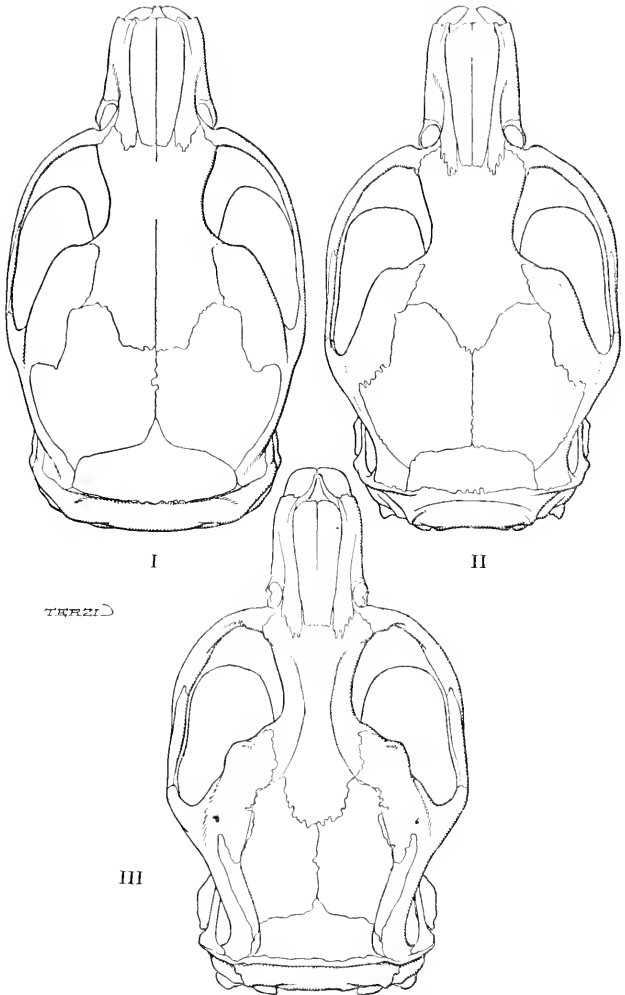


FIG. 1.—*Arricola amphibius* Linnæus.

Dorsal views of skulls in different stages of growth. Condyllo-basal length, Stage I, 25.1 mm., St. II, 31.2 mm., St. III, 35.5 mm.

Figs. 1 and 2 illustrate the changes, which accompany growth, in the relative proportions of the cranial and facial parts of the skull, the progressive constriction of the interorbital region, gradual development, approximation and fusion of the temporal ridges, increasing salience of the post-

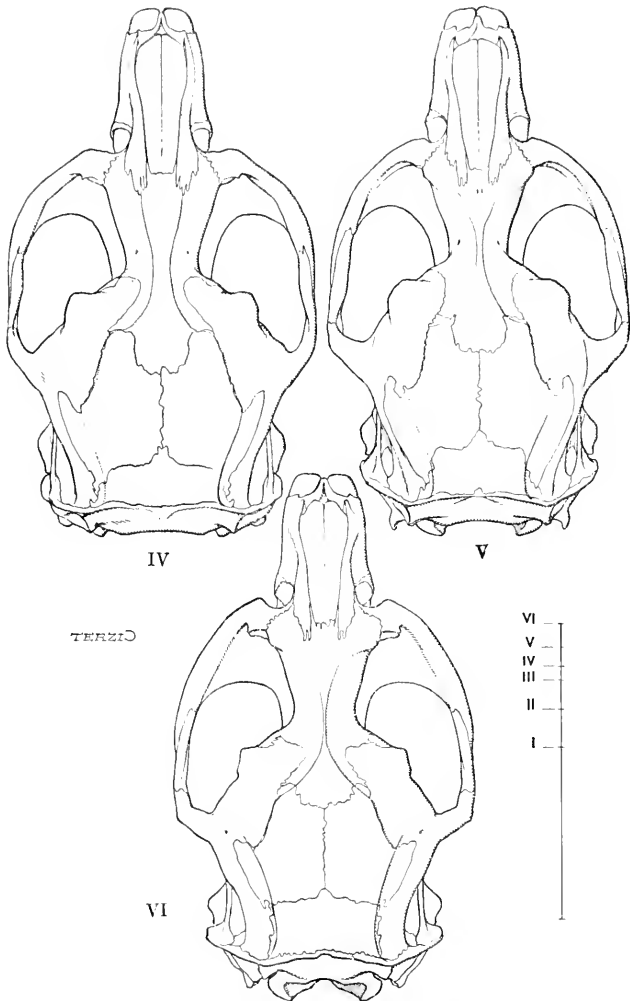


FIG. 2.—*Irricola amphibius* Linnaeus.

Dorsal views of skulls in different stages of growth (continued). Condylobasal length, Stage IV, 37.8 mm., St. V, 40.6 mm., St. VI, 44.3 mm.

orbital crests, and gradual approximation of the squamosals on the fore-part of the braincase. Other changes in the rostrum, zygomata, interparietal and occiput are also shown.

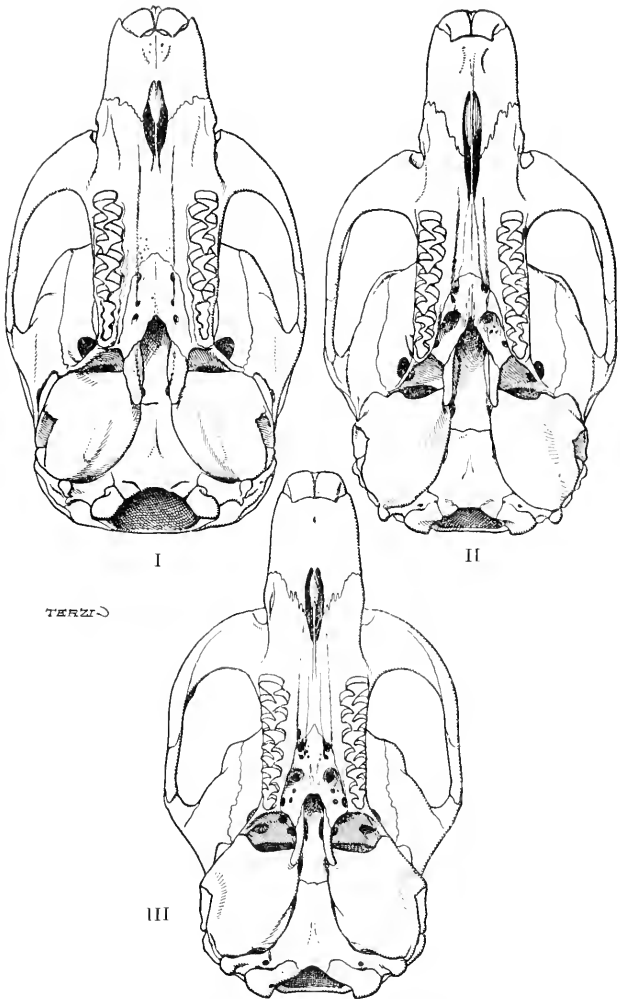


FIG. 3.—*Arvicola amphibius* Linnæus.

Ventral views of skulls in different stages of growth. Stages I, II, and III (same specimens as shown in Fig. 1).

In Stage I the rostrum is short and broad, the molars are relatively large, the palate is simple and level throughout, the pterygoid fossæ are short, and the bullæ are rounded. In the later stages the rostrum becomes progressively longer and narrower as the incisors increase in length, the



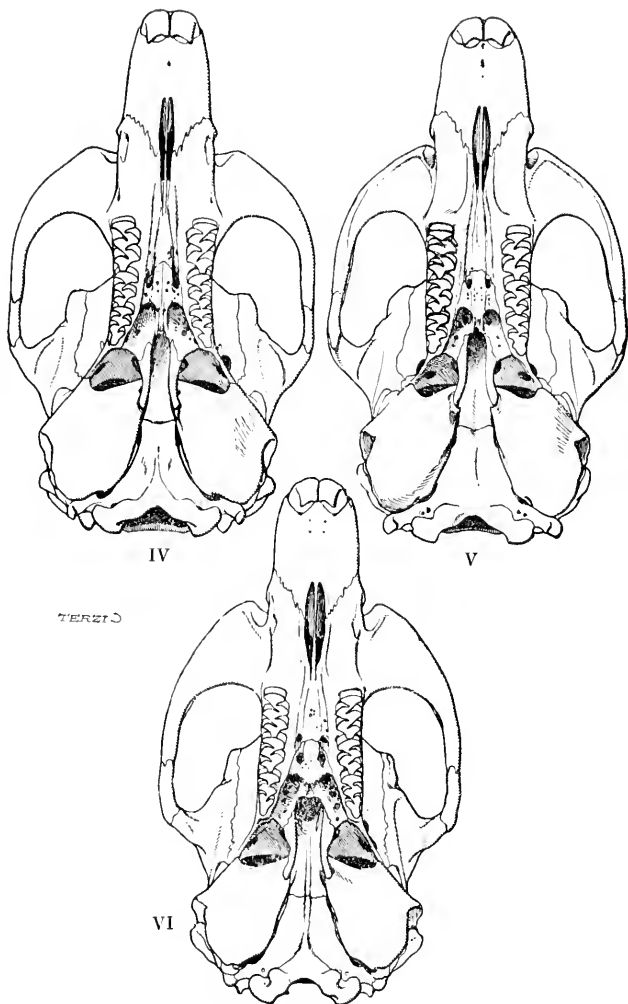


FIG. 4.—*Arvicola amphibius* Linnæus.

Ventral views of skulls in different stages of growth. Stages IV, V, and VI (same specimens as shown in Fig. 2).

molars become relatively smaller, the hinder part of the palate is sculptured in bold relief, the pterygoid fossæ increase in size, and the bullæ develop large eustachian processes.

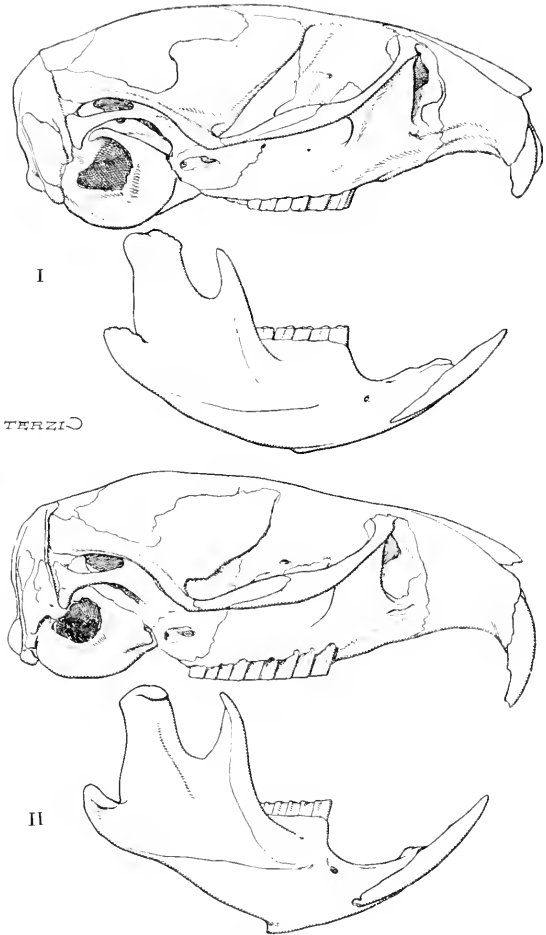


FIG. 5.—*Arvicola amphibius* Linnæus.

Lateral views of skulls in different stages of growth. Stages I and II (same specimens as shown in Fig. 1).

In Figs. 5-7 the progressive flattening of the dorsal surface, the changing direction of the occiput (inclined backwards in Stage I, forwards in Stage VI), the forward migration of the orbit (most marked in Stages V

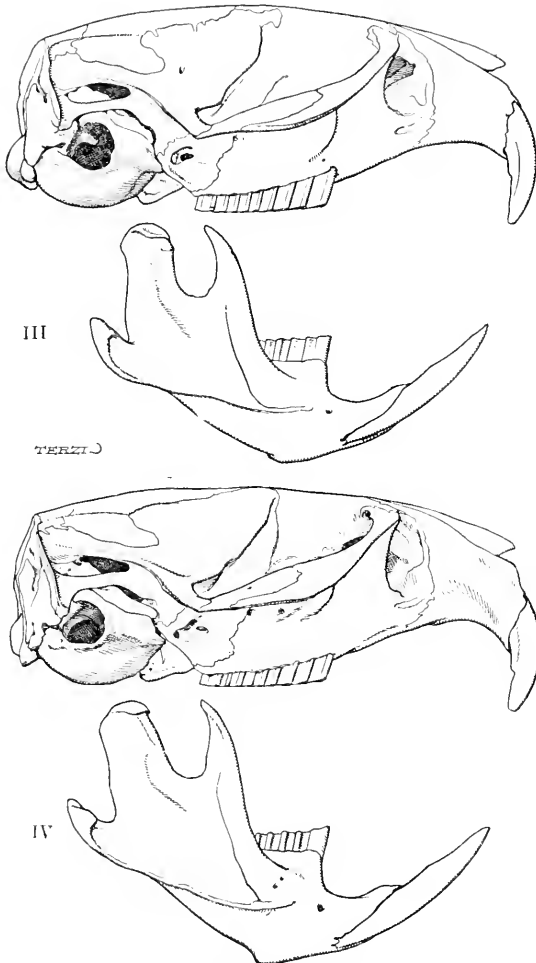


FIG. 6.—*Arricola amphibius* Linnaeus.

Lateral views of skulls in different stages of growth. Stages III and IV (same specimens as shown in Figs. 1 and 2).

and VI), and the changes in the form of the auditory bullæ are features worthy of attention.

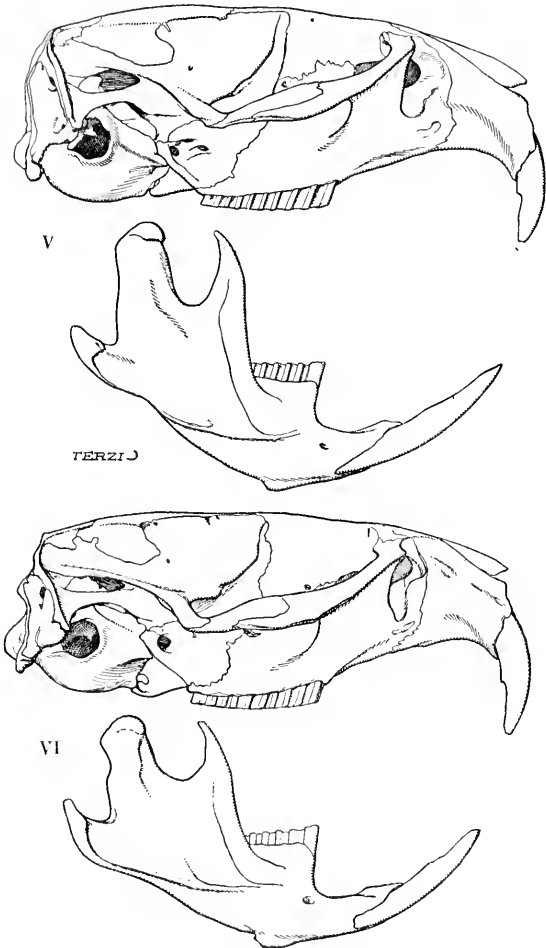


FIG. 7.—*Arvicola amphibius* Linnaeus.

Lateral views of skulls in different stages of growth. Stages V and VI (same specimens as shown in Fig. 2).

encroaching upon the frontals to an unusual extent. In the post-glenoid region there is typically a large fenestration in each squamosal immediately above the auditory bulla; but in some genera the fenestra is represented merely by a small foramen.

The interparietal is usually large. In genera in which the temporal ridges sweep by and do not cross the lateral extremities of the bone its form is to a very large extent influenced by the degree in which those ridges are approximated posteriorly; as the ridges tend to become closer together with age, the interparietal becomes narrower in relation to its length. In genera in which the ridges traverse the interparietal that bone becomes very small, as in *Ondatra* and *Prometheomys*; in the latter genus

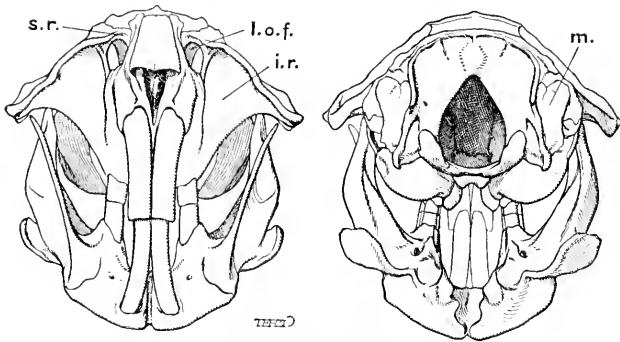


FIG. 8.—*Arvicola amphibius* Linnaeus.

Anterior and posterior views of skull with mandible in position: *s.r.* upper maxillary root of the zygoma; *i.r.* lower maxillary root of the zygoma, forming the outer wall of the infraorbital canal or "masseteric plate"; *m.* mastoid portion of periotic.

the sagittal suture persists, even in old age, dividing the bone into two halves, a character that may be seen occasionally in other voles, e.g., *Phaiomys*.

The anterior palatal foramina are usually moderately large, but in forms showing marked fossorial specialization of the skull they are much reduced in size. From the posterior end of each foramen a well-marked groove, the lateral palatal groove, runs back on each side of a median elevated tract and crosses the maxillo-palatine suture in the neighbourhood of  $m^2$ ; the groove may terminate here in one of the posterior palatal foramina; but, if the postero-lateral bridges are well developed, it usually continues past the foramen, deepens behind it, and passes under (dorsal to) the postero-lateral bridge to effect, as a rule, a junction with the postero-lateral pit ("post-palatine fossa").

The posterior portion of the palate presents characters of

importance to the systematist. In some genera the palate terminates behind in a simple transverse shelf with or without a median process or "nasal spine"; in these the postero-lateral pits lie at a deeper level and pass forwards under (dorsal to) the palatal shelf, and their inner borders do not form any externally visible connection with the shelf or with its "nasal spine" (e.g., *Evoatomyx*, *Dicrostonyx*, *Lemmus*). In other genera the "nasal spine" is elongated, is inclined dorsally instead of being horizontal, and is connected at its tip and sides with the inner borders of the postero-lateral pits, thus becoming converted into a sloping median septum between the pits. In the more primitive of these genera the median septum is short, broad, and ill defined, but in the more specialized ones it is long, narrow, and very sharply defined; frequently the ventral surface of the septum is grooved, and sometimes it is completely cleft. The floors of the postero-lateral pits are usually perforated by numerous small foramina which serve for the transmission of nerves and vessels to the soft palate and upper part of the pharynx; but in *Prometheomys*, in which the hinder part of the palate is generally speaking somewhat intermediate between the two types described above, the floor of each pit is occupied by a single very large foramen.

The pterygoid fossæ vary in size and depth from genus to genus, but the ectopterygoid plates are always well developed. When deepest the floors of the fossæ lie at a level distinctly dorsal to the ventral surface of the basisphenoid and by means of a small transverse canal perforating the latter they are placed in communication with each other. To a large extent the size of the pterygoid fossæ, the width of the choanæ, of the back part of the basisphenoid and of the fore-part of the basioccipital seem to be dependent upon the varying size of the auditory bullæ.

Some of the most characteristic features of the Microtine skull are shown in longitudinal vertical sections (Figs. 9 and 10). In other Muridæ the palatine processes of the maxillary and palatine bones are thin; but in Microtinæ they are enormously thickened, probably in correlation with the unusually tall and robust crowns of the molars and with the powerful development of the jaw muscles. The hinder part of each palatine, *i.e.*, the portion which forms the post-palatal pit, remains thin. The presphenoid, the basisphenoid and the fore-part of the basioccipital are considerably thickened vertically. In the floor of the braincase (Fig. 11) the presphenoid is of unusual length, in correlation with the great length of the tooth-rows; but owing to the intrusion of the alveolar capsules of  $m^2$  and  $m^3$  into the sphenorbital fissure, this bone and the fore-part of the basisphenoid are greatly compressed laterally. The sphenorbital fissure occupies a great area in the cranial floor, but in the more hypsodont genera its outlets are greatly straitened by the tooth capsules, which divide the fissure into two parts, an inner and an outer; the inner division between the tooth capsules and the presphenoid transmits the

first and second branches of the fifth nerve; the outer division between the tooth capsules and the alisphenoid serves for the passage of the internal maxillary artery, which often grooves the outer side of the alveolar capsule of  $m^2$ .

The alisphenoids are very large; of each the ascending process forms a large part of the anterior wall of the braincase, rising in the orbit nearly to the level of the post-orbital process of the squamosal and there articulating with the frontal; the descending process forms an ectopterygoid plate, greatly developed in all Microtinæ, which articulates with the squamosal and auditory bulla behind, and bridges the foramen ovale to serve as a buttress supporting the hinder end of the alveolar portion of the maxilla. The horizontal plate is ankylosed with the basisphenoid as usual; it is pierced at its base by a foramen for some of the cerebral vessels in front of the very shallow pituitary fossa, and externally by the large *foramen ovale*. Just below the front edge of the *foramen ovale* and external to the ectopterygoid plate is a foramen by which the internal maxillary artery enters the outer division of the sphenorbital fissure. There is no distinct *foramen rotundum*, the second branch of the fifth nerve emerging with the first through the sphenorbital fissure. The orbito-sphenoids are small, are completely ankylosed with the presphenoid, and are pierced by the small optic foramina, as usual. Posteriorly the basisphenoid is often notched for the passage of the internal carotid artery; in *Prometheomys* the notch is represented on each side by an oblique tunnel, the mouth of which is a conspicuous feature in the floor of the braincase; small passages from the anterior wall of this tunnel place it in communication with the vascular passages through the base of the alisphenoid and also with the transverse canal, which is constantly present in the Microtinæ and gives passage to a vein that passes from one pterygoid fossa to another through the body of the basisphenoid.

The auditory bullæ are always well developed. When least modified they have thin papery walls; when more specialized their walls are strengthened by bony threads developed in folds of the mucous membrane lining the cavity of the middle ear; and in their most modified condition the walls are formed by a compact mass of spongy bone, and the *tegmen tympani* and mastoid portions are considerably inflated. The external meatus becomes tubular in aquatic forms, and is often much straitened in fossorial genera. The stapedial artery is often enclosed in a bony tube which passes through the stapes.

The mandible always possesses distinct coronoid and angular processes, although the latter are reduced in some genera. The horizontal ramus is characteristically stout, and is considerably thickened for the accommodation of the hypsodont cheek-teeth. At the symphysis the mandibular rami are united, as in other Muridæ, merely by ligament.

*Dentition.*

As usual in Muridæ the dentition of the Microtinæ consists of sixteen teeth, namely a pair of incisors and three pairs of cheek-teeth or molars in each jaw above and below, usually expressed by the formula  $i_1^1 m_3^2 = 16$ . It is, however, questionable whether the three cheek-teeth are in fact the homologues of the teeth called  $m_1^1$ ,  $m_2^2$ , and  $m_3^3$  in other placentals (see p. 124).

As in all other Rodents the incisors are persistently growing

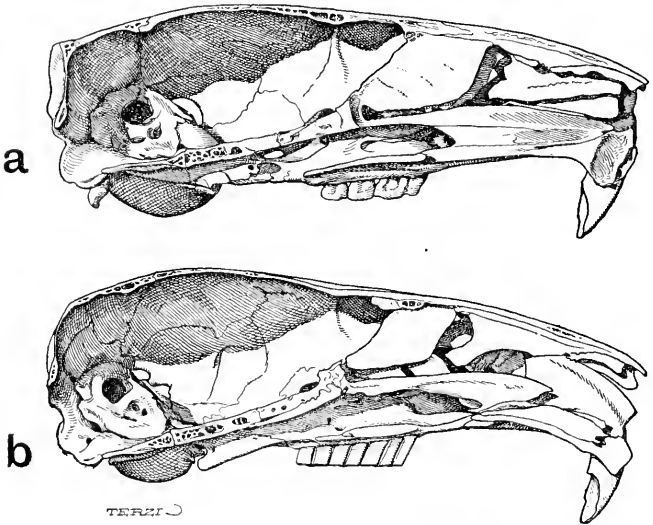


FIG. 9.—Vertical longitudinal sections of skulls of Muridæ (enlarged).

a. *Rattus rattus* Linnæus; b. *Neotoma* sp. (See p. 16.)

teeth. The upper incisors are strongly curved as compared with those of the lower jaw and form larger segments of relatively small circles, whereas their opponents invariably form smaller segments of relatively large circles. Posteriorly the alveolar sheath of each upper incisor passes backwards into the maxillary bone, where it usually terminates just in front of the alveolus of  $m_1^1$ ; in *Ellobius*, however, it pushes its way back on the inner or lingual side of the molar roots to terminate in the hinder part of the maxilla immediately dorsal to the palatal surface of the bone, the termination of the tooth capsule being often marked by a fenestration of the maxilla. Each lower incisor passes backwards through the mandibular ramus. In the Lemmings this tooth lies on the



lingual side of the molars throughout, and its alveolar capsule terminates behind at a point opposite the alveolus of  $m_3$ . In the Voles the tooth is much longer; it passes backwards on the lingual side of  $m_1$  and  $m_2$ , crosses to the labial side of the jaw

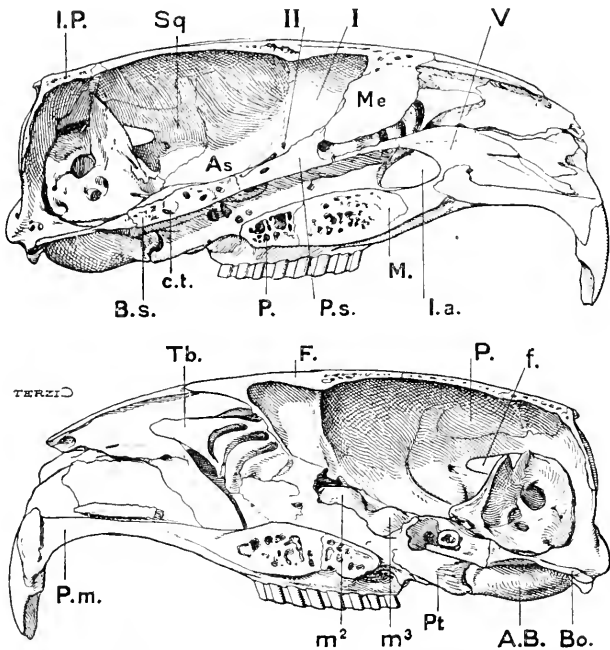


FIG. 10.—Vertical longitudinal sections of skull of *Arvicola amphibius* Linnaeus (enlarged).

*I.P.* interparietal; *Sq.* squamosal; *II.* optic foramen; *I.* olfactory chamber; *V.* vomer; *As.* alisphenoid; *Me.* mesethmoid; *B.s.* basisphenoid; *c.t.* transverse canal; *P.* palatine; *P.s.* presphenoid; *M.* maxilla; *I.a.* alveolus of incisor.

*Tb.* turbinals; *F.* frontal; *P.* parietal; *f.* supratympanic fenestra of squamosal; *P.m.* premaxilla;  $m^2, m^3$  alveolar capsules; *Pt.* pterygoid; *A.B.* auditory bulla; *Bo.* basioccipital.

between  $m_2$  and  $m_3$ , and ascends into the condylar process to a greater or less height, its termination often producing a well-marked hump on the outer surface.

In structure the incisors are quite typical. Each is developed from a persistent pulp lodged in the widely open pulp-cavity at its base. The front face of the tooth is formed by a thick plate of hard enamel which thins out and ends off on the lateral surfaces;

the core of the tooth, exposed on its posterior face, is formed of relatively soft dentine. In transverse section the teeth are usually wider than deep; the enamel is frequently stained by a yellow pigment; the front face of each upper incisor may or may

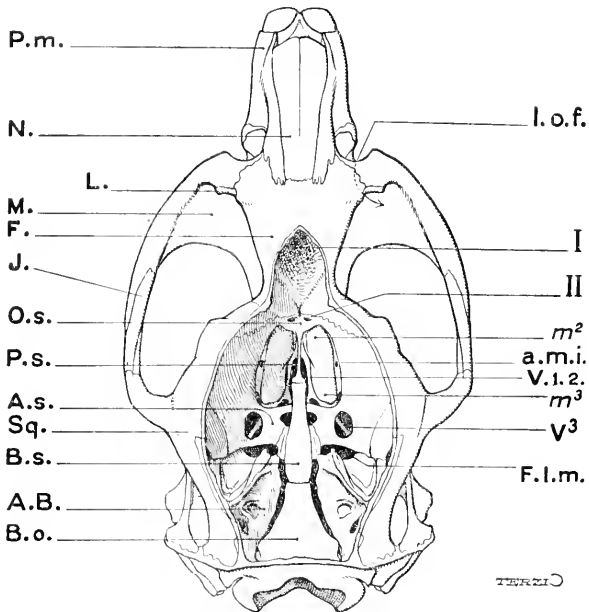


FIG. 11.—Skull of *Arcicola amphibius* Linnæus, with top removed to expose the floor of the braincase.

*P.m.* premaxilla; *N.* nasal; *L.* lachrymal; *M.* maxilla; *F.* frontal; *J.* jugal; *O.s.* orbitosphenoid; *P.s.* presphenoid; *A.s.* alisphenoid; *Sq.* squamosal; *B.s.* basisphenoid; *A.B.* periotic; *B.o.* basioccipital. *I.o.f.* infraorbital canal; *I.* olfactory chamber; *II.* optic foramen; *m*<sup>2</sup>, *m*<sup>3</sup>. alveolar capsules; *a.m.i.* groove for internal maxillary artery; *V.1.2.* exit for first and second branches of fifth nerve; *V*<sup>3</sup>. *foramen ovale*; *F.l.m.* *foramen lacerum medium*.

not be traversed by a longitudinal groove. The teeth differ considerably from genus to genus, and the significance of some of the differences is discussed below.

The cheek-teeth are highly characteristic. In all Microtinæ they are tall-crowned or hypsodont. In some genera they are of limited growth, closing their pulp-cavities and cement-spaces below, developing roots, and wearing out in old age. But in the

majority of the genera they are persistently growing teeth like the incisors, in which development at their bases from ever-active dentinal pulps and enamel organs compensates throughout life for

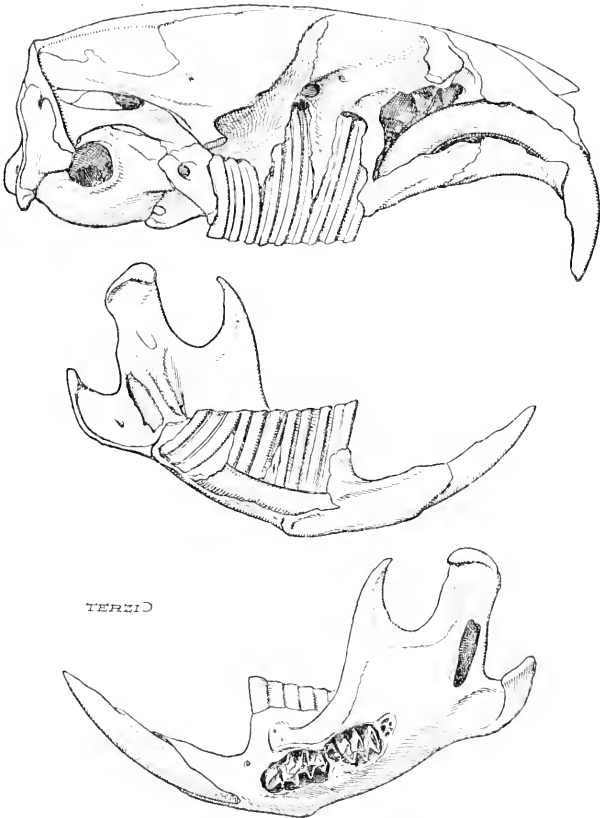


FIG. 12.—*Arvicola amphibius* Linnæus.

Skull and left mandibular ramus dissected to show the alveolar courses of the teeth.

the continuous loss of substance which takes place at the wearing surface of each tooth.

The worn surfaces of these teeth display a peculiar pattern of triangles and transverse loops, produced by the truncation by wear of the ends of the tall columns or prisms of which each

crown appears to be composed, and giving rise to a number of salient angles and re-entrant folds along the inner and outer borders of the tooth. Each triangle or loop is formed by dentine, surrounding an inner core of relatively soft "osteodentine," and bounded externally by a sheet of relatively hard enamel. The front end of each upper molar and the hinder end of each lower molar is formed by a more or less crescentic or pyriform transverse loop, the inner and outer extremities of which form the first inner and first outer salient angles. The triangles behind or in front of this transverse loop are arranged in two series, an inner and an outer, the members of which alternate with each other more or less distinctly and regularly. The apex of each triangle forms a salient angle which is separated from its neighbours by a re-entrant fold or cement space, which in many genera is partly filled with cement. At the hinder part of  $m^3$  and the fore-part of  $m_1$  the triangles are succeeded by a complex structure, the "posterior loop" in  $m^3$ , the "anterior loop" in  $m_1$ ; these terminal loops are often of great systematic importance.

In describing the teeth it is customary to enumerate the salient angles and re-entrant folds from before backwards in upper molars, and from behind forwards in lower molars, the first salient angle on each side being formed by the transverse loop. The differences in the number, form, and relative size of the triangles and salient angles, the degree to which the dentinal spaces are open to or closed off from each other, the greater or less complexity of the anterior loop in  $m_1$  and of the posterior loop in  $m^3$ , the distribution and nature of the enamel sheet in different parts of the periphery, the presence or absence of cement, and above all the circumstance whether the cheek-teeth are of persistent or of limited growth, *i.e.*, rooted or rootless;—all these, when used with discretion, afford excellent characters for the distinction of genera and species. But in using them for such purposes it must always be borne in mind that the pattern is often subject to considerable variation, not only in different individuals, but in different stages of wear in the same individual; the old idea that "prismatic teeth" present the same pattern throughout life is erroneous. These and many other points are discussed below in the section dealing with the evolution of the teeth (p. 102).

#### *Jaw Muscles.*

It is not possible to give a full account of the myology of the Microtinæ in the present work, but the following notes on the more important muscles of the jaws, based chiefly upon several dissections of *Arvicola amphibius*, will give a fair idea of the general arrangement found in the group.

The most important muscles are the *temporalis* and the *masseter* (Figs. 13 and 14). These have played a great part in moulding the outward form of the skull; the effects of their

powerful influence upon the bones to which they are attached are seen not only in passing from genus to genus, but in tracing the life-history of the individual from youth to old age.

**MASSETER LATERALIS.** This muscle consists of two distinct portions; one, anterior and superficial, partly concealing the other, posterior and deep.

The anterior portion arises by a strong tendon from the lower border of the maxilla just in front of and below the mouth of the infraorbital canal. Becoming fleshy and wider, its fibres pass backwards obliquely to their insertion which occupies the thickened lower border of the angular process of the mandible. Along the inner edge of that border the fibres meet the ends of those of the *pterygoid internus* muscle. Owing to the oblique, almost horizontal, course of its fibres this portion of the masseter is that principally concerned in drawing the jaw forwards when the animal is gnawing.

The posterior portion rises by fleshy fibres from the whole outer surface of the outer wall of the infraorbital canal and from the lower border of the zygomatic arch throughout its entire length. The muscle is inserted into the whole length of the masseteric crest of the mandible from a point below  $m_1$  to the end of the angular process behind. The anterior fibres become tendinous towards their insertion, and they have a more nearly vertical direction. The fibres become more and more oblique posteriorly, the hindermost winding round the bases of the angular and condylar processes to be inserted upon the inner surfaces of the upper part of the angular process and the hinder base of the condylar process. This portion of the masseter is very powerful, drawing the jaw forwards and upwards.

**MASSETER MEDIALIS.** This is a comparatively feeble muscle arising by fleshy fibres from the inner surface of the zygomatic arch, the inner surface of the outer wall of the infraorbital canal, and by a small slip, which, passing through the infraorbital canal, arises from the side of the maxilla in the prezygomatic fossa. The anterior fibres, from the infraorbital canal and floor of the orbit, pass downwards and backwards and are inserted by tendon into the fore-part of the masseteric crest under cover of the posterior portion of the *masseter lateralis*. The fibres from the zygomatic arch pass vertically downwards to their insertion by tendon into a groove which rises from the *crista masseterica* below and ascends parallel with the front border of the coronoid process to a point a little below the base of the sigmoid notch; thence the line of insertion passes backwards to the alveolar protuberance of the lower incisor and finally ascends the condylar process to a point a little below the head. The small posterior portion of the muscle arising from the squamosal root of the zygoma and inserted into the line around the sigmoid notch, is usually separable from the chief or anterior portion, a branch of the facial nerve passing out between them. The *masseter medialis* assists the *temporalis* in

closing the jaws, and its most anterior fibres pull the lower jaw forwards as well as upwards.

**TEMPORALIS.** This muscle although varying considerably in size and in its precise relation to the braincase in Microtinae

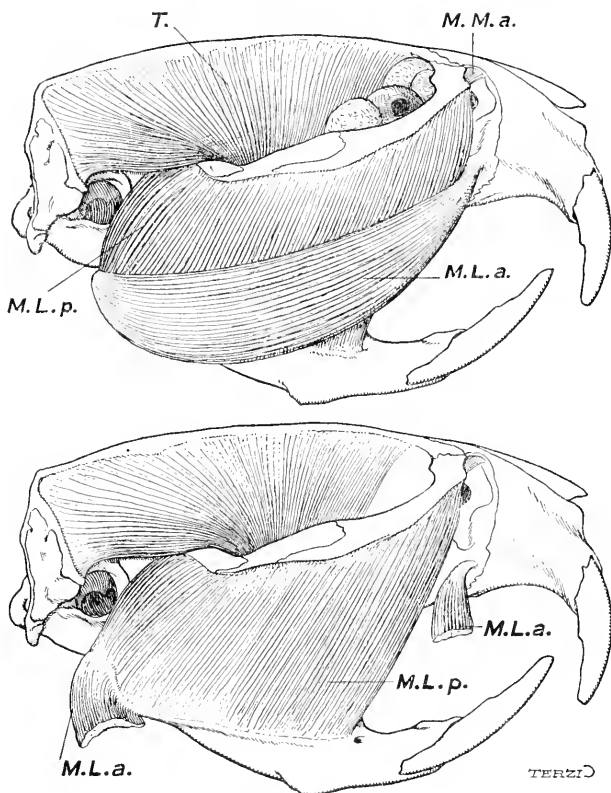


FIG. 13.—*Arricola amphibius* Linnæus.

Jaw muscles: *M.L.a.* anterior or superficial portion of *masseter lateralis*; *M.L.p.* posterior or deep portion of *masseter lateralis*; *M.M.a.* and *M.M.p.* anterior and posterior portions of *masseter medialis*; *T.* *temporalis*.

is always well developed. The temporal fossa extends from the occipital crest to a point more or less far forwards in the inter-orbital region. The muscle is covered by a fascia which extends from the temporal ridge, marking its upper limit of origin, to the

upper border of the jugal and to the lower edge of the temporal fossa in the post-glenoid region. The *temporalis* is formed chiefly by a great fan of fleshy fibres which arise from the floor of the temporal fossa; the more superficial fibres take origin from the

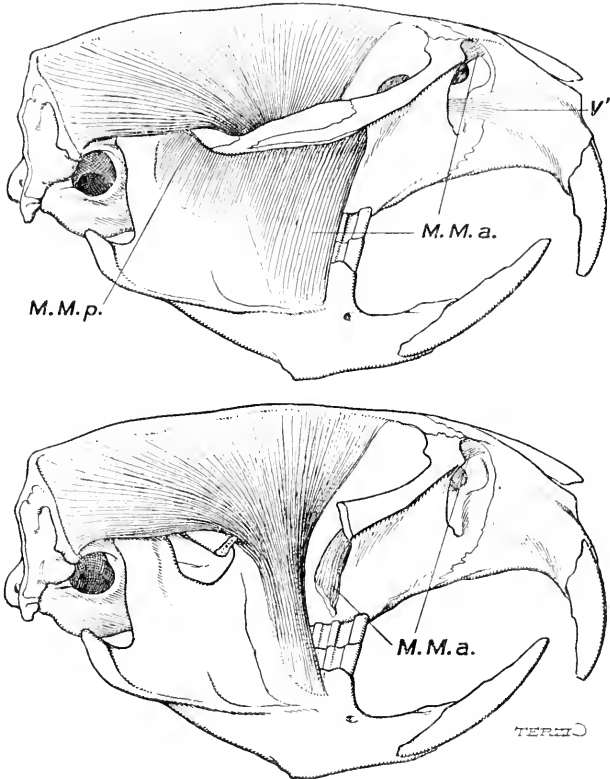


FIG. 14.—*Arricola amphibius* Linnaeus.  
Jaw muscles (continued): letters as in Fig. 13.

under surface of the temporal fascia. The fibres converge to their insertion into the tip and inner face of the coronoid process. The anterior and central portions of the muscle are particularly strong; and some of the deeper fibres arising from the squamosal upon the anterior shoulder of the braincase have a tendinous origin, the tendon producing the post-orbital crest or process of the squamosal which is so characteristic of the subfamily.

Parsons<sup>1</sup> describes and figures the "parietal portion" of the *temporalis* in the Water Vole as being continuous with what is described above as the anterior portion of *masseter medialis*. The foregoing description is based chiefly upon several dissections of the jaw muscles in the same species; I have never found any portion of the *temporalis* going to an insertion external to the coronoid process (apart from the fibres that envelop the tip of the process) and my experience in this respect seems to agree with that of Tullberg.<sup>2</sup>

**PTERYGOID INTERNUS.** This is a short, thick muscle passing obliquely backwards, outwards, and downwards from its origin in the pterygoid fossa to its insertion upon the inner face of the mandibular angular process.

**PTERYGOID EXTERNUS.** A small muscle arising from the ectopterygoid plate and inserted upon the inner face of the condylar process of the mandible.

**DIGASTRICUS.** This muscle arises from the paroccipital process and is inserted into the lower border of the mandible towards the symphysis. Anteriorly its belly is in close contact with that of its fellow of the opposite side. Its function is to retract and depress the mandible.

#### d. THE EVOLUTION AND STATUS OF THE SUBFAMILY MICROTINÆ, AND THE INTERRELATIONSHIPS OF THE GENERA.

There can be no doubt that the Microtinæ have descended from a primitive Myomorphous stock which was also ancestral to all the other groups of Muridæ. Among Muridæ the subfamily is sharply defined by its cranial and dental characters. Of these the most prominent are the firm construction of the skull, shortened rostrum, forwardly placed orbits, peculiarly formed "masseteric" plates, the presence of post-orbital squamosal crests or processes, the thickened palatal processes of the maxillaries and palatines, and the hypsodont prismatic cheek-teeth. The molars of certain Cricetinae (e.g., the North American genera *Sigmodon* and *Neotoma*) show a strong superficial resemblance to the cheek-teeth of Microtinæ; but detailed study shows that similar tooth-patterns have been evolved in somewhat different ways in the two subfamilies. In the remarkable Asiatic genus *Myospalax* ("*Siphneus*") the cheek-teeth are rootless and closely resemble in pattern those of the typical lemmings among Microtinæ. But although the skull (Figs. 15-17) is highly specialized for fossorial habits, it and the jaw muscles resemble those of the Cricetinae in retaining essential features similar to those found in the more primitive of the non-Microtine Muridæ generally, and differing widely from those characteristic of the Microtinæ. Among the most primitive Nesomyinae (c.g., *Nesomys*), now

<sup>1</sup> PARSONS, P.Z.S., 1896, p. 160.

<sup>2</sup> TULLBERG, Ueber d. System der Nagetiere, Taf. xiv, figs. 17 and 20.



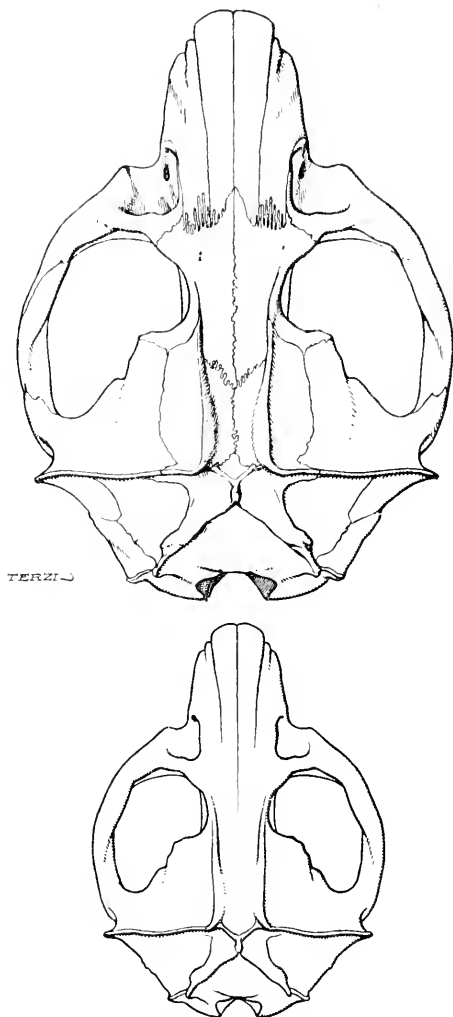


FIG. 15.—*Myospalax fontanus* Thomas.  
Skull of adult, dorsal view, enlarged; the smaller figure natural size  
(B.M., No. 9.1.1.203, Shansi).

confined to Madagascar, we find cheek-teeth which, although very different from those now characteristic of voles, present an arrangement of the crown tubercles similar to that which, in a less reduced condition, probably characterized the molars of the ancestor of the Microtinæ. In one genus of this Malagasy group, *Brachytarsomys*, which has adopted a fossorial vole-like mode of living, the molars, although low-crowned and rooted, have been simplified transversely in such a way that they show all the broader features

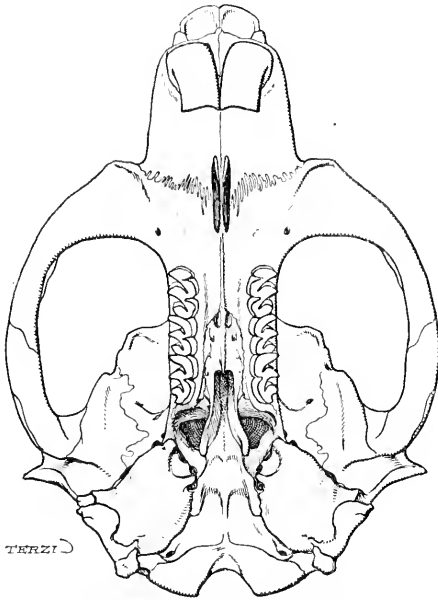


FIG. 16.—*Myospalax fontanus* Thomas.  
Skull of adult, ventral view, enlarged.

observable in the cheek-teeth of voles. It is of great interest to observe that in this genus (and in this genus alone) the jaw muscles have developed exactly as in the highest voles; and the skull of *Brachytarsomys*, although very primitive in many respects, yet makes an undeniable approach towards that of the Microtinæ in all those features which in voles depend upon the special development of the anterior part of the *temporalis* and upon the peculiarities in the arrangement of the *masseter lateralis* muscles. The parallel, indeed, is so close that it may be necessary later on to transfer *Brachytarsomys* to the Microtinæ. The facts

mentioned suggest that the dental, cranial, and myological characters are inseparably linked with each other both in *Brachytarsomys* and in the voles. The problems connected with the evolution of the patterns of the cheek-teeth and their bearing upon relationships are more fully discussed below at p. 102.

The Microtinæ owe their development, special characters, and survival in the face of keen competition, chiefly to the fact that they have acquired the power of subsisting upon coarser, tougher,



FIG. 17.—*Myospalax fontanus* Thomas.  
Skull of adult, lateral view, enlarged.

less inviting and less nutritious vegetable substances than those devoured by their more generalized relatives and rivals. For the most part, too, the Microtinæ have become earth-bound, burrowing creatures, and their fossorial habits have played a great part in moulding both the outward form and the internal structure of most of the living genera.

The immediate ancestor of the Microtinæ must have been a generalized Murine with moderately large eyes and ears, long tail, normal feet and hands, and normal fur. In these respects it cannot have shown a greater degree of fossorial specialization than that exhibited in *Brachytarsomys*. Its skull must have resembled

that of the more primitive Muridæ in its general lightness and delicacy of construction, in the persistence of the median sutures, the flatness of the palate, the wide separation of the temporal

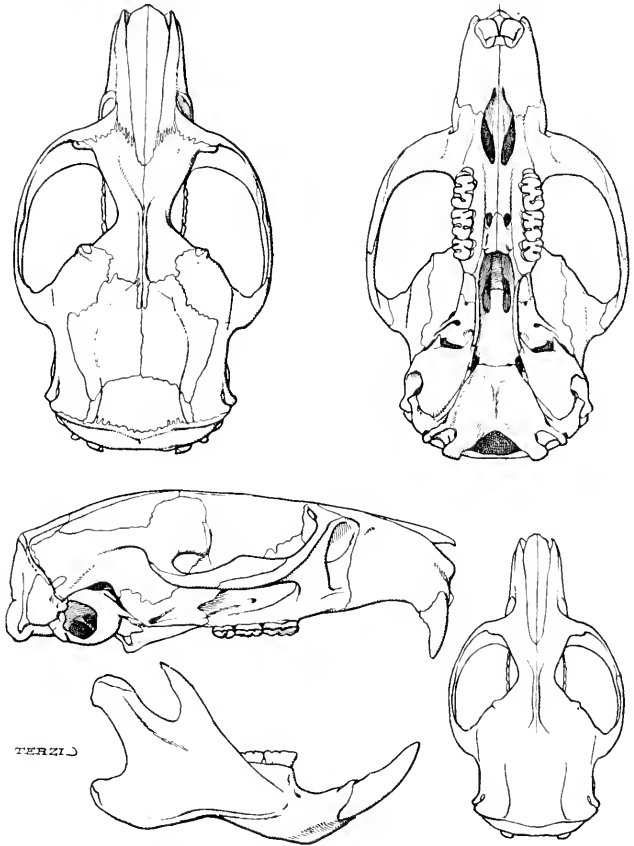


FIG. 18.—*Brachytarsomys albicauda* Gunther.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

ridges, and in many other respects. The upper incisors when unworn retained distinct traces of their original cuspidate crowns (see pp. 99–101). The lower incisors were wholly lingual or inferior to the molars in position; they were very short, so that they did not extend further back than to a point opposite the

hinder edge of the alveolus of  $m_2$ . The cheek-teeth, as explained fully on pp. 102-119, must have been low-crowned, rooted, and multitubercular; their crowns were remarkably complex,  $m_1$  consisting of about twenty-one tubercles; each of the other teeth was composed of about fifteen tubercles, the tubercles being arranged in three longitudinal rows both in upper and lower molars. As in other primitive Muridæ the food was bruised and crushed, the motion of the lower jaw during mastication being transverse or oblique instead of longitudinal in direction. From such a form all known Muridæ living or extinct may well have descended; but in this work we have merely to trace the modifications which have led to the evolution of the Microtinæ from this primitive type.

Representatives of the primitive stock just described appear at different times to have discovered the nutritive value of the coarser vegetable substances such as moss, grass, tough leaves, bark and roots, and by degrees they substituted such unattractive provender for the softer and more succulent fruits, berries, nuts, tender foliage and green shoots eaten by their ancestors and less enterprising rivals. Leaving the dainties to others, they thus tapped vast and never-failing food supplies which have in the course of time enabled their descendants, the Microtinæ, to colonize the Holarctic region more thoroughly and more completely than any of the related groups.

This gradual change in diet induced corresponding gradual changes in the dentition, alimentary canal, and all the related organs. Gnawing, that fundamental habit of Rodentia, lost some of its primitive importance, since the extraction of kernels from hard shells ceased to be one of the chief operations in feeding, and the incisors, free to develop in other directions, were used sometimes as digging instruments, sometimes as forceps for the extraction of seeds, etc., special uses which have led to various modifications in the form of these teeth (see pp. 99-101). The new food made great and ever-increasing demands upon the cheek-teeth, and old normal methods of mastication had slowly to be changed. Bruising and crushing no longer sufficed for the reduction of the food, and were gradually replaced by shearing and slicing. Low-crowned tuberculate teeth, admirably adapted for the earlier use, had to be transformed into tall-crowned, prismatic structures fitted for the new purpose. Mere pressure between the tooth-rows, accompanied by a transverse or oblique rocking motion of the lower jaw, had to be replaced by a powerful gliding stroke from behind forwards. The motion imparted to the jaw by the *masseter lateralis* muscle, used by other Muridæ chiefly in gnawing, had now to become the chief motion in mastication, and the anterior part of the *temporalis* muscle became specially developed as an auxiliary to the *masseter complex* for this purpose. The uneven surfaces of the primitive tubercular teeth had at first to be worn flat in order to permit the lower jaw

to glide forwards when the molars were pressed tightly together: but as the forward stroke became firmly established the crown tubercles gradually ceased to be functional parts of the crowns. The enamel, primitively rather thick, equally developed, and continuous in all parts of the periphery of the crown, became differentiated into thick and thin portions, remaining thick where required, becoming thin or disappearing altogether in situations where it was no longer useful or impeded the stroke of the teeth. In this way the enamel has been re-arranged in upper and lower molars to form a series of appropriately curved cutting blades which shear with each other effectively as the lower jaw is pulled forwards and upwards by the muscles. The apical enamel has atrophied and disappeared to a very large extent, so that the molars of many voles now present as soon as they cut the gum a flat surface upon which hard enamel and soft dentine are already exposed in effective alternation. Step by step, as the food has increased in harshness, the rate at which the substance of the teeth is wasted by attrition has become more rapid; in compensation the crowns of the teeth have become progressively taller, their dentinal pulps and enamel organs more vigorous and more continuously active; and the loss of that vigour and activity has been postponed to a later and later moment in the life of the individual from generation to generation, until at last in the highest *Microtinæ* the molars like the incisors have acquired the power of persistent growth.

Other direct effects of the change of diet are modifications in the alimentary canal. The food of the *Microtinæ* is richer in cellulose than that of less specialized *Muridæ* and the process of digestion is chemically somewhat different. This has led, as in other rodents which subsist upon similar food-stuffs, to marked enlargement of the cæcum and to enlargement and complication of the large intestine.<sup>1</sup>

The increased height of the molar crowns and their robust proportions have necessarily led to the enlargement of the alveolar capsules in which the teeth are developed and supported. In the upper jaw the capsules rise up as conspicuous swellings in the floors of the infraorbital canal and nasal chamber ( $m^1$ ) and in the floors of the orbit and sphenorbital fissure ( $m^2$  and  $m^3$ ); in the lower jaw they fill the body of each horizontal ramus and with the contiguous shaft of the lower incisor impart to the mandible a characteristic robustness of form. In those less specialized *Microtinæ* in which the molar teeth still develop roots in old age, senility is marked by the gradual subsidence and collapse of the alveolar capsules; in these forms, therefore, the alveolar portions of the jaws revert in old age to the condition seen throughout life in primitive *Muridæ*. But in all *Microtinæ* the great size of the alveolar capsules, whether a permanent or a more or less temporary feature, has produced important modifications of the surrounding

<sup>1</sup> TULLBERG, Ueber d. System der Nagetiere, p. 443.

parts. The palatal processes of the maxillaries and the palatines have been deepened vertically; the median sutures of these bones, open throughout life in primitive Muridæ, have closed and disappeared; the ectopterygoid plate of the alisphenoid supporting the hinder end of the maxilla has been greatly developed, and the presphenoid and the fore-part of the basisphenoid, owing to the intrusion of the alveolar capsules into the sphenorbital fissure and the consequent driving inwards of the first and second divisions of the great trigeminal nerve, have become laterally compressed and vertically deepened.

Under the influence of the deep part of the *masseter lateralis* muscle the zygomatic process of the maxilla, particularly its lower root which forms the outer wall of the infraorbital canal, has become unusually strong and characteristically formed. The temporal muscle, and particularly its anterior portion, is greatly increased in size in all Microtinæ; it has made room for itself in the orbito-temporal fossa by driving the zygomatic arch outwards, by compressing laterally the interorbital region which in the highest forms becomes extremely narrow, and by driving the eye forwards. The latter organ, becoming less and less important as Microtinæ become more strictly fossorial, is reduced in size and displaced, being lifted up by the molar capsules as well as pushed forwards by the temporal muscle. The squamosal bone, which gives origin to the greater part of the temporal muscle, has like this muscle risen in importance; it shows a well-marked tendency to encroach upon the frontals anteriorly and upon the parietals and interparietal behind in many Microtine genera, and on the shoulder of the braincase it forms a more or less well-marked post-orbital process or crest for the origin of the tendinous portion of the *temporalis*. Partly in consequence of the increased development of the ectopterygoid plate, but partly owing also to increased size of the *pterygoid internus* muscle, the pterygoid fossa has been deepened on each side. In the mandible the muscular specializations are reflected in the form of the coronoid and angular processes and in the strength of the *crista masseterica*; where the insertions of the *pterygoid internus* and *masseter lateralis* muscles have become tendinous and concentrated, the angular process has suffered reduction.

Fossorial specialization has led to the reduction of the eyes and external ears, shortening of the limbs and tail, broadening of the head and thickening of the body, and to many modifications of the hands, feet, and fur. In the skull it is betrayed by the flattening of the dorsal surface and, in extreme types, by the projecting and straightened (proödont) incisors, shortened nasals, shallowed rostrum, and forwardly inclined occiput. The auditory bullæ become specially developed for underground life; the cavities of the middle ear, mastoid portion, and the swollen *tegmen tympani* are filled, in the most modified forms, with spongy tissue, and the *canaliculus tympanicus* becomes completely

ossified. In the pelvis the pubic symphysis is characteristically shortened.

Many of the interpretations of Microtine structure given in the foregoing paragraphs have already been made by Winge.<sup>1</sup> I have, however, worked through and reflected upon the whole subject for myself many times, and have arrived in my own way at my own opinions and conclusions. These differ, in many important respects,<sup>2</sup> considerably from those of my illustrious predecessor, to whom I am gratefully indebted for much kindness and instruction, and it is therefore necessary for me to shoulder responsibility for the whole.

That the evolution of the Microtinæ has proceeded along the lines described above and for the general reasons given, becomes evident not only when we review the known genera, but when we follow the post-natal development of the individual. Comparison of unworn tooth-germs with specimens in successive stages of wear confirms the views expressed above as to the character of the dentition of the ancestor and with regard to the manner in which the ancestral molars have been modified (see the special sections dealing with the dentition at pp. 99-124). Similarly the post-natal growth of the skull in various genera recapitulates many of the chief evolutionary processes which have resulted in the skull forms characteristic of the adult stages of growth in the most highly specialized genera. For example, new-born skulls of *Dicrostonyx*, *Evotomys rufocanus*, *Arvicola*, and *Ondatra* (Plate II) are all much alike and closely similar to the skull in adults of the most primitive Muridæ. They naturally show the beginnings of the Microtine specialization; but most of the essential characters of the group become more and more evident in later stages of growth.

In two respects the Microtinæ, judged by their most primitive forms, stand lower in the scale than all other Muridæ. Firstly, their cheek-teeth retain more of the primitive longitudinal complexity than do those of any other subfamily. Secondly, in the lowest Microtinæ, the Lemmi, the lower incisor is unusually short, not extending backwards beyond  $m_3$ , and is wholly lingual to the molars in position. In all other respects, the Microtinæ have been carried by the two-fold specialization described above to a level far above that attained by any of those members of other subfamilies of Muridæ that have specialized in somewhat similar directions.

<sup>1</sup> WINGE, "Om Græske Pattedyr," Vidensk. Medd. Naturhist. Foren. Kjöbenhavn, 1881, pp. 36-50. "Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa," E. Mus. Lundii, 3, pp. 123-126, 1887. "Grönlands Pattedyr," Meddelelser om Grönland, 21, 1902, pp. 358-360, 382-386. "Danmarks Pattedyr," 1908, pp. 50-55, 68-79. "Pattedyr Slægter," 2, 1924, pp. 37-45, 137-143.

<sup>2</sup> As long ago as 1914 Winge and I were comparing our views on this subject, and he told me that I had got everything upside down. No doubt others will be of the same opinion to-day!



Among the Microtinæ (excluding *Brachytarsonmys*) the LEMMI are at once the oldest and fundamentally the most primitive. The remarkable shortness of the lower incisor in all lemmings proves that the group diverged from the primitive Murine stock before that tooth had attained its full development; the development of the incisor in the lemmings was arrested by the decline of the gnawing habit sooner than in the voles. Other circumstances which point to the relatively greater antiquity of the lemmings are firstly, the fact that they are all peripheral forms with a relatively restricted and a waning distribution; secondly, that whereas the Microti are represented by numerous genera, including many in which the molars in adult stages of growth develop roots, the Lemmi are now represented only by a few genera in which, without exception, the cheek-teeth have acquired fully the power of persistent growth. In other words, only the most highly specialized Lemmi have survived; the more primitive forms with rooted molars having utterly disappeared before the competition of the newer and less primitive group of voles.

DICROSTONYX is fundamentally the most primitive of the lemmings, and is by its structure one of the most isolated genera of the subfamily. Its cheek-teeth, when quite unworn, have members of the three primitive longitudinal rows of tubercles distinctly developed; they retain, in adult stages of wear, many of the primitive terminal elements which are suppressed in most other genera, and their re-entrant folds lack cement. This primitive type has survived either by colonizing, or else by remaining in, the high north, where it has adapted itself to the rigorous conditions now obtaining in that region and to subsistence upon the unusually harsh and poor diet offered by that inhospitable land. The primitive characters are therefore hidden beneath a mask, the product of intense and two-fold specialization. The fur has become very thick and subject to both seasonal and geographical variations of length, density, and colour, being shorter, thinner, and darker in summer, in warmer regions, and in the young; longer, denser, and whiter or paler in winter, in the bleaker regions, and in old age. The peripheral parts are shortened and withdrawn to the shelter either of the dense fur or of the general integument of the trunk; thus the outer ears are reduced each to a mere fold of naked skin hidden in the fur; the arms and legs protrude but little from the general covering of the body; the caudal vertebræ are shorter than the dense brush which envelops them. The hands and feet have become exceptionally broad, partly for digging, and partly for locomotion upon snowy wastes; their palms and soles are densely clothed with crisp, curling fur, and the pads, having ceased to be of functional importance, are represented only by some feeble vestiges which can be found by clipping the hair away from the soles. The claws have become large and sharp, those of the third and fourth manual digits being highly modified for digging and subject to a remarkable and unique

seasonal change; with the approach of winter these two claws grow to an extraordinary size and develop a peculiar supplementary ventral portion which sometimes surpasses the main part of the claw in length; but with the return of spring this ventral portion is shed and the main claw is then worn down to normal length. The bones of the fore-arm, particularly the ulna, are greatly strengthened for the attachment of the powerful muscles which move the fossorial hand.

In this genus the incisors have become slender, straightened,

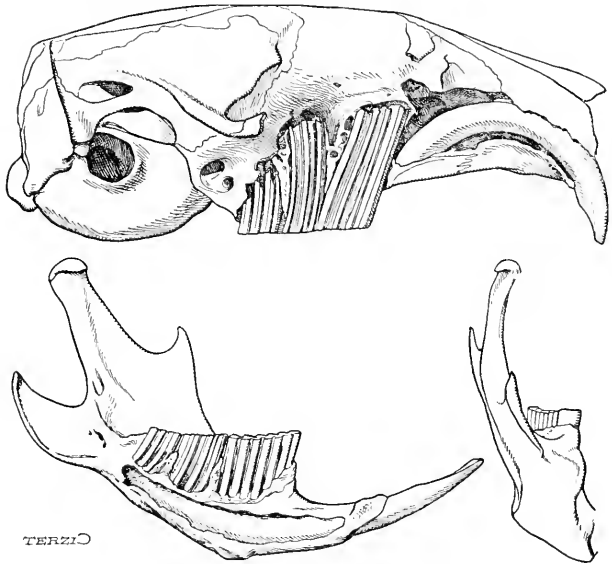


FIG. 19.—*Dicrostonyx granlandicus* Traill.

Skull and left mandibular ramus dissected to show the alveolar courses of the teeth (enlarged).

and more or less protruding; and they retain at the most but a very feeble vestigial trace of an anterior groove. The cheek-teeth, as in all other known lemmings, have become hypsodont, persistently growing, broad-crowned, with their enamel differentiated into thick and thin portions and reduced even to disappearance on those portions of the periphery of the crown where enamel is no longer of functional importance. The intrusion of the alveolar capsules of  $m^2$  and  $m^3$  into the sphen-orbital fissure has resulted in the lateral compression of the presphenoid, which is reduced to a slender rod in most species. The temporal muscles produce a salient ridge upon each side of

the braincase and the attachment of their post-orbital tendons is marked by the prominent peg-like post-orbital process of each squamosal; the anterior parts of these muscles produce an elevated

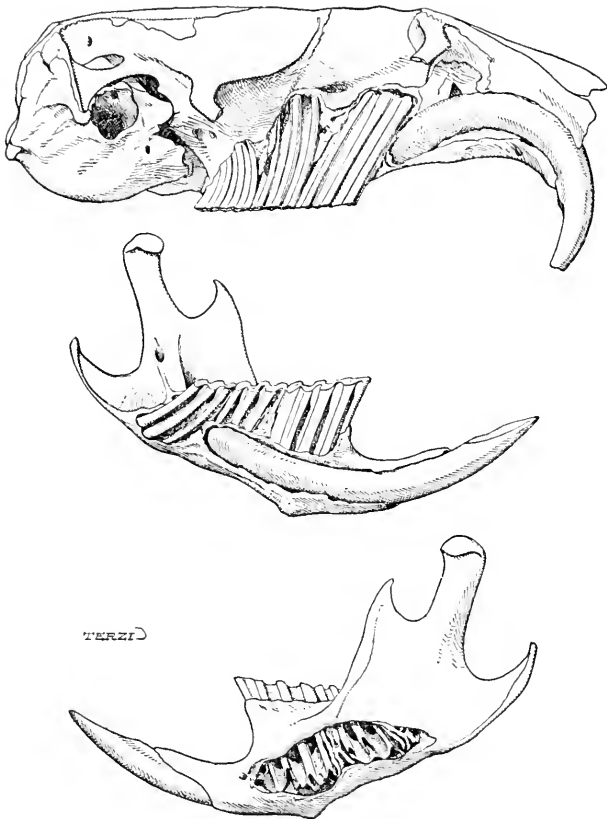


FIG. 20.—*Lemmus lemmus* Linnæus.

Skull and left mandibular ramus dissected to show the alveolar courses of the teeth (enlarged).

superciliary ridge on each side, but they are not strong enough as a rule to cause these ridges, even in old age, to fuse into an inter-orbital crest and the squamosal bones remain widely separated anteriorly. The cavity of the middle ear is partly filled with a dense sponge of bone.

The true lemmings, *Synaptomys*, *Myopus* and *Lemmus*, form an interesting group which stands on a higher plane than *Dicrostonyx*. In the shortness and wholly lingual course of the lower incisors the members of this group agree with *Dicrostonyx* and differ from the rest of the Microtinæ, and when most modified the external form shows a specialization which in some respects is analogous to that seen in *Dicrostonyx*. But in other essential respects the group differs as widely from *Dicrostonyx* as it does from the voles. The persistently growing cheek-teeth are characterized by the reduction and loss of many of their primitive terminal elements, so that their patterns are as simple longitudinally as in the highest voles; they are further characterized by the reduction of the outer salient angles in lower and of the inner salient angles in upper teeth; by the tendency of the outer folds above, and the inner folds below to retain their original character of transverse valleys; by their great breadth, by well-differentiated enamel, and by the presence of cement in the re-cntrant folds. In correlation with the more highly specialized molars, the anterior portions of the temporal muscles have apparently gained in strength and they produce more marked effects upon the portions of the skull directly under their influence; thus the post-orbital tendon stimulates the squamosal on each side to develop a long, shelf-like, post-orbital crest; the superciliary ridges fuse sooner or later to form an interorbital crest; the interorbital region itself is much constricted and the squamosals, in the adults of the highest forms, tend to meet anteriorly.

Of the three genera of this group *SYNAPTOMYS* is the most primitive. Externally it differs little from such voles as *Evotomys* and wholly lacks the outward specialization for fossorial habits or a boreal habitat which characterizes the recent species of *Lemmus*; the large ears and the, for a lemming, long and thinly clad tail are particularly noticeable. Other primitive characteristics are shown in the general lightness of the skull and but slight modification of the zygomatic arches, in the large anterior palatal foramina, in the opisthodont and grooved upper incisors, and in the persistence of vestiges of the middle row of tubercles in the molars of some species. On the other hand the posterior border of the palate, the floor of the braincase, and the auditory bullæ show specializations which lead away from *Myopus* and *Lemmus* and afford parallels with those seen in some of the higher voles.

Of the two subgenera, *Mictomys* and *Synaptomys*, into which the genus is divided, *Mictomys* is the more primitive in some respects. In it the lower incisor ends on the lingual side of the molars opposite the posterior end of  $m_2$ , whereas in *Synaptomys* it is a little longer, ending slightly behind the anterior end of  $m_3$ ; the mammary formula is  $2 - 2 = 8$  in *Mictomys*, instead of  $1 - 2 = 6$  as in *Synaptomys*. But in certain other features *Mictomys* is the more specialized. The strongly curved upper

incisors are very broad and have the enamel brightly stained throughout in *Synaptomys*; but in *Mictomys* they are more slender and the staining is weaker, disappearing towards the outer edge of the tooth; in both subgenera each incisor bears a groove near its outer border in front, a memorial of the former cuspidate condition of these teeth. In correlation with the difference in the upper incisors, the rostral part of the skull is stouter in *Synaptomys* than in *Mictomys*. The cheek-teeth have essentially the same patterns as those of *Lemmus*, but they present, frequently and persistently, traces of the median row of tubercles (*y*, *z*, etc.), and these traces indicate that although the tubercles in question have blended with the so-called principal cusps they are of large size and therefore of much importance. In  $m^1$  and  $m^2$  the enamel folds are a little more transverse in direction than in *Lemmus* and consequently they appear to be a little deeper; in *Mictomys* these teeth show a vestige of cusp *n*, but in *Synaptomys* the postero-internal corner of each tooth is rather more reduced than in *Lemmus*. In both subgenera  $m^3$  is peculiar, having the second transverse loop separated from the third principally by the very deep second outer fold, the first inner fold being very slightly developed. In the lower molars of *Mictomys* the outer folds are so slightly developed that the teeth have crenulate outer margins and no closed triangles; but in the lower molars of *Synaptomys* the outer folds are deep, closing off external triangles as in *Lemmus*. In general the molars of *Mictomys* are more primitive than those of *Synaptomys*, since they retain more of the primitive transverse arrangement, whereas those of *Synaptomys* have acquired more of that alternation of inner and outer elements which is perfected in *Lemmus*.

In the genus *Synaptomys* the skull is less specialized than in *Lemmus*. The tips of the nasals project in front of the incisors. As in *Lemmus* the zygomatic arches are widest anteriorly, but their expansion is not so great; the planes of their outer surfaces are nearly vertical instead of being convergent dorsally, and the upper borders of the jugals are much less boldly convex. The post-glenoid part of the braincase is not shortened; the braincase is therefore longer and narrower, as well as less massive. Most of these characters are due to weaker temporal muscles and the absence of extreme fossorial specialization. The palate posteriorly is as in *Microtus*; in the subgenus *Synaptomys* it is much as in *Microtus arvalis*, but in *Mictomys* the posterior pits are extended at the expense of the median septum, which has become long and thin as in "*Stenocranium*," and of the postero-lateral bridges, which are slender and incomplete. The molars are considerably narrower in proportion to their length than in *Lemmus*, but they diverge posteriorly as in that genus. The pterygoid fossæ are a little longer than in *Lemmus*, but rather shallow, their floors being scarcely dorsal to the ventral surface of the basisphenoid.

In *MYOPUS* the external form is also vole-like, although more thickset than in *Synaptomys*. The skull and teeth agree in essential respects with those of *Lemmus*, although the skull is distinguished from that of *Lemmus* by its smaller size, lighter build, rather less expanded zygomata, anteriorly more widely separated squamosals, larger anterior palatal foramina, and more globular auditory bullæ. In these various characters the genus shows itself to be more specialized than *Synaptomys*, although outwardly, and to some extent in cranial characters, more primitive than *Lemmus*.

In *LEMMUS* the characters of the group reach their highest expression, the whole animal being greatly modified for fossorial habits. Outwardly this is shown by the extremely robust general form, small eyes, small ears hidden in the fur and destitute of meatal valves, large and broad hands and feet, enlarged fore-claws, peculiar large and flattened thumbnail, hairy palms and soles, with the pads reduced to functionless vestiges, and short, thick, and densely clothed tail. Under the influence of the powerful temporal muscles and of fossorial habits the skull has become massive, broad, and depressed, with very strongly built, abruptly and widely expanded zygomata; in the inter-orbital region the temporal ridges fuse to form a median crest; the squamosals form strong post-orbital crests and tend to approach each other anteriorly as age advances; the braincase is square, its post-glenoid portion much shortened, and it seems to have been pushed forwards, encroaching upon and reducing the size of the temporal portions of the orbito-temporal vacuities; the cheek-tooth rows diverge rapidly behind; the palate terminates simply behind, the posterior median sloping septum being represented merely by a short, free, spinous process; the pterygoid fossæ are very short and deep. The auditory bullæ are less inflated than in the related genera, but the cavity of the middle ear is filled with a dense sponge of bone. The incisor teeth are rather slender, the upper ones rather strongly curved and without well-marked anterior grooves. The cheek-teeth are broad and heavy, with the salient angles on the inner sides of the upper molars and the outer sides of the lower molars squarely truncated.

The lowest *MICROTI* retain many primitive characters not found among the highly specialized genera which alone are known to represent the Lemmi. But in one important respect the most primitive voles stand upon a higher plane than any of the lemmings. The lower incisor in all voles has pushed its way backwards through the jaw to a point considerably behind  $m_3$ , a character which indicates much later divergence from the primitive Murine stock by *Microti* than by Lemmi. The shaft of the lower incisor, lingual to the molars anteriorly (as it is throughout its course in the lemmings), crosses obliquely below or between the roots of  $m_2$  and  $m_3$  to the labial side of the jaw, where the growing base of the tooth invades and finally, in the most

highly specialized forms, colonizes the condylar process. If we admit that the great backward extension of the incisor is a more

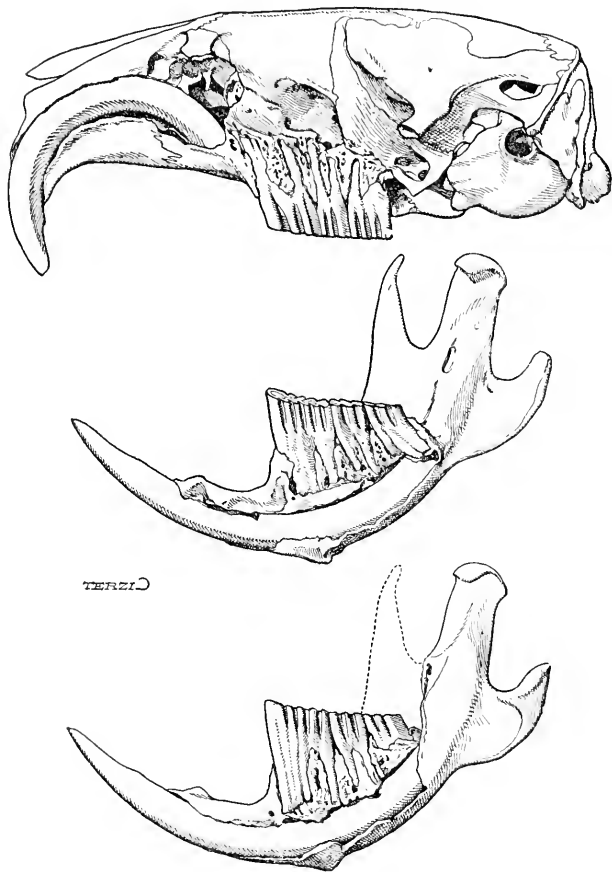


FIG. 21.—*Ondatra zibethica* Linnæus.

Skull and right mandibular ramus dissected to show the alveolar courses of the teeth; the bottom figure shows the left mandibular ramus dissected from the outer side (enlarged).

ancient feature in voles than is the hypsodonty of the molars, the peculiar relation of the molars to the lower incisor, just described and so characteristic of all *Microti*, is easily explained;

the molars as they have become hypsodont have invaded deeper levels of the jaw, and there they have had to mould themselves and adjust their curvatures to the shaft of the incisor already present. In the lemmings it is otherwise; the molars have become hypsodont much sooner, probably before the growing base of the incisor had pushed back to the level of  $m_2$ .

Among the voles *EVOTOMYS* is one of the most primitive genera, although its species show a fairly wide range in the degrees of specialization which they have severally obtained. In this genus, and in the closely related but more progressive genera discussed below, the skull is characterized by the structure of the bony palate, which terminates behind as a simple, thin-edged, transverse shelf, not provided with a postero-median sloping septum; deep postero-lateral pits are, however, present, but they pass forwards freely under the edge of the shelf. The palate of *Evotomys* is thus very similar to that of *Dicrostonyx* and *Lemmus*, and strikingly dissimilar in appearance from that of *Synaptomys* and the higher voles such as *Arvicola* and *Microtus*. The auditory bullæ are always well inflated, thin walled, and simple, and in nearly all species they lack all trace of internal spongy tissue. The cheek-teeth are of limited growth, developing two roots each in adult stages of wear; in pattern they are more or less simplified or reduced longitudinally; cement is present in their re-entrant folds. In outward form the species show few signs of specialization in any particular direction.

In the most primitive species (members of the *glareolus* group) the skull is rather lightly and delicately built, with the temporal ridges weakly developed and widely separated in the interorbital region, and with the post-orbital crests of the squamosals small though distinct. The cheek-teeth are small and the incisors slender; the lower incisor passes from the lingual to the labial side of the jaw as in all voles, but its passage between  $m_2$  and  $m_3$  takes place at such a low level in relation to  $m_3$  that this tooth is not noticeably displaced. The dentinal spaces of the molars are characteristically confluent, semi-opposed and not perfectly alternating as in the higher voles, and the salient angles, in adult stages of wear, are peculiarly rounded;  $m^1$ ,  $m^2$ ,  $m_2$ , and  $m_3$  are reduced as in normal species of *Microtus*;  $m^3$  in its least-reduced form presents five salient angles on each side;  $m_1$  is typically reduced to a pattern somewhat resembling that seen in the  $m_1$  of such voles as *Microtus nivalis*, and consists of a posterior loop, five triangles, and a short anterior loop. This pattern is an old one in the genus, dating from at least the Upper Pliocene, and in normal members of the *glareolus* group young examples of the  $m_1$  show no trace of ephemeral complications in the anterior loop; but in some far-eastern forms traces of a fourth outer fold, which is reduced by insulation of its internal part, may be seen.

At the other end of the series, though apparently connected with the more primitive forms by a long series of gentle grada-



tions, are the members of the *E. rufocanus* group. These are specialized for subsistence upon a coarser and tougher diet than that used by the *glareolus* group. The general size of the animal is increased. The cheek-teeth have become taller-crowned and more robust; the alveolar capsules of  $m^2$  and  $m^3$  rise up prominently in the sphenorbital fissure, subsiding only in old age, after the failure of the dentinal pulps and the formation of roots to the teeth;  $m_3$  is encapsulated and noticeably displaced by the shaft of the lower incisor. In pattern the teeth are somewhat modified; the inner and outer salient angles acquire a perfect alternation and in middle stages of wear the dentinal spaces are tightly closed, although they are confluent in young stages of wear and again acquire an " *Evotomys*-like " confluency in extreme old age;  $m^3$  is reduced in adults and has only three salient angles on each side; but when young both it and  $m_1$  show commonly ephemeral complications. One character in which the members of this group are rather more primitive than are most of the other species of *Evotomys* may be mentioned;  $m^1$  and  $m^2$  in young stages of wear frequently show traces of cusp *n*. In correlation with the larger and heavier molars the temporal muscles have become stronger, and under their combined influence the skull has acquired a massiveness and angularity which resembles that seen in many species of *Microtus*. In the interorbital region, which becomes more constricted, the temporal ridges approach each other with age and in extreme old age may even come in contact, although usually they remain separated by a deep and narrow sulcus.

ASCHIZOMYS, known from only one individual, is certainly a remarkable member of this group in which the outward form has become lemming-like. The skull is described as being essentially as in normal *Evotomys*, broad, depressed, lightly built, smooth and rounded. The cheek-teeth are said to be persistently growing, but with the general pattern and rounded salient angles so characteristic of less specialized *Evotomys*;  $m^3$  is small and weak with a well-developed fourth outer angle; in the mandible  $m_3$  is encapsulated and displaced by the incisor as in the *E. rufocanus* group. These cranial and dental characters, coupled with my own experience of the younger stages of growth of *E. rufocanus*, lead me, however, as explained below, to suspect that *Aschizomys* is not of generic value, but that it is based upon an adolescent specimen of a more or less aberrant member of the *E. rufocanus* group.

EOTHENOMYS is apparently descended from some primitive form of *Evotomys*. Externally the only important modification is seen in the mammary formula which is reduced from the normal  $2 - 2 = 8$  to  $0 - 2 = 4$ . In all essential respects the skull resembles that of *Evotomys*. The cheek-teeth have become completely hypsodont and rootless, and in the lower jaw  $m_3$  is noticeably displaced by the incisor. In one respect the molars

are more primitive than those of *Evotomys*; in most of the species cusp *n* is largely developed in  $m^1$  and  $m^2$ , in which teeth it forms a large extra postero-internal salient angle.

ANTELIOMYS is a closely related genus which goes a little further than *Eothenomys* in three respects:—the temporal ridges tend to fuse in the interorbital region, the palate develops a conspicuous though horizontal median spinous process posteriorly, and cusp *n* is more reduced in  $m^1$  and  $m^2$  than is usual in *Eothenomys*. In one respect it is more primitive;  $m^3$  is much more complex, having five or even six salient angles on each side. The first outer fold of this tooth is usually shallow, leaving the first outer triangle confluent with the anterior loop—a character seen in other genera, such as *Alticola*.

ALTICOLA is also an offshoot from some primitive form of *Evotomys*, as is clearly shown by the structure of the palate and the general form of the molars. The cheek-teeth have become rootless, and  $m_3$  is noticeably displaced by the incisor. The molars are characterized by the great width of the re-entrant folds, which contain very little cement, and by rather perfect alternation of the inner and outer elements; these features give the teeth in most species a peculiar long-drawn-out appearance. In pattern  $m^1$ ,  $m^2$  and all the lower molars are about as reduced as in normal *Evotomys*;  $m^3$  shows from species to species an interesting series of gradations, beginning with forms in which the tooth is about as complex as in *Antelionomys*, and ending with others in which there are only three outer and two inner salient angles; the first outer fold of this tooth is, as already mentioned, almost invariably shallow. The skull is lightly built and in essential respects closely resembles that of *Evotomys*. The temporal ridges are widely separated in the interorbital region; the post-orbital squamosal crests are moderately developed; in the palate the lateral bridges are frequently incomplete and the hinder edge is often furnished with a blunt median spine. The auditory bullæ are simple, thin walled, and sometimes greatly inflated; they are destitute of spongy tissue within, and the stapelial artery is naked. The species are more or less highly specialized for life at high altitudes; the more primitive, with relatively complex teeth, normal *Evotomys*-like essential external characters, including long, thinly-clothed tails and naked soles, occur at lower elevations; the more specialized forms, with simplified teeth, short and densely clothed tails, and hairy soles, inhabit higher regions. Some remarkable species, inhabiting the bare talus slopes of Central Asia, have acquired remarkably flattened skulls fitting them for life in rock crevices; these have been referred to a special subgenus *Platycranius* by Kascenko, but apart from the peculiar flattening of the skull there is nothing to distinguish them from the more specialized forms of *Alticola*.

HYPERACRIUS is apparently a peculiar descendant from some form of *Alticola*. The genus has become specialized for

fossorial life; the fur is short and dense and in one species (*H. wynnei*) it is highly modified and mole-like; the eyes and ears are reduced, the fore-claws are slightly lengthened, the tail is shortened, but fully clothed; the mammary formula is reduced to  $1 - 2 = 6$ . The temporal muscles are greatly increased in size and strength and the reduction of the eyes is no doubt partly correlated with this muscular increase. In the skull the temporal ridges fuse, at an early age, to form a linear median interorbital crest, and the squamosals, frontals, parietals, and interparietal all show a characteristic temporal modification; the post-orbital crests of the squamosals are greatly lengthened, extending from the interorbital region outwards and backwards on each side almost to the glenoid articulation. The anterior palatal foramina are reduced to more or less shortened, narrow slits. The palate in the smaller species is essentially as in *Alticola*; but in the largest form (*H. wynnei*) the posterior median sloping septum is represented by a short spine, in form rather like that seen in *Antelionomys*, but differing in that it is not horizontal but sloping; if this spine were directly connected laterally with the post-palatal pits, the palate in *H. wynnei* would be similar to that of many species of *Microtus*; as it is the pits have already very definite, salient, inner borders, which run forwards to effect a junction with the dorsal surface of each lateral bridge near the base of the spine; thus the structure of the palate in this species may be said clearly to foreshadow the palate of the higher voles. The presphenoid is reduced to a slender bar in all species of *Hyperacrius*, and a similar reduction is to be seen in some but not in all species of *Alticola*. The auditory bullæ are as in *Alticola* as regards essential structure; but they are considerably smaller and less inflated. The cheek-teeth are light, rootless and tall-crowned; they have normally differentiated enamel, but their re-entrant folds lack cement. The enamel pattern is essentially as in *Alticola*; but  $m^3$  is simplified and its posterior end is more reduced and shortened than in any species of *Alticola*.

DOLOMYS apparently represents or at least is very nearly related to forms which must have been directly ancestral to the Water Voles (*Arvicola*). Its fossil remains have been found, hitherto, only in the Upper Pliocene of Hungary; but recently a living species has been discovered on the mountains of Montenegro, where, secure from competition, the genus has survived until the present day. This living species is a large, soft-furred, long-tailed vole, bearing such a close outward resemblance to the Alpine Voles (*Microtus (Chionomys) nivalis*) that it was at first mistaken for a member of that group.

As in other primitive voles the cheek-teeth are rooted in adults; indeed, in this genus the teeth appear to be more brachyodont than is usual in such genera, for even in the living species the cement spaces and pulp cavities close at the bases of

the teeth in individuals so young that they have not yet fully acquired the adult pelage. In pattern the teeth are not very different from those of *Evotomys*; but  $m_1$ , which possesses five alternating triangles between the posterior and anterior loops, shows in young stages of wear some vestigial and ephemeral complications of the anterior loop; whereas  $m^3$  is reduced and has only three or four outer and three inner salient angles. Cement is present in the re-entrant folds of the teeth in the recent species, but is not developed in those of the Pliocene forms.

The genus is most satisfactorily distinguished from *Evotomys* and placed upon a higher plane by its skull. The hinder portion of the palate shows a very broad and ill-defined median sloping septum, small, shallow and indefinite postero-lateral pits, and more or less incompletely developed lateral bridges. In *Dolomys*, therefore, we see the beginnings of that palatal structure, which is better developed in *Arvicola*, and becomes perfected in the most specialized species of *Microtus*. The temporal ridges, in the recent species at all events, fuse anteriorly to form a median interorbital crest in adults and posteriorly they are fairly closely approximated. The alveolar capsules of the cheek-teeth do not rise up in the floor of the orbit or in the sphenorbital fissure. The auditory bullæ lack internal spongy tissue, but they are large and considerably inflated; the stapedia artery is enclosed in a bony tube as far as the stapes. The mandible is normal;  $m_3$  is not noticeably displaced by the shaft of the incisor. The upper incisors are strongly curved and sometimes show a slight trace of an anterior groove.

APISTOMYS, described from the Upper Pliocene of Hungary and known only from fragmentary remains, is scarcely to be distinguished as a genus from *Dolomys*. In it  $m_1$  has a general "arvaloid" appearance, whereas in *Dolomys* this tooth is more like that of some forms of *Evotomys* or *Microtus nivalis* in general form.

MIMOMYS is a very interesting and important genus, represented by numerous species in the Upper Pliocene of Europe and by one species in the early Pleistocene of Britain. It appears to have descended from some primitive species of *Dolomys*, i.e., from a form more primitive in skull structure than is the only living representative of the latter genus. So far as is known, the temporal ridges remained rather widely separated in the interorbital region in *Mimomys*, instead of fusing into a weak linear crest as in recent *Dolomys*. But in other respects *Mimomys* has gone much further than *Dolomys*, and in the later Pliocene and earlier Pleistocene deposits of Britain species of *Mimomys* shade off imperceptibly into forms which cannot be distinguished with available materials from the genus *Arvicola*. The palate is essentially as in *Arvicola*, its postero-median sloping septum being short, broad, but rather well defined.

As in *Dolomys* the cheek-teeth of *Mimomys* develop roots in

adult stages of wear. But as we trace the genus onwards from earlier to later horizons we observe that the species become more and more hypsodont, the growth of the molars ceasing and roots being developed at later moments in the life of the individual in the more modern species than in the earlier members of the genus. Simultaneously the teeth undergo a process of simplification, visible not only as we trace the genus forward from one geological horizon to another, but as we follow the development or wear of the individual tooth from infancy to age. The genus thus presents us with some beautiful examples of recapitulation which are described in detail below (p. 111). The most interesting tooth, as always in voles, is  $m_1$ . In the most primitive forms it no doubt resembled the corresponding tooth of *Dolomys* in possessing not fewer than five closed triangles between the posterior and anterior loops; in addition the third outer salient angle was complicated by a large vestige of one of the tubercles of the primitive median row giving rise to a peculiar feature which I have called the "prism-fold." In early species, like *M. pliocenicus*, the third outer re-entrant fold becomes reduced in early middle age by the conversion of its internal portion into an enamel islet, and this islet and the "prism-fold" persist until a very advanced stage of wear has been reached. When very young the  $m_1$  of a late species, e.g., *M. intermedius*, resembles a young  $m_1$  of *M. pliocenicus* in all essential respects. In exactly the same way it is reduced by the conversion of the third outer fold into an enamel islet, and as wear proceeds the islet disappears and a simplified pattern showing only three triangles between the posterior and anterior loops is brought to light on the surface of the crown. This simplified pattern is the characteristic adult pattern of the tooth in the later species, and it is developed and perfected long before the tooth ceases to grow. The archaic elements in the later species are confined to the apical portions of the crown, and the process of reduction, though in every detail a faithful repetition of that seen in *M. pliocenicus*, is performed within the first few weeks or days of the individual's existence instead of occupying most of its life as in the older form.

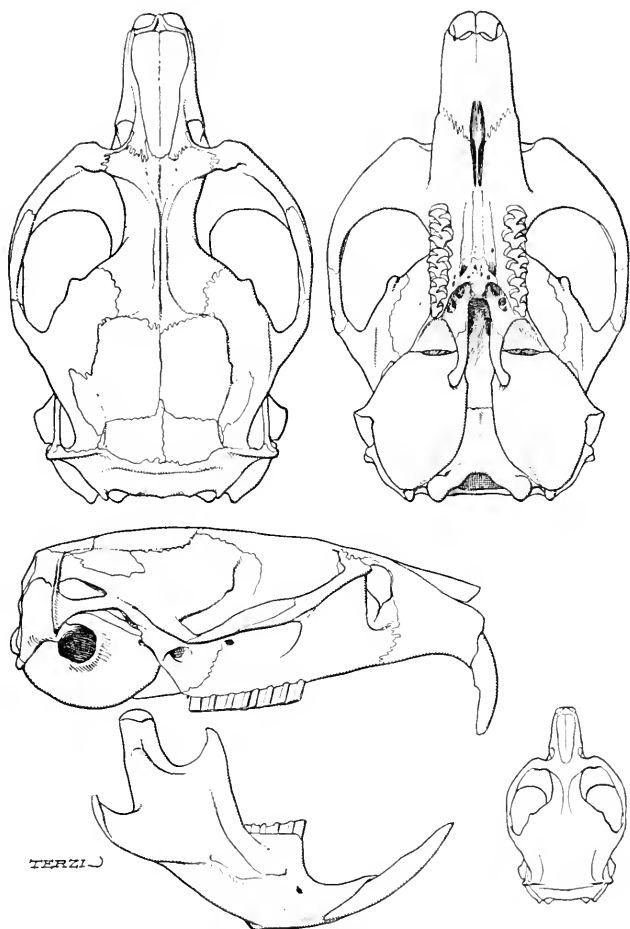
In adult stages of wear the cheek-teeth of the later species of *Mimomys* are not to be distinguished from those of *Arvicola* by pattern alone, and as the general progress is towards hypsodonty and persistent growth there comes a moment in the geological scale when, with existing materials, it is impossible to say definitely whether we are dealing with *Mimomys* or with *Arvicola*. If the teeth could be shown to develop roots in old age they would be referred to the former genus; but as no sign of roots, not even an incipient closure of the cement spaces or pulp cavities, can be detected, the remains in question, from the later Cromerian beds of Bacton and the early Middle Terrace deposits of the Thames, have to be referred to *Arvicola*.

ARVICOLA is thus shown to be a direct descendant of *Mimomys*; but the species now so widely spread over Europe and Asia are probably not to be regarded as the immediate offspring of *M. intermedius* and allied British species; for certain dental reasons it is more probable that they have come down from close relations of *M. intermedius* which once existed in Eastern Europe or Asia. The living members of the genus all show well-marked fossorial specialization which tends to become extreme in members of the *A. scherman* group; in the more familiar riparian species slight specializations fitting these voles for aquatic habits have been superimposed upon fossorial characters.

Modern species of *Arvicola* are large voles with massive, strongly ridged, and angular skulls when adult. The temporal ridges fuse in the interorbital region, and the squamosals, with well-developed post-orbital crests, approach each other, encroaching upon the frontals anteriorly as age advances. The palate posteriorly is now essentially as in normal voles; the pterygoid fossæ are deep. The auditory bullæ are rather small but now show a slight development of spongy tissue within, and the stapedia artery is completely enclosed in a bony tube. In the more fossorial species the occiput is characteristically inclined, pressed forwards above, and the upper incisors are noticeably straightened and protruding, the animal evidently using the skull and incisor teeth as one of its chief tools in digging. The cheek-teeth are persistently growing, with normally differentiated enamel, and with cement present in the re-entrant folds. The enamel pattern is characterized by the simplicity of  $m^3$ , with only three salient angles on each side, and of  $m_1$  in which there are only three closed triangles between the posterior and anterior loops. In very young stages of wear the anterior loop of  $m_1$  shows some extremely interesting ephemeral complications which are described at p. 107.

In this genus, as in many other members of the Microtinæ, persistent growth of the cheek-teeth appears to be accompanied by persistent growth of the skeleton; in the oldest individuals examined, among the enormous amount of fossil and recent material at my disposal, not only are the molars still in vigorous growth but the epiphyses of the limb-bones are still unfused with their shafts (Plates III and IV). Apparently, that is so far as actual observation goes, voles of this genus are animals that never stop growing and never grow old. But no doubt, if one could keep the vole alive in natural conditions, but secure from the fatal stroke of accident, a time would come when cheek-teeth and skeleton would cease to grow and the animal would become senile and die in the normal manner.

PHAIOMYS is an interesting genus restricted to the highlands of Central Asia, in which region it is usually found inhabiting the damp meadows bordering the Alpine water-courses. It is closely related to *Arvicola*, and seems like the latter to be descended



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FIG. 22.—*Phaiomys leucurus* Blyth.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

from some close ally of *Mimomys intermedius*. The cheek-teeth have become persistently growing, and  $m_3$  is a little reduced; but otherwise their pattern and particularly that of the  $m_1$ , is exactly as in adult *M. intermedius*. In the skull the temporal ridges fuse to form a median interorbital crest, but the squamosals, which have small but rather conspicuous post-orbital crests, remain widely separated anteriorly. The palate is essentially as in normal *Microtus*, but its postero-median sloping septum is rather short and broad. Traces of the median suture of the palate and of the sagittal suture of the interparietal sometimes persist. The auditory bullæ are well inflated and their walls are strengthened by a thick development of dense spongy tissue; the mastoid portion is also slightly inflated, and the stapedia artery passes through the stapes enclosed in a bony tube. Externally *Phaiomys* is evidently modified for fossorial

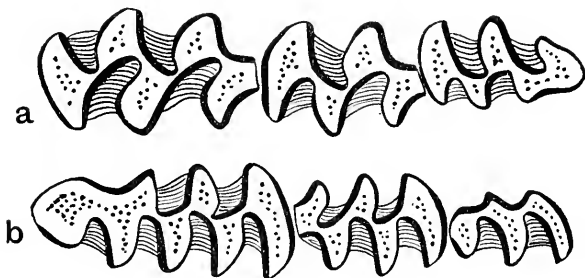


FIG. 23.—*Phaiomys leucurus* Blyth.

Crown views of cheek-teeth: *a.* right upper, *b.* right lower molars.

habits and for life in its special station; the fur is peculiarly long and soft; the tail is shortened and densely clothed; the palms and soles are overgrown with hair, and the claws, both of the hands and feet, have been considerably lengthened.

The North American genus *PHENACOMYS* appears to represent, in its essential characters, the common stock from which two of the most important groups, namely, *Pitymys* and its associates and *Microtus* and its closest allies, have descended. In external appearance most of the living species of *Phenacomys* do not differ much from typical voles; they possess moderately large eyes, well-developed ears, normal hands and feet, and a moderately long, well-clothed tail. Two or three forms, sometimes placed in a special subgenus *Arborimus*, have, however, remarkably long tails, and they retain the arboreal habits which may have characterized the long-tailed ancestor of all voles.

The skull resembles that of the more primitive species of *Microtus* in general form, having a moderately long rostrum,



rather broad interorbital region, and oblong and depressed braincase. The temporal ridges are widely separated in the interorbital region and behind; the squamosals have moderately salient post-orbital crests and are widely separated anteriorly, although in old age they show a slight tendency to encroach upon the frontals and approach each other. The upper border of each jugal bone is convex, giving a fusiform expansion to the central part of the zygomatic arch. The upper portion of the infraorbital canal is more spacious than usual. The palate posteriorly is formed nearly as in *Microtus*, but the postero-lateral bridges are usually absent, the postero-median septum is short and horizontal, and the postero-lateral pits are very shallow; these features of low relief in the palate may be correlated with the brachyodonty of the cheek-teeth, and cause the palate of adult *Phenacomys* to resemble that of *Microtus* and other more highly developed voles in young stages of growth. The pterygoid fossæ are shallow, their floors being nearly flush with the ventral surface of the basisphenoid. The palate, choanæ, basisphenoid, and basioccipital are broad. The auditory bullæ are small, globular, simple and without internal spongy tissue; the stapedial artery is naked as it approaches the stapes. The mandible is nearly normal, but  $m_3$  is not displaced by the shaft of the lower incisor, which passes below  $m_3$  to terminate in the base and at the hinder margin of the condylar process below the dental foramen; the groove between the alveoli of the cheek-teeth and the ascending ramus is not "pocketed" posteriorly by the alveolar sheath of the lower incisor as in *Microtus*, but remains open behind as in *Evtomys*.

Although some primitive characters are thus to be observed in the skull and mandible of *Phenacomys* the claim of the genus to a lowly position among voles rests chiefly upon the evidence of the cheek-teeth. These are very light and of limited growth, each molar developing two roots when adult. The enamel shows the beginning of a normal differentiation, being slightly thicker on the concave than on the convex sides of the salient angles. The re-entrant folds are narrow and transversely deep, giving to the teeth a characteristic longitudinally crowded appearance, but they do not contain cement. The enamel pattern is peculiar, characterized especially by the approximate equality of the inner and outer salient angles and infolds in upper molars and by their disparity in lower molars, in which the inner salient angles are conspicuously larger and the inner infolds much deeper than those of the outer side;  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  are essentially as in normal voles, the last-named tooth being, however, in living species of *Phenacomys*, usually a little more reduced than usual, its antero-external angle becoming obsolete;  $m^3$  is also noticeably reduced in living species, having only three salient angles on each side;  $m_1$  is a complex tooth with four or five outer and six inner salient angles, consisting

of a posterior loop, followed by from three to seven substantially closed alternating triangles, and terminated by an anterior loop of crescentic shape formed chiefly by the

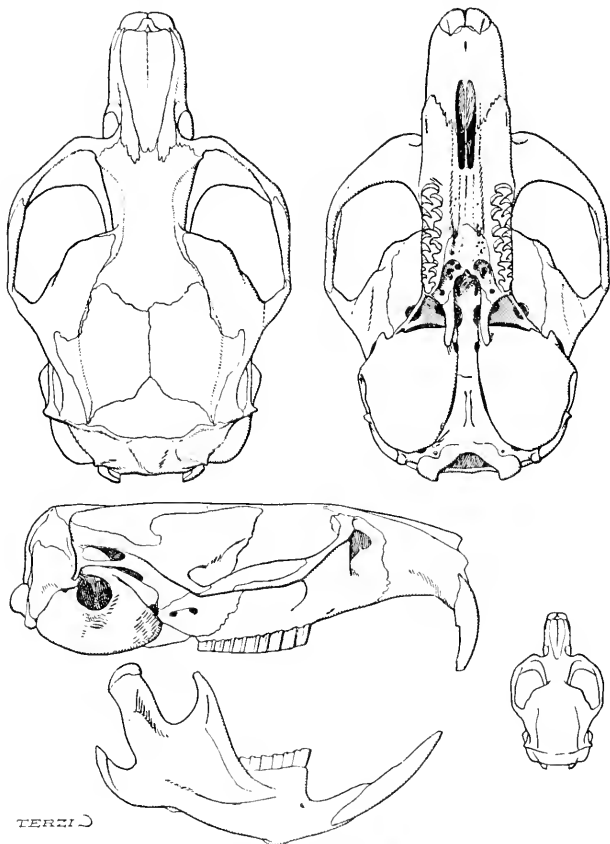


FIG. 24.—*Pitymys planiceps* Miller.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size (B.M., No. 10.7.7.219, type and only known specimen).

fifth and sixth inner salient angles; in young stages of wear the outer side of the anterior loop shows some minute and quite ephemeral complications. The interest of this tooth in *Phenacomys* lies in the unusual variability which it displays, from

species to species, in the number of closed triangles; in some species only the three posterior are closed, those in front being

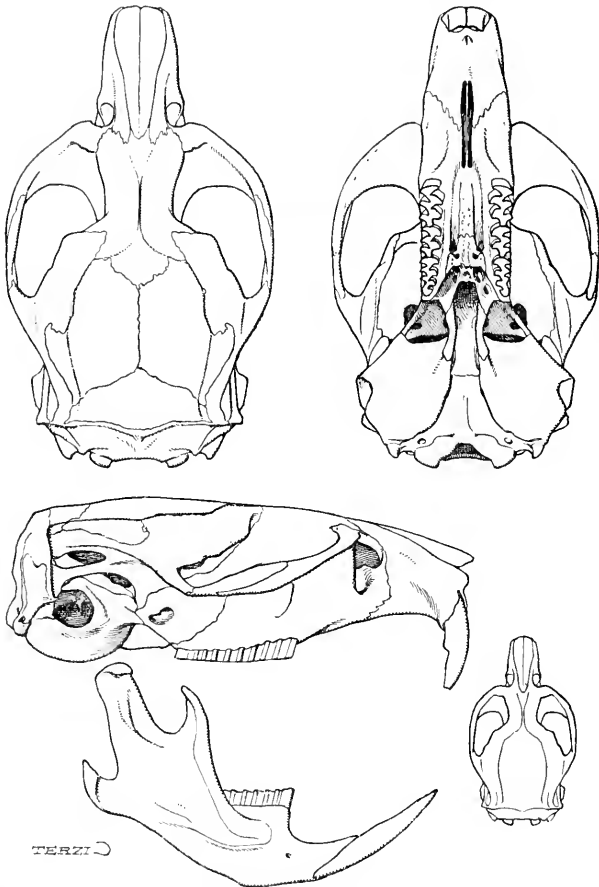


FIG. 25.—*Neodon sikimensis* Hodgson.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

more or less confluent with each other and with the anterior loop, the tooth presenting an appearance which elsewhere is characteristic of genera like *Pitymys*; in other species four, five, six, or even seven triangles may be closed, the tooth resembling

that of genera like *Microtus*. Among other voles (*Mimomys*, *Arvicola*, *Pitymys*, *Microtus*, etc.), with the exception of *Orthromys* and *Herpetomys*, the possession by  $m_1$  of three closed triangles only, on the one hand, or of four or more on the other, has been a distinction of generic importance since Pliocene times at least; but in *Phenacomys* both types of  $m_1$  are associated, and the distinction between them, if it be of any systematic value at all, is of no more than specific importance. Ancient species of *Phenacomys*, in which the outward characters may have been a little more primitive, those parts of the skull under the direct influence of the temporal muscles a little less modified, and  $m^{1-3}$  a little less reduced than they are in the living species of  $m_{2-3}$  this genus, may thus well have been the ancestors common to both *Pitymys* and *Microtus*, with their respective adherents; indeed, such forms may well have been ancestral to all the

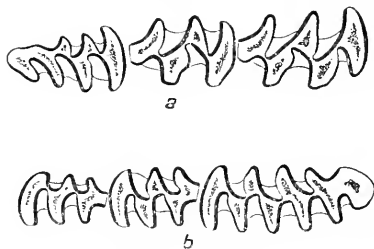


FIG. 26.—Cheek-teeth of *Pitymys subterraneus* de Selys-Longchamps.  
Crown views: a. right upper, b. left lower molars.

other known voles as well. Unfortunately, nothing is at present known of the palæontological history of *Phenacomys*.

PITYMYS is an ancient genus, now widely distributed in Central and Southern Europe and in South-eastern North America. The earliest remains are apparently those obtained from the later Pliocene (Cromerian Beds) of Britain; these consist of teeth and fragmentary lower jaws, indicating the presence of several species, which in size and form agree in all essential respects with the teeth and lower jaws of recent *Pitymys*. But whether these ancient fossils belonged to *Pitymys*, as we now understand it, or to *Neodon*, *Tyrrhenicola* or some other genus, cannot be determined with the material at present available.

The living members of the genus are small voles with very small eyes, small ears, short tails, and soft, short, dense and more or less mole-like fur. They have large hands provided with rather long claws, relatively short feet with claws rather shorter than those of the fingers, moderately hairy soles and

only five plantar tubercles. Flank glands are present in adult males. In the typical subgenus the mammary formula is reduced to  $0 - 2 = 4$ ; in the subgenus *Micrurus*, which is slightly less modified, the mammary formula is  $1 - 2 = 6$ .

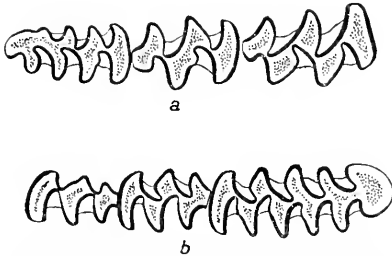


FIG. 27.—Cheek-teeth of *Pitymys majori* Thomas.  
Crown views: a. right upper, b. left lower molars.

The general external characters have thus been considerably modified in relation to the subterranean habits of these voles.

The skull is more or less evidently modified for fossorial life, usually with a rather smooth, delicately built, more or less depressed braincase. The temporal ridges are weakly developed

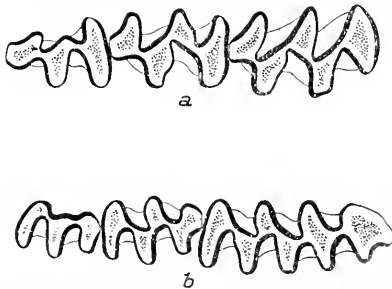


FIG. 28.—Cheek-teeth of *Pitymys ibericus* Gerbe.  
Crown views: a. right upper, b. left lower molars.

and are widely separated in the interorbital region; the post-orbital crests of the squamosals are usually feeble. The palate is normal and the pterygoid fossæ are deep. The auditory bullæ are usually swollen, their mastoid portions also being inflated; the walls of the bullæ are strengthened by spongy tissue and the stapedia artery is enclosed in a bony tube which passes through the stapes. The mandible and incisors are normal.

The cheek-teeth are rootless, with normally differentiated

enamel, and cement is present in the re-entrant folds. The enamel pattern is closely similar to that of *Microtus*, but  $m_1$  has only three closed triangles in front of the posterior loop, the fourth and fifth triangles being more or less broadly confluent with each other and with the anterior loop. In some species  $m^3$  shows some interesting phases in its reduction.



Fig. 1a.



Fig. 2a.



Fig. 3a.



Fig. 4a.



Fig. 5a.

FIG. 29a.—Check-teeth of *Neodon*.

## a. Right upper molars.

1. *N. sikimensis* Hodgson (B.M., No. 15.9.1.218).
2. *N. forresti* Hinton (type).
3. *N. irene* Thomas (B.M., No. 12.3.18.13).
4. *N. carruthersi* Thomas (B.M., No. 9.4.3.93).
5. *N. oniscus* Thomas (B.M., No. 11.11.1.3).

In face of the severe competition offered to it in Europe and N. America by the very numerous species of *Microtus*, *Pitymys* has been forced to adopt fossorial habits; it owes not only its continued existence, but its outward and cranial specialization, and probably its present wealth in species, entirely to these habits.

In those parts of the highlands of South-eastern Central

Asia, where no species of *Microtus* occurs, members of the *Pitymys* group have been able to persist on the surface of the ground, leading the lives of normal Microtines, and they have undergone a process of cranial specialization exactly parallel with that which, in other places, has been undergone by the species of *Microtus*. These peculiar Asiatic representatives of the genus *Pitymys* constitute the genus *Neodon*.



Fig. 1b.



Fig. 2b.



Fig. 3b.



Fig. 4b.



Fig. 5b.

FIG. 29b.—Cheek-teeth of *Neodon*.

b. Left lower molars (same specimens as in Fig. 29a).

In *NEODON* the fur is soft and full, but is not highly modified as is usual in *Pitymys*; the moderately large ears, provided with a distinct antitragus, are evident above the fur; the tail is moderately long and is fairly well clothed; the fore and hind claws are about equal; usually the sole has six pads, although these are sometimes reduced to five. The mammary formula is the primitive one,  $2 - 2 = 8$ .

The skull is nearly as in *Microtus*. The temporal ridges fuse in adults to form a weak but linear median interorbital crest; the squamosals, frontals, and parietals are correspondingly modified with age. The palate is normal. The auditory

bullæ have only a weak development of spongy bone within. The dentition is essentially as in *Pitymys*,  $m_1$  differing from that of *Microtus* in having only three closed triangles in front of the posterior loop.

TYRRHENICOLA, a fossil genus known from the Pleistocene deposits of some of the Mediterranean islands, is very closely related to *Neodon*. Only one well-marked species is known, a large vole with a skull in which the facial portion is unusually long and narrow, and the braincase is lofty and subcylindrical. The temporal muscles were evidently powerfully developed, the temporal ridges fusing in the much constricted interorbital region to form a median linear crest; the post-orbital processes of the squamosals are moderately developed. The pterygoid fossæ are very deep, indicating powerful pterygoid muscles. The palate is highly specialized, resembling that of "*Stenocranium*" in the

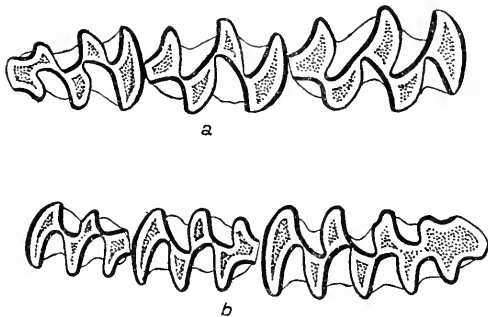


FIG. 30.—Cheek-teeth of *Pedomys haydenii* Baird.  
Crown views: a. right upper, b. left lower molars.

genus *Microtus*. The auditory bullæ are small. The incisors are rather slender, but are normal in other respects. The cheek-teeth are persistently growing, and in other respects are essentially like those of *Pitymys* and *Neodon*.

PEDOMYS is a North American genus apparently closely related to *Neodon*. It is slightly more highly specialized than the latter externally, having long, coarse, not specially modified fur, small ears, concealed in the fur, but provided with a large antitragus, broad hands and feet, with the hind-claws slightly longer than those of the hand, with five plantar tubercles, and with hairy soles; the tail is short; the mammary formula is reduced to  $1 - 2 = 6$ . The skull and teeth are essentially as in *Neodon*, but the mastoid portions of the rather small auditory bullæ are considerably inflated.

ORTHRIOMYS and HERPETOMYS are two very closely related genera, each represented by a single species of restricted distribution, the one stranded upon Mount Zempoaltepee, Mexico,



at altitudes above 8000 feet, the other upon the mountains of Guatemala at altitudes above 9000 feet. They have apparently descended from a primitive *Phenacomys*-like stock and have

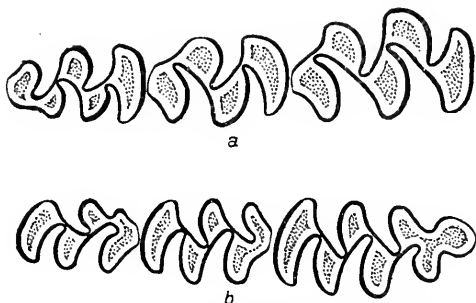


FIG. 31.—Cheek-teeth of *Orthriomys umbrosus* Merriam.

Crown views : *a*. left upper, *b*. left lower molars.

evolved in the direction of true *Microtus*; but although they have gone too far in certain respects to be regarded as members of this genus, or as representing its ancestors, the characters suggest that all three may have been derived from a common *Phenacomys*-like ancestor. The cheek-teeth in both

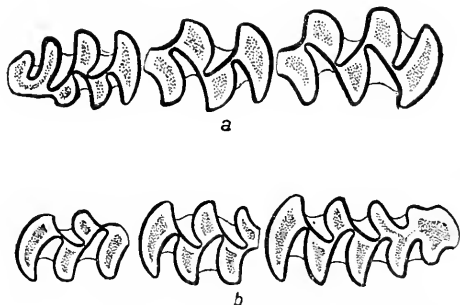


FIG. 32.—Cheek-teeth of *Herpetomys guatemalensis* Merriam.

Crown views : *a*. left upper, *b*. left lower molars.

*Orthriomys* and *Herpetomys* have become completely hypsodont and persistently growing; the temporal muscles have become stronger than in the parent form, producing in the adult skull more salient ridges which fuse anteriorly to form a median interorbital crest. In the general character of the enamel pattern of its molars, small size of the auditory bullæ, general

structure of the skull, and longer tail, *Orthriomys* remains nearer to *Phenacomys* than does *Herpetomys*, which in the features mentioned makes a nearer approach to *Microtus*. In both genera the number of closed triangles in front of the posterior loop in  $m_1$  varies between three and five, and in this they agree with *Phenacomys*, in which  $m_1$  displays a similar though wider (3-7) variability; elsewhere in the group we find that the possession of only three closed triangles by  $m_1$  is a most constant generic character of ancient standing dating, in the case of *Pitymys*, at least from the Pliocene period, and that variability in the number of closed triangles in  $m_1$  is shown only by those genera in which less than four never occur. In the atrophy or complete suppression of the inguinal mammæ, *Orthriomys* and *Herpetomys* differ rather strikingly from other members of the subfamily, in which usually the inguinal pairs are constant and the pectoral pairs are liable to reduction. The flattening of the skull in

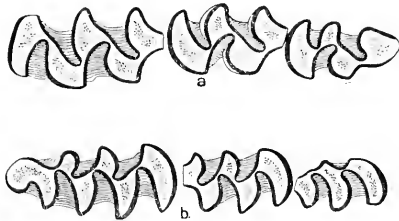


FIG. 33.—Cheek-teeth of *Proedromys* Thomas.  
Crown views: a. left upper, b. right lower molars.

*Orthriomys* is, no doubt, as in the genus *Pitymys*, a specialization correlated with its more fossorial habits.

Of the genera constituting the *Microtus*-group, PROEDROMYS, known from a single specimen collected in Western China, is in two respects the most primitive. Its upper incisors are very broad, recurved, and grooved, and its lower incisors are remarkably short, scarcely invading the condylar process behind. But in the other characters of the skull and teeth it is quite highly specialized. The cheek-teeth are rootless, tall-crowned, and broad, with normally differentiated enamel, and with cement in the re-entrant folds. The enamel pattern is generally as in *Microtus*, but  $m^3$ ,  $m_1$ , and  $m_3$  are somewhat more reduced than usual;  $m^3$  has only three outer and two inner salient angles, its posterior loop formed mostly by the third outer angle;  $m_1$  has only four closed triangles, the fifth triangle or fourth inner angle being broadly confluent with the short, rounded anterior loop; in  $m_3$  the third outer angle is obsolete. The skull is massively built. The temporal ridges probably fuse in extreme

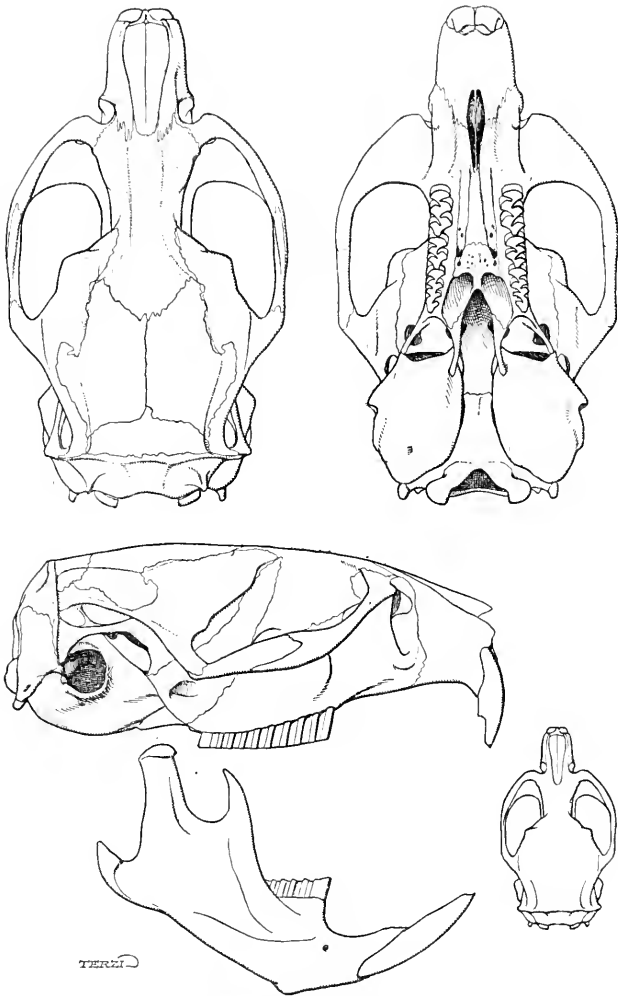


FIG. 34.—*Microtus calamorum* Thomas.

Dorsal, ventral, and lateral views of subadult skull, enlarged; the small figure shows the skull in dorsal view, natural size.

old age in the interorbital region; the post-orbital processes of the squamosals are prominent and peg-like, but the squamosals

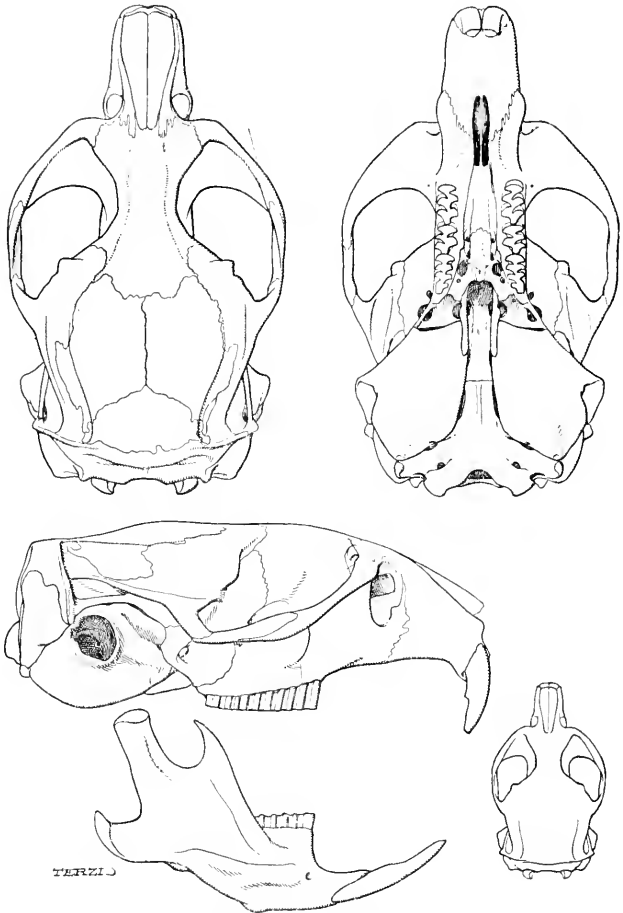


FIG. 35.—*Microtus hartingi* Barrett-Hamilton.

Dorsal, ventral, and lateral views of subadult skull, enlarged; the small figure shows the skull in dorsal view, natural size.

do not appear to approach each other or to encroach upon the frontals with advancing age. The palate is normal; the

auditory bullæ contain spongy tissue. Externally *Proedromys* is a very ordinary looking vole with long coarse fur, a moderately

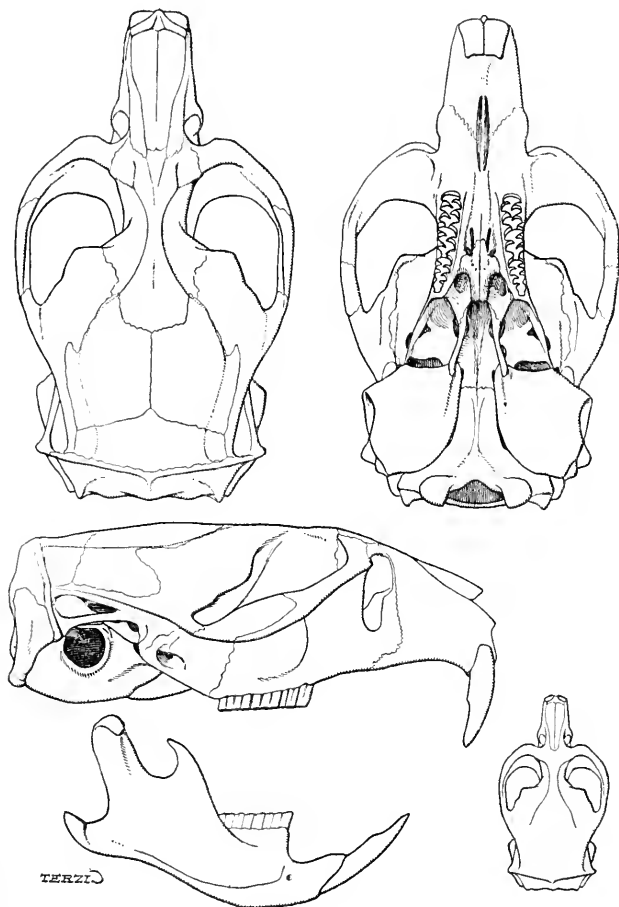


FIG. 36.—*Microtus ratticeps* K. & Blasius.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

long tail, and six plantar tubercles. The mammary formula is  $2 - 2 = 8$ .

MICROTUS is the largest and the most widely distributed

genus in the subfamily, comprising a very large number of recent and fossil forms and ranging over most of the Palæarctic and

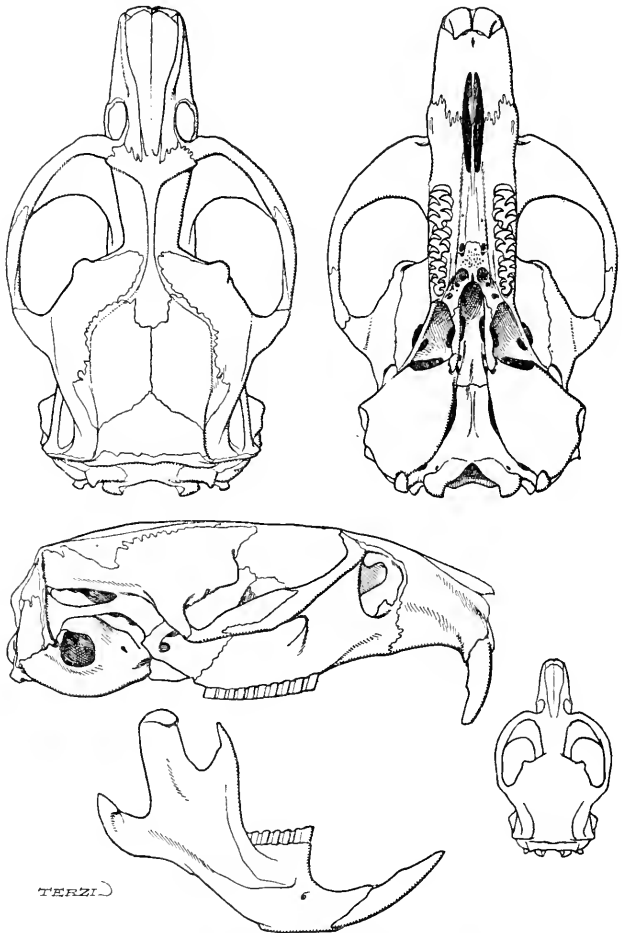


FIG. 37.—*Microtus orcadensis sandayensis* Miller.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

Nearctic regions. The oldest known remains are those found in the later Pliocene (Cromerian Beds) of Britain; but these

consist chiefly of more or less fragmentary jaws and isolated teeth, representing three or four species, and do not throw any

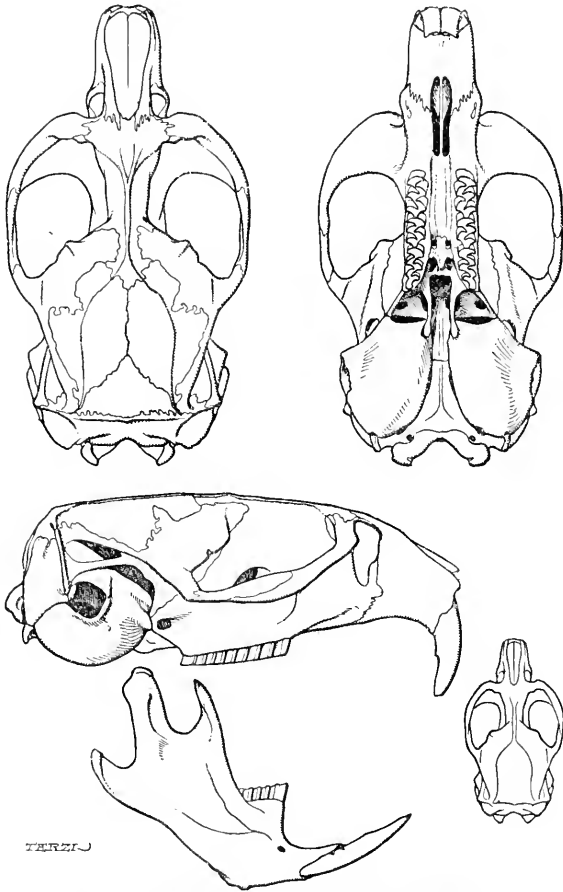


FIG. 38.—*Microtus (Stenocranius) ravidulus* Miller.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

particular light upon the ancestry or relationships of the genus. It is more convenient to reserve the discussion of the various subgeneric groups into which the numerous species of *Microtus*

fall for detailed treatment under the genus. None of the species is specially modified for fossorial or aquatic habits. All have normal coats, moderately developed eyes and ears, and normal hands and feet, with claws of normal length, those of the hind-foot being the longer, with moderately hairy soles and with six plantar

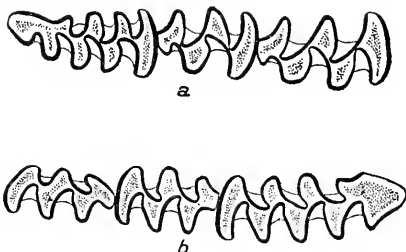


FIG. 39.—Cheek-teeth of *Microtus roberti* Thomas.  
Crown views : a. right upper, b. left lower molars.

tubercles ; the tail is short, or of medium length, and the mammary formula is  $2 - 2 = 8$  (except in the small *mexicanus* group, where it is reduced to  $1 - 1 = 4$ ). The skull is normal, varying in shape, massiveness, and angularity with the species. The temporal ridges, stronger or weaker, fuse (at all events in old age) in the interorbital region ; the post-orbital processes of the

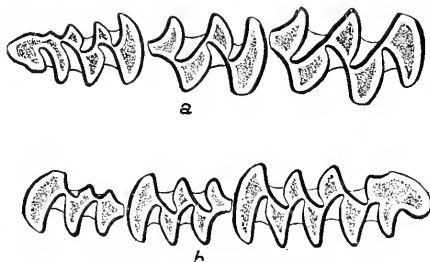


FIG. 40.—Cheek-teeth of *Microtus calamorum* Thomas.  
Crown views : a. right upper, b. left lower molars.

squamosals are more or less developed and an anterior encroachment of the squamosals upon the frontals is more or less evident. The palate is of normal type in all, and in some forms becomes highly specialized by the extension of the post-palatal pits and the attenuation of the postero-median septum. The pterygoid fossæ are deep. The auditory bullæ contain spongy tissue and the stapedial artery is enclosed in a bony tube. The mandible



and incisor teeth are normal. The cheek-teeth are endowed with persistent growth, and have the enamel normally and sometimes conspicuously differentiated, thick enamel forming the concave sides of the salient angles, thin enamel forming their convex sides; cement is present in the infolds. In pattern  $m^1$ ,  $m^2$ ,  $m_2$ , and  $m_3$ , are normal, with or without clear traces of cusp  $n$ ;  $m^3$  has from three to five salient angles on each side;  $m_1$  consists of a posterior loop, usually followed by five substantially closed triangles and terminated by an anterior loop; in some forms the fifth triangle (fourth inner angle) is confluent with the anterior loop; in others, in which the anterior loop is extraordinarily complex, additional triangles may be closed off from the base of the loop so that the number of the closed triangles rises to six, seven or even eight.

CHILOTUS, represented by a few species in North America and Asia, is very closely related to *Microtus*, but it is somewhat

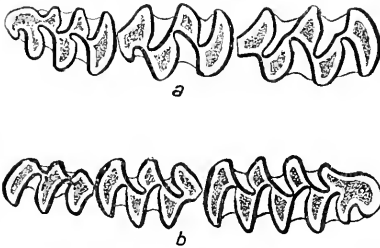


FIG. 41.—Cheek-teeth of *Microtus clarkei* Hinton.

Crown views : *a.* right upper, *b.* left lower molars.

modified for more fossorial habits, or possibly for creeping under logs or stones. Its skull is curiously depressed, and the mastoid portions of the auditory bullæ are distinctly inflated. The fur is short and dense, without any admixture of stiff hairs. The ears are rather small, and the plantar tubercles are reduced to five. In all other respects it agrees with typical *Microtus*.

LASIPODOMYS is a small but rather remarkable Asiatic genus. Closely related to *Microtus*, as is shown by the almost typical skull and teeth, it is considerably specialized externally for fossorial habits, somewhat in the manner of *Lemmus* or *Phaiomys*. The fur has become soft and fine; the ears are short, scarcely appearing above the fur, and are nearly naked. The fore-claws are considerably lengthened, and the thumb is armed with a sharp claw instead of the usual flattened nail. The soles of the hind-feet are densely haired, and although six pads are present, the two posterior are very small, placed low down, and completely hidden beneath the hair. The tail is short and densely clothed. The skull is broad and rather flat, with normal

palate; the temporal ridges fuse anteriorly in old age. The auditory bullæ are densely spongy within, and their mastoid portions are noticeably inflated. The persistently growing cheek-teeth are substantially as in *Microtus*; but  $m^3$  has only three salient angles on each side, and  $m_3$  has the third outer angle obsolete;  $m_1$  is of characteristic form, with a posterior loop, five closed triangles, and a small anterior loop of peculiar squarish shape.

LAGURUS, widely distributed in Eastern Europe, Asia, and Western North America, is a remarkably isolated, in some respects a very primitive, in others a highly specialized genus. It appears on the whole to be most closely related to *Microtus* and its nearer allies, and no doubt traces its descent from some primitive *Phenacomys*-like vole. The external form is highly modified for fossorial habits, the general appearance of the animal being very Lemming-like. The fur is long and very soft. The eyes are moderate. The ears, without an antitragus, are very small and hidden in the fur. The hands and feet are short and broad; the thumb bears a small pointed nail; the claws are of moderate length, the hind ones very slightly the longer; there are five plantar tubercles, but they are completely concealed beneath the dense hairy covering of the soles. The tail is very short and is densely clothed, the hair forming a short terminal pencil. The mammary formula is  $2 - 2 = 8$ .

The short and broad skull has a remarkable superficial resemblance to that of *Dicrostonyx* in dorsal view. The rostrum is moderately short and broad, and the zygomata leave its sides squarely, without any prezygomatic notch. The interorbital region is moderately constricted, but the temporal ridges, although very salient in adults, are rather widely separated anteriorly by a deep median sulcus much as in *Dicrostonyx*; the ridges are rather closely approximated behind, compressing the interparietal, which is abruptly truncated laterally. The squamosals are widely separated anteriorly, with rather small but prominent peg-like post-orbital processes. The palate is essentially as in *Microtus*, with a long postero-median sloping septum. The pterygoid fossæ are short and deep, their floors lying at a level considerably dorsal to the ventral surface of the basisphenoid. The auditory bullæ are very large and are highly modified, with the external meatus shortly tubular and much straitened; the cavity is partly filled with a dense sponge of bone; the mastoid portion and *tegmen tympani* are similarly enlarged and spongy, the mastoid part bulging outwards rather conspicuously between the paroccipital process and the lateral process of the supraoccipital; the stapedia artery is enclosed in a bony tube. The mandible is normal, although the angular process is rather small; the lower incisor displaces  $m_3$  as usual. The upper incisors are strongly curved or slightly "opisthodont."

The cheek-teeth are persistently growing and exceedingly

tall-crowned, their alveolar capsules rising high in the floors of the orbit and sphenorbital fissure. The enamel is differentiated

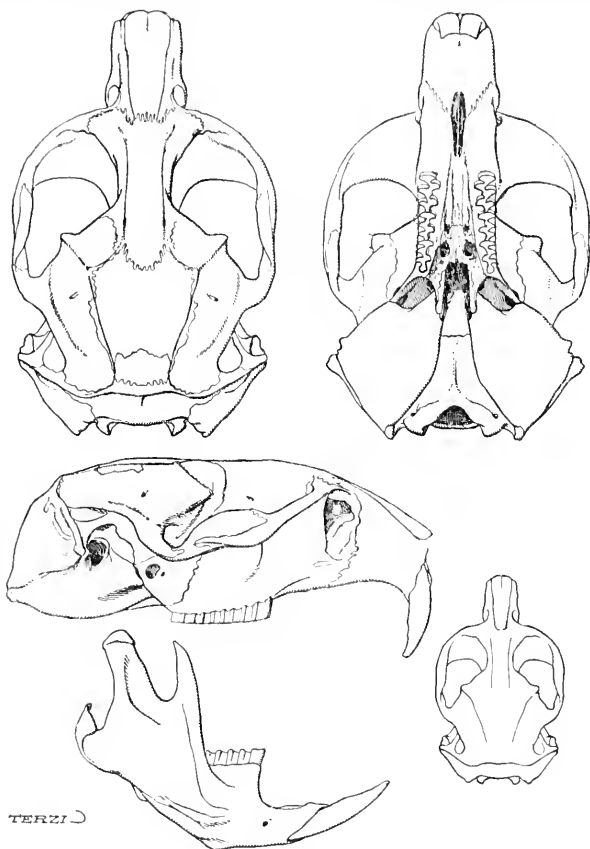


FIG. 42.—*Lagurus luteus* Eversmann.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size (B.M., No. 12.4.1.121; the median dorsal suture is quite obliterated in this specimen).

as in *Microtus*, but the re-entrant folds lack cement. The enamel pattern is characterized by the great width of the re-entrant folds, perfect alternation of the salient angles, long-drawn-out appearance of the teeth, and usually by the retention

in  $m^1$  and  $m^2$  of distinct vestiges of one or more of the "intermediate" tubercles;  $m^1$  and  $m^2$  apart from the generic peculiarities are normal, but the second inner fold of  $m^1$  and the inner fold of  $m^2$  are usually complicated by a vestige of the "protoconule" (cusp  $y$ );  $m^3$  is more or less simplified, with three or four outer and two or three inner salient angles. In general appearance the upper molars, particularly  $m^3$ , show a strong likeness to those of *Alticola*. In the mandible  $m_1$  has five closed triangles between the posterior and anterior loops as in *Microtus*;  $m_2$  and  $m_3$  are normal, but the last-named tooth has its outer angles and infolds less reduced than usual.

Notwithstanding its high specialization for aquatic life ONDATRA, peculiar to North America, is apparently more closely related to *Phenacomys* than to any other Microtine genus, and it has descended from some primitive *Phenacomys*-like stock. In one respect, the palate, it is even a little more primitive than

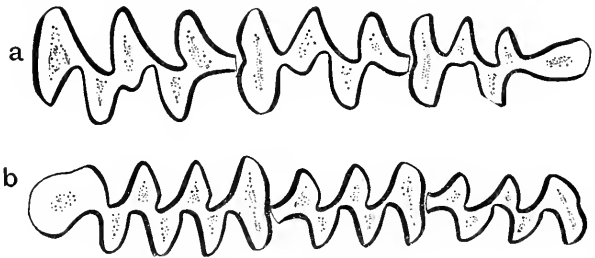


FIG. 43.—Cheek-teeth of *Lagurus luteus* Eversmann.

Crown views: *a.* left upper, *b.* right lower molars.

is any known *Phenacomys*. The cheek-teeth are distinctly primitive and *Phenacomys*-like; they develop roots when adult and have enamel of about equal thickness on the concave and convex sides of the salient angles; the re-entrant folds are partly filled with cement and close the dentinal spaces rather tightly; the depth and narrowness of these folds, coupled with the great breadth of the crowns, impart to the teeth an appearance of longitudinal crowding. The enamel pattern of  $m^1$ ,  $m^2$ , and  $m_2$ , is normal;  $m^3$  has three or four salient angles on each side;  $m_1$  is a complex tooth with a posterior loop, five to seven closed triangles, and a short anterior loop which shows remarkable ephemeral complications when unworn (see p. 115). In  $m_3$  the outer salient angles are somewhat reduced in size, but the outer infolds are deep, so that the first pair of triangles following the posterior loop are substantially closed, and the second pair are not more widely confluent than are the corresponding triangles of  $m_2$ . Obscure traces of "intermediate" tubercles are frequently to be seen in adult or well-worn teeth.

In the skull there are two primitive features; the palate is abnormal posteriorly, lacking postero-lateral bridges, having the postero-median septum represented merely by a slender and free spinous process, and having the postero-lateral pits small and ill defined; the auditory bullæ are small and lack internal spongy tissue, although the external meatus is distinctly tubular, and the stapedia artery is enclosed in a bony tube as far as the stapes. The mandible is nearly normal, but

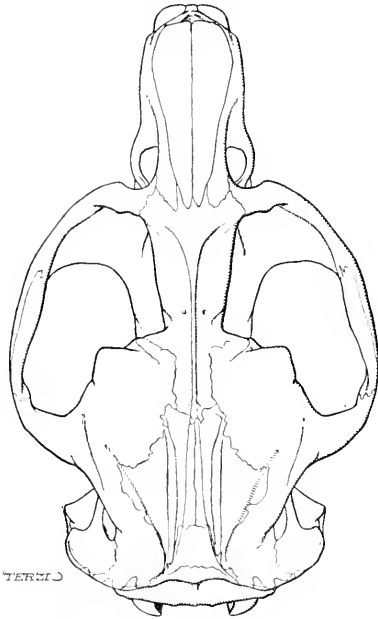


FIG. 44.—*Ondatra zibethica* Linnæus.

Dorsal view of skull (enlarged).

it shows one primitive character; the lower incisor passes backwards below the molar roots to terminate in the lower part of the condylar process, displacing  $m_3$  lingually to a very slight extent. The upper incisors are normal, without grooves, and terminate in the maxilla immediately in front of the anterior root of  $m_1$  as usual (Fig. 21).

In all other respects *Ondatra* is greatly modified for its peculiar habits. Its size has greatly increased beyond that of its terrestrial relatives. The fur is waterproof, made up of very dense, long, fine, and silky under fur, overlaid and more or less completely

concealed by the longer, stiffer, and peculiarly glossy contour hairs. The eyes are small. The ears, provided with a distinct antitragus, are small, densely haired, and almost completely concealed in the fur. The hands are nearly normal and moderately large, with naked palms; the fingers, including the small thumb, all bear long claws. The feet are relatively large, and are slightly twisted, metatarsal IV forming most of the anterior border of the foot (in its natural position); as is common in

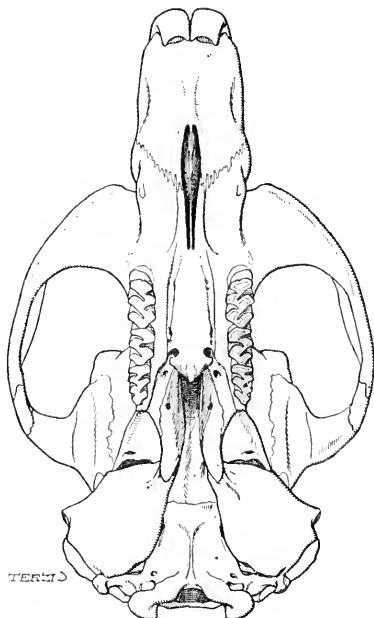
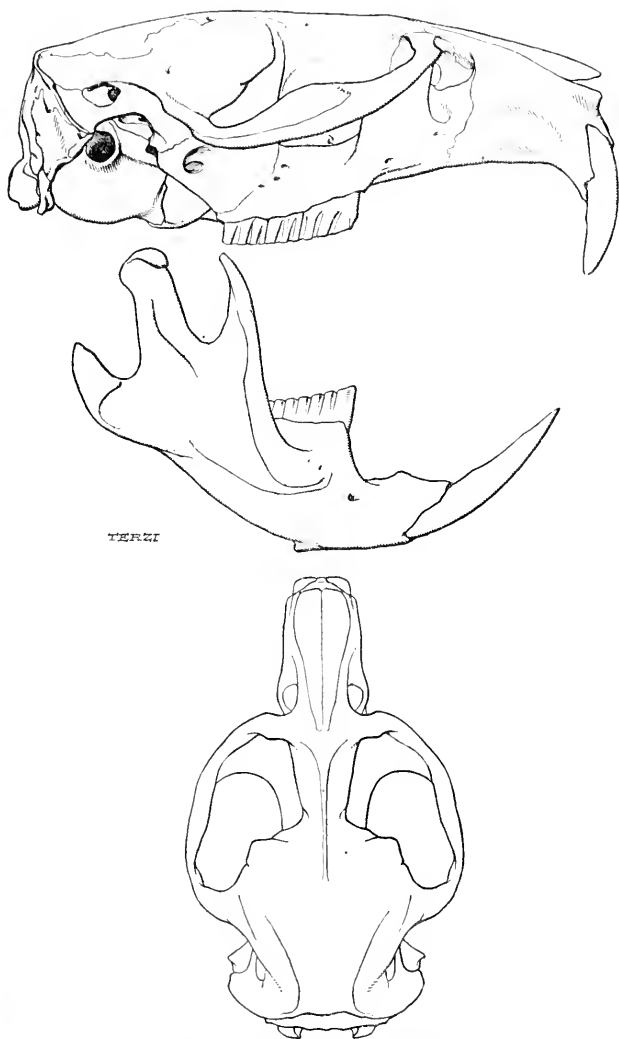


FIG. 45.—*Ondatra zibethica* Linnæus.  
Ventral view of skull (enlarged).

aquatic mammals digit IV tends to be slightly longer than digit III, which is ordinarily the longest toe; all the toes bear claws which are stouter and sometimes longer than those of the fingers; the soles are naked, with five or four plantar tubercles, of which the postero-internal is very large and elongate; the normal postero-external pad is not developed, and the pad which in other voles is usually present between the bases of digits III and IV is sometimes present, sometimes absent. The lateral borders of the foot and of each toe are furnished with conspicuous "swimming-fringes" of stiff hairs,



TERZI

FIG. 46.—*Ondatra zibethica* Linnæus.

Lateral view of skull, enlarged; the small figure shows the skull in dorsal view, natural size

and similar though weaker fringes are developed along the margins of the hands. The tail is very long, about two-thirds of the head and body length, laterally compressed, covered with small scales, and most inconspicuously clothed over its general surface with short stiff hairs; but along the mid-dorsal and mid-ventral borders the hair is longer and denser, completely hiding the skin, and producing behind a very short stiff terminal pencil. The mammary formula is  $1 - 2 = 6$ . Perineal glands, secreting a powerful musk, are well developed.

Apart from the primitive characters above mentioned the skull is highly specialized; it is very large and massive, and in general form and structure closely resembles the skull of the more highly specialized species of *Microtus*. The interorbital region is greatly constricted. The temporal ridges in adults are relatively closely approximated throughout, fusing anteriorly to produce a sharply salient, median interorbital crest. The squamosals are large, relatively closely approximated both anteriorly and posteriorly, with their post-orbital crests strongly developed and extensive, forming the square shoulders of the braincase. The rostrum is long and slender, to accommodate the large incisors. The pterygoid fossæ are deep, their floors distinctly dorsal to the ventral surface of the basisphenoid.

NEOFIBER is another North American genus of great interest. It is represented by a single species known to occur only in eastern and central Florida. Like *Ondatra* it is specialized, though less profoundly, for aquatic life; but in its dental characters it has progressed much further than that genus. *Neofiber* is a very large vole, although considerably smaller than *Ondatra*. The fur, eyes, and ears are substantially as in the latter, but the long contour hairs produce a sort of dorsal keel in the neighbourhood of the rump. The hands and feet are moderately large, with naked palms and soles; the hind claws are distinctly longer and stouter than those of the fingers; the foot is less evidently twisted than in *Ondatra*, and there are five plantar tubercles, the postero-external one being suppressed and the postero-internal pad rounded. The "swimming-fringes" on the borders of the feet and toes are much weaker and less conspicuous than in *Ondatra*, but that along the outer border of the hand is better developed than in that genus. The tail is long, as in *Ondatra*, but is of quite different form, being terete and fully clothed with long stiff hairs. The mammary formula is  $1 - 2 = 6$ . Flank glands are conspicuously developed in both sexes, even in the young.

The skull is essentially like that of *Ondatra*, but is characterized by its great fronto-palatal depth, evenly convex antero-posterior dorsal contour, and conspicuously salient post-orbital squamosal processes. The temporal ridges are more widely separated, the intertemporal portions of the parietal and interparietal being relatively broad. The palate is essentially as in



*Ondatra*, but the postero-lateral bridges are more developed, though slender and incomplete. The choanæ, pterygoid fossæ and auditory bullæ are as in *Ondatra*.

The mandible and incisors are normal; the shaft of the lower incisor displaces  $m_3$  lingually. The cheek-teeth have acquired the power of growing persistently, although in other respects (enamel, tight closure of dentinal spaces, presence of cement in infolds, and general pattern) they closely resemble those of

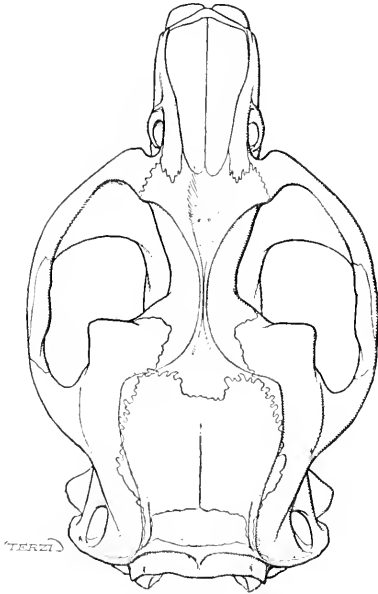


FIG. 47.—*Neofiber alleni* Truc.

Dorsal view of skull (enlarged).

*Ondatra*. The enamel pattern of  $m^3$ ,  $m_1$ , and  $m_3$  is, however, somewhat simplified;  $m^3$  has only three salient angles on each side;  $m_1$  has a posterior loop, five closed triangles, and a short anterior loop (which shows more or less ephemeral and vestigial traces of reduced and obsolete elements); in  $m_3$  the antero-external angle is suppressed, although the triangles following the posterior loop are substantially closed.

Two genera of extraordinary interest, namely, *Prometheomys* and *Ellobius*, remain for discussion. Certain characters, partly primitive, partly progressive, shared in common, show that these two genera are closely related; but in spite of this close

relationship and of the fact that each has been profoundly modified for fossorial habits, they are very unlike. Each has solved the problems of fossorial life in its own peculiar way.

Among the characters common to the two genera may be mentioned the brachyodonty of the cheek-teeth, which develop roots in adult stages of growth; the peculiar reduction of  $m_3^2$ ; the simplification of  $m_1$ ; the absence of cement from the reentrant folds of the teeth; the remarkable relation of the roots

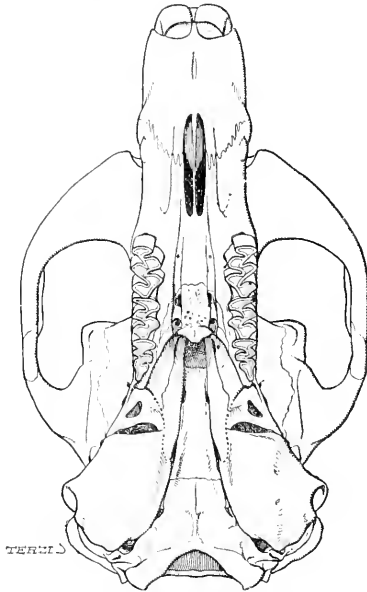


FIG. 48.—*Neofiber alleni* True.

Ventral view of skull (enlarged).

of  $m_3$  to the shaft of the lower incisor. The lower incisor passes from the lingual to the labial side of the jaw between  $m_2$  and  $m_3$  as in other voles; but the implanted part of  $m_3$  curves sharply backwards and follows the curve of the dorsum of the incisor upon its lingual aspect, instead of continuing straight down transversely across the shaft of the incisor.

PROMETHEOMYS, represented by a single species living in the mountains of the Caucasus, is in many ways the more primitive genus. It is a rather large vole, with long and soft fur, very small eyes, and moderately large, naked and rounded ears which are provided with a large antitragus and are not concealed by the fur.

The hands bear enormous claws, those of the three central digits being especially lengthened, slender and recurved; the thumb

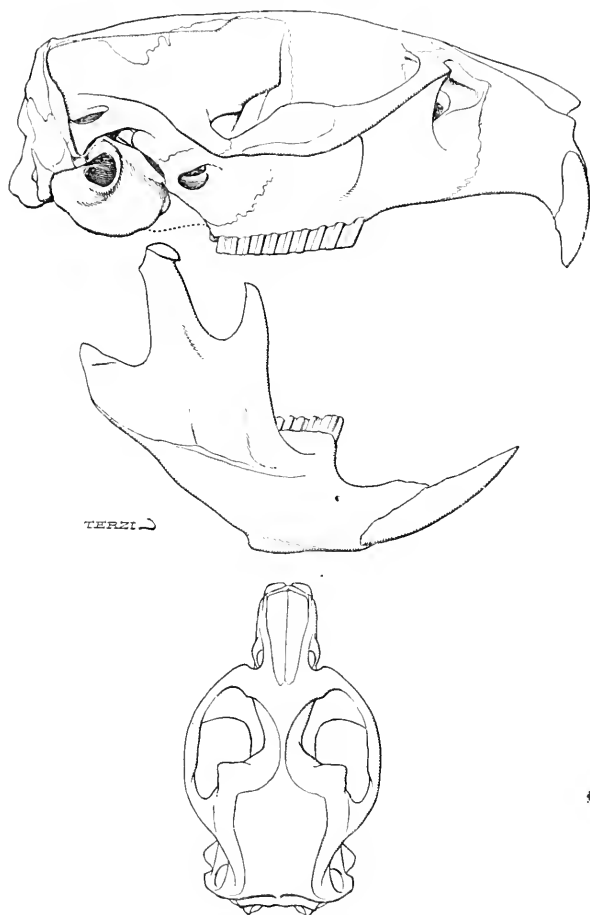


FIG. 49.—*Neofiber alleni* True.

Lateral view of skull; the small figure shows the skull in dorsal view, natural size.

bears a short, stout, curved claw; the palm is naked between the pads, of which there are the usual five. The foot is also provided with large claws, but these are only half as long as those of the

hand; there are five plantar tubercles; the sole is naked between the pads, but is densely haired posteriorly. The tail is about half the length of the head and body, thick, and densely clothed with hair. The mammary formula is  $2 - 2 = 8$ .

In general form the skull is much as in other voles, with moderately long and broad rostrum, rather sharply constricted interorbital region, squarish braincase, normal zygomata, and with the infraorbital canal and its outer wall of the usual form. The rostrum is not unusually shallow; the occiput is vertically truncated. One primitive feature of the dorsal surface is worthy of special remark; traces of the sagittal suture can be seen, even in old adults, between the nasals, frontals and parietals, and posteriorly the suture usually persists, dividing the remarkably small interparietal into two halves. In adults the temporal ridges are fused to form a sagittal crest which ultimately extends backwards from the middle of the interorbital region to the occiput; this crest reaches its greatest height on the posterior part of the frontals, and in all but the very oldest specimens the crest subsides in the mid-parietal region and the ridges, thence feebly marked, diverge slowly to the occiput, crossing the interparietal obliquely; the interparietal, at all times small in *Prometheomys*, diminishes with age. The squamosals are very large, forming the whole dorso-lateral surface of the braincase, their upper borders being parallel; the lateral wings of the parietals, so constantly present in voles, are obsolete; the post-orbital crests, though fairly extensive, are very weak, and the squamosals anteriorly show no special tendency to approach each other by encroaching upon the frontals. These characters are correlated with the great development of the temporal muscles, of which the middle and hinder portions are especially strong; a parallel development is seen in *Ellobius*, and a somewhat similar, but, for Microtinæ, far less abnormal condition occurs in *Ondatra*. The alveolar capsules of the cheek-teeth are, in young specimens, protuberant in the floors of the orbit and the sphenorbital fissure, but these protuberances subside in adults as the crown stumps are pushed out of the capsules by the more slender roots; the capsule of  $m^3$  is nearly clear of the braincase. The antero-palatal foramina are moderately large. The palate is abnormal behind, more primitive than in any other member of the subfamily, but foreshadowing the palate of *Ellobius*, etc.; it is sculptured in low relief, with broad and complete postero-lateral bridges, but with the median septum represented only by a broad irregular nasal spine; the floors of the homologues of the postero-lateral pits lie slightly dorsal to the general surface of the palate, but they are cut off from it by the lateral extensions of the fore-part of the mesopterygoid fossa; each pit is formed as usual by the ventral surface of the palatine bone, but each is perforated by a large foramen which occupies fully half the area of the pit. By filling up the foramina, deepening the pits, placing their edges in continuation with the nasal

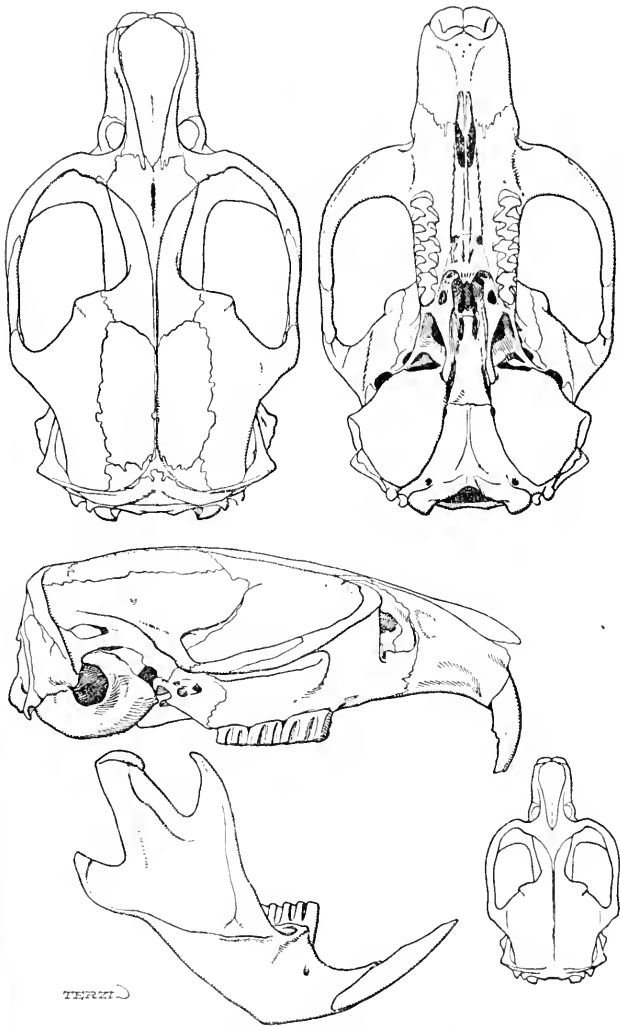


FIG. 50.—*Prometheomys schaposchnikowi* Satunin.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size. (In this specimen the median suture of the interparietal has been obliterated.)

spine, and tunnelling under the postero-lateral bridges we would convert the palate of *Prometheomys* into one like that of *Microtus*.

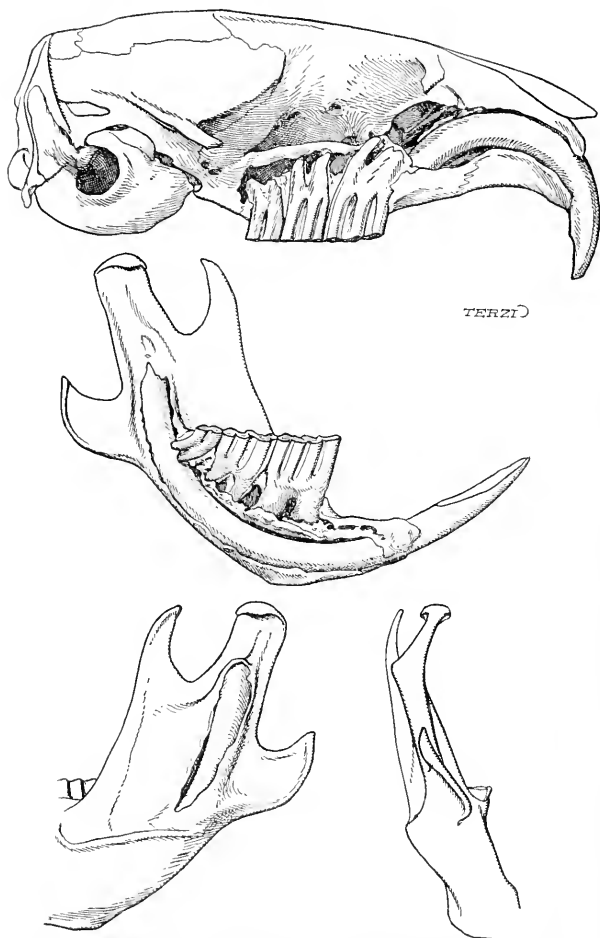


FIG. 51.—*Prometheomys schaposchnikowi* Satunin.  
Skull and left mandibular ramus dissected to show the alveolar courses of the teeth (enlarged).

The pterygoid fossæ are fairly large but are not deep, their floors being about level with the ventral surface of the basisphenoid;

anteriorly they are perforated and placed in rather broad connection with the orbit—a very unusual feature in voles. The auditory bullæ are moderately large, with short tubular external meatus; the *tegmen tympani* articulates with the squamosal in front and the mastoid portion is not inflated; the cavity of the bulla does not contain spongy tissue, but its walls are strengthened by several incomplete perpendicular septa; the stapedia artery is not enclosed in a bony tube. The mandible is normal; the lower incisor produces a strong alveolar hump upon the outer surface of the condylar process well below the level of the condyle.

The upper incisors are strongly curved, their front surfaces flush with the nasal tips and their growing bases lying in the maxillaries immediately in front of  $m^1$ ; they are broad teeth, each with a weak groove on the outer third of its anterior surface; the enamel is stained bright yellow. The lower incisors are not peculiar.

The cheek-teeth are rooted, each tooth with two roots; in  $m^1$  a vestige of a third root, supporting the second inner angle, such as occurs in some of the earlier species of *Mimomys*, is sometimes present; in  $m^2_3$  the two roots may coalesce. The enamel is rather thick throughout, but shows feeble traces of a normal differentiation. Cement is not present in the rather wide re-entrant folds. The outer folds both in upper and lower molars tend to leave the opposed dentinal spaces confluent with each other. The enamel pattern in general is like that of *Ellobius*;  $m^1$ ,  $m^2$ , and  $m_2$  are essentially normal;  $m^3$  has three outer and two inner salient angles, divided into two lobes by the second outer and single inner infolds; its outer salient angles are very much reduced, with the first outer triangle very small and broadly confluent with the anterior loop, an exaggeration of the tooth form seen in *Alticola* and *Hyperacrius*; the opposed tooth  $m_3$  is also greatly reduced and divided into two lobes, of which the posterior consists of the posterior loop proper and the first inner triangle, which are broadly confluent in consequence of the reduction of the first inner fold; the anterior lobe is formed by the second outer and third inner salient angles, broadly confluent with each other; the third outer angle is obsolete;  $m_1$  has three outer and four inner salient angles, consisting of a posterior loop, three substantially closed triangles, and an anterior loop formed by the broadly confluent fourth and fifth triangles which open into the short anterior loop proper. Young specimens of the molars show traces of the "intermediate" tubercles and other ephemeral complications (see p. 117).

ELLOBIUS is widely distributed in Eastern Europe and Asia, and its range, as shown below, appears formerly to have extended into Northern Africa as far west as Tunis and Algeria—the only Microtine known from the African continent. Like *Prometheomys* it is highly specialized for fossorial habits; but its mining operations are conducted in a totally different way, and because the methods employed by the two animals are and have always

been different, fossorial habits moulding what is essentially one and the same primitive stock have in the end produced two totally different results. *Prometheomys* digs its quite shallow but extensive burrows with its hands and throws out the earth in small heaps like a mole; its powerful incisors are used chiefly for the purpose of cutting roots which may obstruct its progress, and for cutting the roots of the subalpine grasses upon which it feeds. The hands, feet, and fur are the organs therefore chiefly affected by the fossorial habits of *Prometheomys*; these habits have not directly influenced either its skull or its teeth to any great extent, and the chief cranial modifications of the genus are correlated with the peculiar development of the temporal muscles and therefore with the peculiarities of the food. *Ellobius*, on the other hand, uses its incisor teeth and skull as a powerful shovel and drill, in the manner of *Spalax*; accordingly the head and fur are highly specialized in this genus, but the hands and feet remain comparatively unmodified.

In *Ellobius* the fur is very fine, short, dense, and mole-like; the eyes are small; the ears are reduced to a mere fold of naked integument surrounding the external meatus and completely hidden in the fur. The hands and feet are of moderate size, armed with very small claws, and with naked palms and soles; there are five palmar and six plantar pads as usual, the plantar pads being all moderately developed or small. The lateral borders of the hands and feet are fringed with stiff hairs, those on the outer margins being especially well developed. The tail is very short, and is fully clothed with stiff hairs, which form a long thin terminal pencil.

The skull shows extreme fossorial specialization, being cuneate in profile, with straightened and far-protruding incisors, extremely shallow and slender rostrum, depressed anterior nares, flattened dorsal surface, and slightly inclined occiput. The zygomata are moderately stout and diverge posteriorly. The orbito-temporal vacuities are rather small; the interorbital region is short and wide, about as broad as the rostrum. The temporal ridges are closely approximated throughout, tending to fuse or in old age fusing to form a sagittal crest extending from the interorbital region backwards to the occiput as in *Prometheomys*. The interparietal is very small, its sutures obliterated in old age. The squamosals are large but do not show any tendency to encroach upon the frontals anteriorly; their post-orbital crests are distinct, but the shoulders of the braincase fall away from the interorbital region much less abruptly than in *Prometheomys* and normal voles. The infraorbital canal is modified; its upper portion for the transmission of the infraorbital portion of the *masseter medialis* muscle is somewhat enlarged, and the lower slit-like portion normally serving for the transmission of the nerves and vessels has disappeared. The rostrum in ventral view is long and slender; the anterior palatal foramina are very small. The palate



is essentially as in *Microtus*, the postero-median septum being sharply defined and the postero-lateral pits deep and extensive.

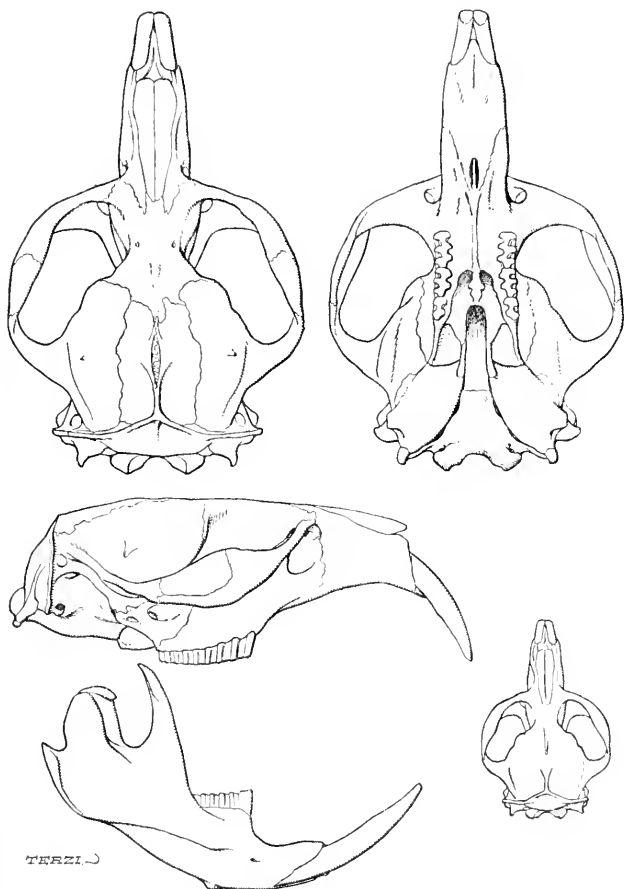


FIG. 52.—*Ellobius fuscocapillus* Blyth.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure shows the skull in dorsal view, natural size.

The pterygoid fossæ are deep, their floors being slightly dorsal to the ventral surface of the basisphenoid, and they are closed anteriorly. The auditory bullæ are very small and but slightly

inflated; their external apertures are very small and their walls are strengthened by a stout and wide meshwork of bony trabe-

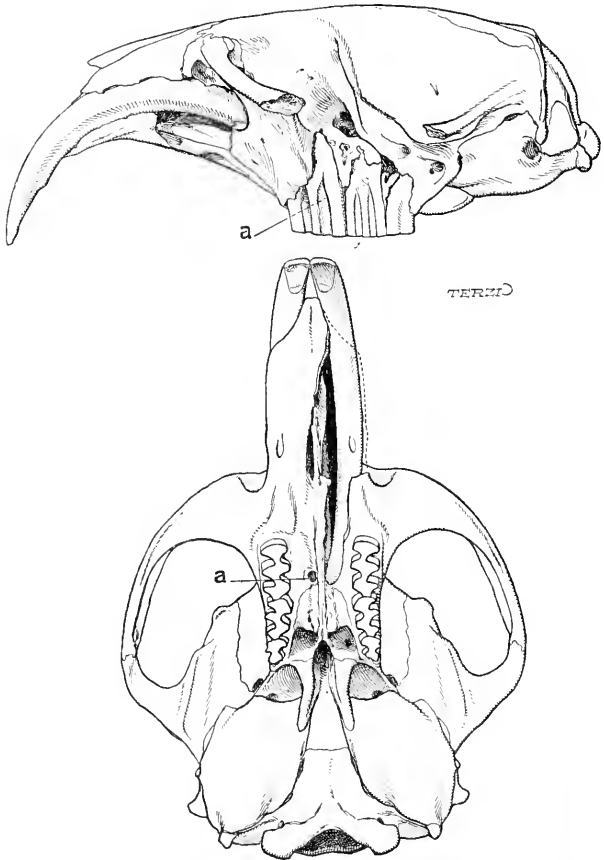


FIG. 53.—*Ellobius taureci* Blasius.

Lateral and ventral views of a skull dissected to show the alveolar courses of the teeth (enlarged); *a.* marks the position of the growing base of the upper incisor and in the ventral view points to the maxillary fenestra.

culæ; the stapedia artery is enclosed throughout in a bony tube. The mandible has lofty recurved coronoid processes, and the angular processes are reduced in each ramus to a mere ridge

bordering the alveolar sheath of the lower incisor as it ascends the condylar process.

The incisor teeth are highly specialized; they are much lengthened and straightened, forming smaller segments of much larger circles than usual; they are without grooves, and, as is very commonly the case in Rodent incisors showing fossorial adapta-

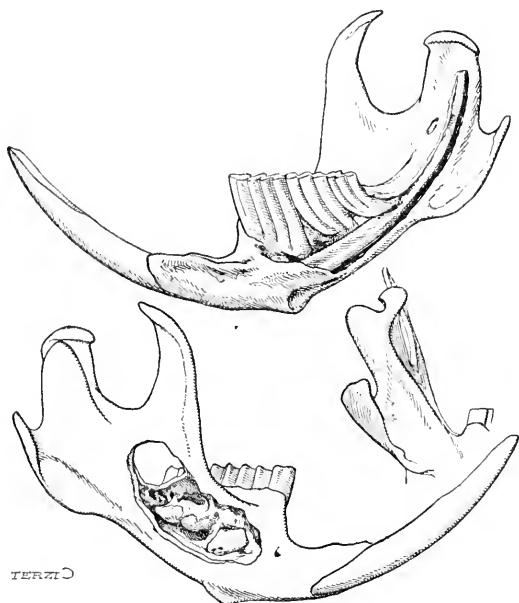


FIG. 54.—*Ellobius tanerci* Blasius.

Right mandibular ramus dissected to show the alveolar courses of the teeth. The small figure represents the left mandibular ramus in oblique posterior view and shows the relation of the alveolar protuberance of the incisor to the condyle (enlarged).

tion, their enamel is white and they tend to be rounded in transverse section. The upper incisors extend much further backwards in the maxillary bones than in any other Microtine genus, their alveolar capsules terminating just dorsal to the surface of the palate between the molars at a point near the hinder end of  $m^1$ ; in some species the ends of the capsules actually appear on the surface of the palate, a fenestra by absorption of bone being opened in the maxilla before the advance of the growing tooth. The lower incisors are also very long, ascending the condylar

process to a point just below the condyle, where their capsule projects, and rises to about the level of the condyle itself.

The cheek-teeth are rooted in adults. The enamel is rather thinner than in *Prometheomys* and about equally thick on the concave and convex sides of the salient angles. Owing partly to the shallowness of the re-entrant folds, which do not contain cement, and partly to the imperfect alternation of the inner and outer angles, the dentinal spaces show an unusual degree of confluence. Apart from their generic peculiarities  $m^1$ ,  $m^2$ , and  $m_2$  are in pattern essentially as in normal voles, but  $m^2$  occasionally shows traces of the cusp  $x^1$  and of the fold which primitively separates that cusp from 6—a very archaic character;  $m^3$  is greatly reduced in much the same way as in *Prometheomys*, but the reduction goes even further, the first outer triangle and the

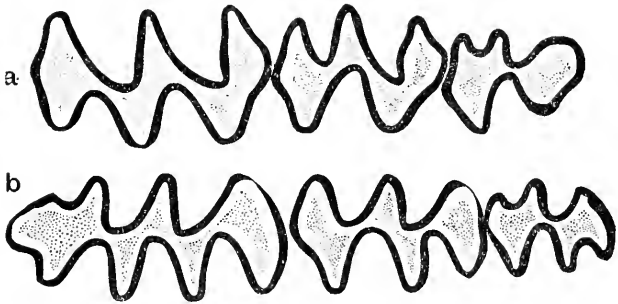


FIG. 55.—Cheek-teeth of *Prometheomys schaposchnikowi* Satunin.

Crown views : a. left upper, b. right lower molars.

infold primitively separating it from the anterior loop being reduced to microscopic vestiges, and although  $m^1$  and  $m^2$  develop two roots each  $m^3$  acquires but a single fang. In the lower jaw  $m_1$  consists of a posterior loop, three to five alternating triangles, and a short anterior loop; its posterior loop is usually substantially closed in front, but the triangles are more or less confluent with each other and with the anterior loop; the degree to which the fourth and fifth triangles are differentiated from the base of the anterior loop varies with the species, the individual, and with age;  $m_2$  is essentially as in normal voles apart from its confluence;  $m_3$  is like  $m_2$ , but is a little more reduced, its antero-external angle being obsolete;  $m_1$  and  $m_2$  have two roots each, which pass down through the jaw to the labial side of the incisor;  $m_3$  has a single fang, lying on the lingual side of the incisor, but sharply curved backwards to follow the dorsal curvature of the incisor, instead of continuing nearly straight downwards as in all other voles with the exception of *Prometheomys*. This abrupt backward

curvature of the tooth and its root is an exaggeration or accentuation of the gentle backward curvature of the  $m_3$  seen in nearly all voles; in those in which the teeth have acquired the power of persistent growth the curvature becomes marked and it is one of the means of keeping the teeth "keyed" together tightly at the grinding surface; but what the mechanical significance of this character is in *Prometheomys* and *Ellobius* I am not prepared at present to say. That it is a character indicating, like others, a special relationship between the two genera, I do not doubt; it may be a character of accommodation, the  $m_3$  having come into relation with the shaft of the incisor at a different moment in its developmental history from that in which these two teeth have come into relation with each other in other voles.

"*Bramus barbarus*" Pomel,<sup>1</sup> from the Quaternary Phosphorites

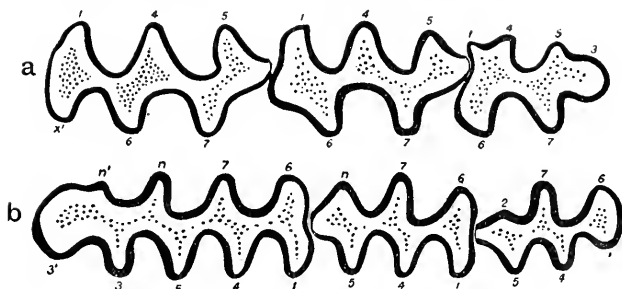


FIG. 56.—Cheek-teeth of *Ellobius talpinus* Pallas.

Crown views: *a.* left upper, *b.* right lower molars lettered according to the homologies of the cusps.

of Tunis, is a most interesting fossil form known to science only from the original description. Miller,<sup>2</sup> in 1896, thought it "probable that *Bramus* is the type of a group differing too widely from any of the recent *Microtinae* to be united with them in one subfamily;" but in 1918 Miller and Gidley<sup>3</sup> placed the genus in the family Rhizomyidae, forming for it a special subfamily *Braminae*. After carefully studying Pomel's most lucid though unfortunately unillustrated account of the fossil species, I have come to the conclusion that *Bramus* must be regarded as a synonym of *Ellobius*. Every detail mentioned by Pomel, namely, the form of the molars, the characters of their roots, the relation of  $m_3$  to the shaft of the lower incisor, the form of the mandibular angle, the character of the infraorbital foramen and the form of the interorbital region, appears to be exactly as in *Ellobius*. The occurrence of this

<sup>1</sup> POMEL, Comptes Rendus, Paris, 114, p. 1159, 1892.

<sup>2</sup> MILLER, N. Amer. Fauna, No. 12, p. 74, 1896.

<sup>3</sup> MILLER and GIDLEY, Journ. Washington Acad. Sci., 8, p. 438, 1918.

genus in the Pleistocene or even at the present day in North Africa would, of course, be in complete harmony with what is now known about the faunistic relations of North Africa with South-eastern and Central Asia.

c. KEY TO THE GENERA OF MICROTINÆ.

GROUP LEMMI.

Lower incisor short, wholly lingual to the molars, and terminating posteriorly in the horizontal ramus opposite or in front of the alveolus of  $m_3$ .

I. Cheek-teeth rooted in adults.

(None yet discovered.)

II. Cheek-teeth rootless and persistently growing, with well-differentiated enamel.

A. Cheek-teeth longitudinally complex; with the inner and outer salient angles and re-entrant folds approximately equal in size or depth; re-entrant folds without cement;  $m^1$  with four salient angles on each side;  $m^2$  with four outer and three inner salient angles; postero-external angle ("cusp  $n$ ") in  $m^1$  and  $m^2$  much smaller than the other salient angles;  $m_1$  with at least five outer and six inner salient angles, and with at least seven closed triangles in front of its posterior loop.

Skull with prominent peg-like post-orbital processes; temporal ridges separated in interorbital region by a median sulcus. Auditory bullæ with dense internal sponge of bone.

Ears vestigial and concealed. Hands and feet short and broad; palms and soles densely clad with crisp hair; palmar and plantar pads vestigial; fore-claws greatly enlarged and apparently double in winter; thumb with minute nail. Tail shorter than foot, densely clothed, with a long terminal pencil. Mammæ  $2 - 2 = 8$  . . . . . **Dicrostonyx.**

B. Cheek-teeth longitudinally simplified; inner salient angles of upper, and outer salient angles of lower molars smaller than those of opposite sides; re-entrant folds with cement;  $m^1$  with three salient angles on each side;  $m^2$  with three outer and two inner salient angles;  $m^3$  apparently consisting of four transverse loops;  $m_1$  with three outer and four inner salient angles and with three closed triangles only in front of the posterior loop. Molars broad-crowned; some of the inner salient angles in upper teeth and of the outer salient angles in lower teeth presenting an appearance of square truncation.

Skull with shelf-like post-orbital crests; temporal ridges fusing sooner or later in the interorbital region.

Thumb with large flattened, strap-shaped nail.

1. Palatal surface of skull not terminating posteriorly as a simple transverse shelf; its median spinous process

forming an inclined septum between the postero-lateral pits (as in *Microtus*).

Upper incisors strongly curved, each with a well-marked anterior groove; second and third transverse loops of  $m^3$  separated chiefly by second outer infold.

Skull lightly built, long and narrow. Auditory bullæ large and globular, internally with a wide meshwork of bony trabeculæ.

General outward form vole-like; ears evident above fur; palms and soles naked between pads; palmar tubercles 4, plantar tubercles 6; claws and thumb-nail not specially enlarged; tail slightly longer than hind-foot, rather thinly clad . . . . . **Synaptomys.**

- a. Lower molars with closed triangles, their outer infolds and salient angles well developed.

Upper incisors very broad.

Rostral part of skull very stout; palate without long posterior spine.

Mammæ 1 - 2 = 6 . . . . . Subgenus **SYNAPTOMYS.**

- b. Lower molars without closed triangles; their outer infolds and salient angles not well developed.

Upper incisors not very broad.

Rostral part of skull slender; palate with long posterior spine.

Mammæ 2 - 2 = 8 . . . . . Subgenus **MICTOMYS.**

2. Palatal surface of skull terminating behind as a simple transverse shelf; its median spinous process when present horizontal and ending freely (as in *Evotomys*).

Upper incisors less strongly curved, without well-marked anterior grooves, and with much hollowed tubular worn surfaces; second and third transverse loops of  $m^3$  separated by first inner and second outer folds.

Skull relatively massive, broad and depressed.

Mammæ 2 - 2 = 8.

- a. External form vole-like, but more thick-set than in *Synaptomys*; fore-claws and thumb-nail not specially enlarged, and skeleton of hand not specially modified.

Skull rather lightly built; zygomata less widely expanded; squamosals relatively widely separated in front. Auditory bullæ globular . . . . . **Myopus.**

- b. External form highly modified for fossorial habits. Ears hidden in the fur. Hands large and broad, the claws and thumb-nail greatly enlarged; metacarpals shortened and ungual phalanges lengthened for support of claws. Feet short and broad, with large claws. Palms and soles densely haired; palmar and plantar tubercles vestigial. Tail short, robust, densely clothed, and with a long terminal pencil.

Skull massive, broad and depressed; zygomata very heavy, strong, and widely expanded; squamosals more closely approximated in front. Auditory bullæ ovate or pyriform, not greatly inflated; densely spongy within . . . . . **Lemmus.**

## GROUP MICROTIL.

Lower incisor long, passing from the lingual to the labial side of the molars between the bases or roots of  $m_2$  and  $m_3$ , and ascending for a greater or less distance behind the molars to terminate within or near the condylar process.

- I.  $m_3$  not extremely reduced, never conspicuously smaller than  $m_2$ ; implanted portion of  $m_3$  not sharply recurved and never approximately concentric with the alveolus of the lower incisor.

- A. Skull with palate terminating behind as a transverse shelf, with or without a median spinous process; the latter when present free, its tip never connected with the inner borders of the postero-lateral palatal pits. Auditory bullæ without spongy tissue.<sup>1</sup>

1. External characters never modified for aquatic habits; size small or medium.

Skull with the temporal ridges usually separated in the interorbital region of the adult (*Hyperacrius* excepted). Auditory bullæ thin-walled; stapedia artery naked as it passes through stapes.

Dentinal spaces of cheek-teeth not always substantially closed;  $m_3$  never with closed triangles.

- a. Cheek-teeth rooted in adults;  $m_1$  with four outer and five inner angles.

External form normal.

Mammæ 2 - 2 = 8

**Evotomys.**

1. Cheek-teeth relatively weak; dentinal spaces of  $m_1$  and  $m_2$  more or less confluent in middle life;  $m_3$  not encapsulated or noticeably displaced by the shaft of the incisor.

Skull not exceptionally massive or angular.

Normal *Evotomys*.

2. Cheek-teeth robust; dentinal spaces of  $m_1$  and  $m_2$  tending to be tightly closed in middle life;  $m_3$  noticeably displaced by the shaft of the incisor and encapsulated on the lingual side of the jaw.

Skull massive and angular, resembling that of *Microtus* in general appearance. *rufocanus* group.<sup>2</sup>

- b. Cheek-teeth rootless and persistently growing.

1. External form Lemming-like. Cheek-teeth tall-crowned but light, in pattern resembling those of normal *Evotomys*;  $m_3$  displaced by the shaft of the incisor and encapsulated. **Aschizomys.**<sup>3</sup>

2. External form essentially normal, not Lemming-like. Lower molars nearly as in normal *Evotomys*.

- a. Skull with the temporal ridges not fused in the interorbital region; post-orbital crests of squamosals never very long; anterior palatal foramina not greatly reduced. Auditory bullæ never very small. Re-entrant folds of the cheek-teeth partly filled with cement. External

<sup>1</sup> The only exception to this is afforded by *Evotomys kennardi*, a fossil species from the Pleistocene of Britain. The bullæ of this form contain a little spongy tissue.

<sup>2</sup> Owing to the existence of intermediate forms it is not possible to separate the *rufocanus* group subgenerically from normal *Evotomys*.

<sup>3</sup> As to the validity of *Aschizomys* see pp. 43, 279.



characters not highly modified for fossorial life; ears moderately or well developed; plantar tubercles 6; fore-claws not noticeably lengthened; fur never highly modified.

α. Mammæ 0 - 2 = 4.

\*.  $m^1$  usually with four,  $m^2$  usually with three well-developed salient angles on the inner side;  $m^3$  with three or four salient angles on each side, its first outer infold usually deep.

Skull relatively broad, the temporal ridges feeble and widely separated in the interorbital region; palate without conspicuous spinous process behind.

#### Eothenomys.

\*\**. m<sup>1</sup> and m<sup>2</sup> normal, the former with three, the latter with two well-developed inner salient angles; m<sup>3</sup> very complex, with five or six salient angles on each side, its first outer infold usually shallow, leaving the anterior loop and first outer triangle broadly confluent.*

Skull long and narrow; temporal ridges stronger, tending to approach in the interorbital region; palate with well-developed, horizontal, median spine behind. **Antelionomys.**

β. Mammæ 2 - 2 = 8.

Cheek-teeth with characteristic long-drawn-out appearance;  $m^1$  and  $m^2$  normal;  $m^3$  variable, sometimes complex, sometimes simplified, with from three to six outer and from two to five inner salient angles, its first outer infold usually shallow and its posterior loop very long and narrow in the more reduced forms of the tooth.

Skull with the temporal ridges weak and widely separated in the interorbital region.

#### Alticola.

\*. Skull normal, not conspicuously depressed.

Subgenus ALTICOLA.

\*\**. Skull greatly depressed.*

Subgenus PLATYCRANIUS.

b. Skull with the temporal ridges fused in the interorbital region; post-orbital crests of squamosals noticeably lengthened, extending backwards towards the glenoid region; anterior palatal foramina small. Auditory bullæ very small. Re-entrant folds of cheek-teeth without cement;  $m^1$  and  $m^2$  normal;  $m^3$  simplified, with three outer and two inner salient angles, its posterior loop short and broad, its first outer infold shallow.

External characters more or less evidently modified for fossorial habits; fur short and dense, sometimes mole-like; ears small; tail short. Mammæ 1 - 2 = 6 . . . **Hyperacrius.**

2. External characters highly modified for aquatic habits; under fur very dense and fine, contour hairs long, stiff and glossy; palms and soles naked; hands and feet furnished with "swimming-fringes"; claws enlarged. Mammæ 1 - 2 = 6. Size very large.

Skull with the temporal ridges fused in the inter-orbital region when adult. Auditory bullæ small; external meatus tubular; stapedia artery enclosed in a bony tube as far as stapes.

Dentinal spaces of cheek-teeth always closed;  $m_3$  with closed triangles; re-entrant folds partly filled with cement.

- a. Cheek-teeth rooted in adults;  $m^3$  with three or four salient angles on each side;  $m_1$  with five outer and six inner salient angles and from five to seven closed triangles;  $m_3$  with three outer salient angles.

Skull with temporal ridges closely approximated throughout; its dorsal contour flattened from before backwards; post-orbital processes of squamosals forming shelf-like crests.

Tail laterally compressed and sealy. Feet obviously twisted; lateral margins of toes conspicuously fringed; fore and hind claws subequal.

Contour hairs not forming a "dorsal keel" on rump . . . . . **Ondatra.**

- b. Cheek-teeth rootless and persistently growing;  $m_3$  with three salient angles on each side;  $m_1$  with four outer and five inner salient angles and five closed triangles;  $m_3$  with two outer salient angles only.

Skull with temporal ridges widely separated on the braincase; its dorsal contour convex from before backwards; post-orbital processes of squamosals prominent and peg-like.

Tail terete, densely haired. Feet less noticeably twisted; "swimming-fringes" less developed on borders of digits; hind-claws longer and stouter than fore-claws.

Contour hairs forming a "dorsal keel" in neighbourhood of rump . . . . . **Neofiber.**

- B. Skull with palate not terminating behind as a transverse shelf; median spinous process always present, converted into a sloping septum between the postero-lateral palatal pits, the inner borders of these pits always continuous with the tip or sides of the median process. Auditory bullæ with or without spongy tissue.

1. Cheek-teeth rooted in adults. Bony palate with postero-median sloping septum short and broad.

- a. Skull with the temporal ridges fused in the interorbital region when adult; palate with postero-lateral pits shallow and ill defined, the postero-lateral bridges sometimes absent. Auditory bullæ large with thin walls; mastoid portion slightly inflated; stapedia artery enclosed in bony tube as far as stapes.

Mandible with  $m_3$  not noticeably displaced by shaft of incisor.

Cheek-teeth with the inner and outer salient angles and infolds approximately equal; re-entrant folds with or without cement, not unusually narrow or deep;  $m^3$  with three or four outer and three inner salient angles;  $m_1$  with five closed triangles.

1. General form of  $m_1$  "nivaloid." Palate narrower. External characters normal; fur, feet and pads not specially modified; ears moderately large; tail long . . . . . **Dolomys.**
2. General form of  $m_1$  "arvaloid." Palate broader. . . . . **†Apistomys.**

b. Skull with temporal ridges widely separated in interorbital region of adult.

1. Lower incisor short, terminating posteriorly in base of condylar process, its shaft not noticeably displacing  $m_3$ . Palate with postero-median septum but little inclined, the postero-lateral pits very shallow, and the postero-lateral bridges usually absent. Auditory bullæ small; stapedial artery naked.

Cheek-teeth characterized by the small size of the outer salient angles of the lower molars; re-entrant folds narrow (giving the teeth a longitudinally crowded appearance), not containing cement; enamel thicker on concave than on convex sides of salient angles;  $m^3$  with three salient angles on each side;  $m_1$  complex with four or five outer and six inner salient angles, its closed triangles varying in number from three to seven.

External characters normal . . . . **Phenacomys.**

2. Lower incisor ascending the condylar process for a greater or less distance, its shaft (at all events in later species) noticeably displacing  $m_3$ . Palate with postero-median septum, postero-lateral pits and bridges well defined.

Cheek-teeth with the outer and inner salient angles and re-entrant folds approximately equal; re-entrant folds of normal width and depth, usually, but not invariably, containing cement; enamel usually thicker on convex than on concave sides of salient angles;  $m^3$  with no more than three salient angles on each side, its second inner infold sometimes persistent, sometimes subject to reduction by insulation of its internal portion;  $m_1$  never with more than three closed triangles in adult stages of wear, its third outer fold sometimes persistent, but usually reduced by insulation of its internal portion. (In older species the molar roots are developed sooner; in newer species at a later moment in the life of the individual; the islet representing the internal portion of the third outer fold of  $m_1$  is a long persistent feature in the earlier forms, but becomes quite ephemeral in later species.)

† **Mimomys.**

2. Cheek-teeth rootless and persistently growing. Bony palate normal; usually boldly sculptured in adults. Mandible with  $m_3$  noticeably displaced by shaft of incisor. Auditory bullæ with the stapedia artery enclosed in a bony tube.

a. Inguinal mammæ always present and functional;  $m_1$  with its fourth and fifth triangles, according to the genus, either constantly closed off from, or constantly open to each other.

1. Enamel pattern of  $m^3$  and  $m_1$  simplified;  $m^3$  with three salient angles on each side;  $m_1$  with three outer and five inner salient angles, its third outer fold more or less reduced, with three closed triangles only and all parts in front of the third triangle merged in the anterior loop.

Skull with the temporal ridges fused in the interorbital region when adult.

External form always more or less modified for fossorial or for aquatic habits.

a. Size medium to large.

Skull massive, strongly ridged and angular when adult; post-orbital crests of squamosals well developed; squamosals tending to approach each other anteriorly with advancing age. Auditory bullæ small, with a slight development of spongy bone tissue within.

External form modified slightly for aquatic habits, but in some species rather more markedly for fossorial life. Hind-claws slightly longer than fore-claws; palms and soles naked; hands and feet slightly fringed laterally. Tail about half length of head and body. Mammæ  $2 - 2 = 8$  . . . . . **Arvicola.**

b. Size small or medium.

Skull less strongly built; post-orbital crests small but salient; squamosals widely separated anteriorly. Auditory bullæ large, their walls strengthened by dense spongy bone tissue; mastoid portion slightly inflated.

External form modified for fossorial life; fur long and soft; palms and soles densely haired, the pads concealed; claws unusually long. Tail short, about one-fourth length of head and body. Mammæ  $3(2) - 2 = 10(8)$ . **Phaiomys.**

2. Enamel pattern of  $m_1$  less reduced, its third outer infold always well developed, and one or more of the dentinal spaces in front of the third closed triangle always separated from the anterior loop.

a.  $m_1$  with only three closed triangles, the fourth and fifth triangles confluent with each other and substantially closed off from the parts anterior to them. Re-entrant folds of cheek-teeth partly filled with cement.

a. Cranial and external characters modified for fossorial life.

Skull with the temporal ridges widely separated in the interorbital region; post-orbital crests of squamosals weak; braincase smooth, depressed, and delicately built. Auditory bullæ well inflated, with spongy tissue within.

Fur soft, dense, and more or less mole-like. Eyes and ears small, the latter concealed. Soles moderately hairy; plantar tubercles 5; claws slightly lengthened. Tail short.

**Pitymys.**

\*. Mammæ  $0 - 2 = 4$  . . . Subgenus **PTYMYS**.

\*\* Mammæ  $1 - 2 = 6$  . . . Subgenus **MICRURUS**.

β. Cranial and external characters not specially modified for fossorial life.

Skull with the temporal ridges fused in the interorbital region when adult; post-orbital crests moderate; squamosals tending to approach each other anteriorly with advancing age.

\*. Skull with facial portion not unusually elongate; palate normal. Auditory bullæ strengthened by net of bony trabeculæ within.

†. Braincase not specially deep and sub-cylindrical. Auditory bullæ moderately large; mastoid portion not noticeably inflated.

Fur soft and full. Ears evident above the fur. Claws of hands and feet rather long, subequal; soles not densely hairy; plantar pads usually 6, but sometimes reduced to 5. Tail rather long, from one-third to half the length of the head and body. Mammæ  $2 - 2 = 8$  . . . **Neodon**.

††. Braincase deep and subcylindrical. Auditory bullæ small; mastoid portion inflated.

Fur long and coarse. Ears small, concealed in fur. Hands and feet broad; hind-claws slightly longer than fore-claws; soles hairy; plantar tubercles 5. Tail shorter, rather less than one-third the length of the head and body. Mammæ  $1 - 2 = 6$  . . . **Pedomys**.

\*\* Skull with facial portion unusually elongate; palate with deep and extensive postero-lateral pits and very long and narrow postero-median septum. Auditory bullæ small . . . † **Tyrrenicola**.

b.  $m_1$  usually with five or more closed triangles, never less than four; the fourth triangle never confluent with the fifth.

α. Vestiges of "intermediate tubercles" ("protoconule," "metaconule," etc.) normally

absent from cheek-teeth; cement present in re-entrant folds;  $m_3$  without closed triangles.

- \*. External characters normal, not obviously modified for fossorial habits.

†. Upper incisors grooved, broad and recurved; lower incisors short, scarcely invading the condylar process;  $m^3$  with three outer and two inner salient angles;  $m_1$  with four closed triangles, the fifth triangle confluent with the short anterior loop;  $m_3$  with its third outer angle obsolete.

Skull massive; temporal ridges fused in the interorbital region; post-orbital processes prominent and peg-like; palate normal. Auditory bullæ with spongy tissue within.

Fur long and coarse; tail moderately long; plantar tubercles 6. Mammæ  $2 - 2 = 8$  . . . . . **Proedromys.**

††. Upper incisors normally without grooves, not unusually broad or recurved; lower incisors long, ascending the condylar process to a greater or less extent.

Skull with temporal ridges fused in the interorbital region when adult; palate normal. Auditory bullæ with spongy tissue within . . . . . **Microtus.**

- \*\* External form and cranial characters modified for fossorial life. Skull broad and flat; temporal ridges fusing in interorbital region in old age. Auditory bullæ densely spongy within; mastoid portion inflated. Ears small.

†. Fur short and dense; claws not lengthened; plantar tubercles 5. Mammæ  $2 - 2 = 8$  . . . . . **Chilotus.**

††. Fur soft and fine; fore-claws considerably lengthened; soles densely haired; plantar tubercles 6, very small, crowded together, and concealed; tail short;  $m^3$  with three salient angles on each side;  $m_1$  with five closed triangles and small squarish anterior loop.

**Lasiopodomys.**

- β. Vestiges of "intermediate tubercles" ("protoconule," "metaconule," etc.) normally present in upper molars. Re-entrant folds wide, without cement;  $m_1$  with five closed triangles;  $m_3$  with closed triangles.

Skull short and broad; temporal ridges salient but separated in the interorbital region by a median sulcus; squamosals widely separated anteriorly, their post-orbital processes peg-like and prominent;

palate normal. Auditory bullæ very large; mastoid portion and *tegmen tympani* swollen; densely spongy within.

Upper incisors strongly curved.

External form Lemming-like; fur long and soft; ears very small, concealed in fur; claws moderate, the hind ones slightly the longer; soles densely haired; plantar tubercles 5, concealed; tail very short. Mammæ  $2 - 2 = 8$  . . . . . **Lagurus.**

- \*. External form more Lemming-like; tail shorter;  $m_3$  with four closed triangles and three outer salient angles.

Subgenus LAGURUS:

- \*\* External form less Lemming-like; tail longer;  $m_3$  with three closed triangles and two outer salient angles.

Subgenus LEMMISCUS.

- b. Inguinal mammæ absent or functionless;  $m_1$  with its fourth and fifth triangles indifferently closed or open, the number of closed triangles varying individually between three and five. Re-entrant folds of cheek-teeth deep and narrow, partly filled with cement;  $m_3$  with closed triangles, its first outer fold deep.

Skull with temporal ridges fused in the inter-orbital region when adult. Auditory bullæ with a small amount of spongy tissue within; stapedia artery enclosed in bony tube.

Fur long and soft; ears large; plantar tubercles 5.

1. Skull long, narrow, and somewhat depressed. Auditory bullæ small. Cheek-teeth, particularly the upper molars, like those of *Phenacomys* in general appearance;  $m^3$  with three salient angles on each side;  $m_1$  with three or four outer and four inner salient angles;  $m_3$  with three salient angles on each side. Tail long, half length of head and body. Mammæ  $2 - 0 = 4$ .

**Orthriomys.**

2. Skull less depressed. Auditory bullæ large. Cheek-teeth of more normal general appearance;  $m^3$  with three outer and four inner salient angles;  $m_1$  with four outer and five inner salient angles;  $m_3$  with two outer and three inner salient angles. Tail shorter, about one-third length of head and body. Mammæ  $2 - 1 = 6$  . . . . **Herpetomys.**

- II.  $m_3^3$  extremely reduced;  $m^3$  always and  $m_3$  sometimes conspicuously smaller than  $m_2^2$ ; implanted portion of  $m_3$  sharply recurved, lying upon and tending to be concentric with the lingual aspect of the dorsal surface of the alveolus of the lower incisor.

Cheek-teeth rooted in adults; re-entrant folds wide and shallow, without cement; inner and outer dentinal spaces mostly confluent, forming or tending to form transverse pairs; enamel thick not clearly differentiated; enamel pattern simplified, that of  $m^1$ ,  $m^2$ , and  $m_2$  essentially normal.

Skull with temporal ridges closely approximated or fusing throughout; squamosals very large, their upper borders tending to be parallel, the lateral wings of the parietals obsolete.

Highly modified for fossorial life.

- A. Skull of nearly normal general form; interorbital region much constricted; post-orbital crests of squamosals shelf-like though weak; infraorbital canal normal; anterior palatine foramina large; palate abnormal, inner borders of postero-lateral pits not directly connected with palatal shelf, each pit with a large foramen. Auditory bullæ moderately large, without spongy tissue, but their walls strengthened by incomplete perpendicular septa; external meatus tubular; stapedia artery naked.

Mandible normal, with well-developed angular and obliquely inclined coronoid processes; alveolar protuberance of incisor well below the level of the condyle.

Upper incisors strongly curved, ending nearly flush with nasals in front and terminating in maxilla just in front of  $m^1$  behind, broad, each with a weak anterior groove; enamel of incisors yellow.  $m^3$  bilobular, with three very small outer and two large inner salient angles, its first infold very shallow leaving the first outer triangle broadly confluent with the anterior loop;  $m_1$  with three outer and four inner salient angles, and three alternating substantially closed triangles;  $m_3$  bilobular with two outer and three inner salient angles, the first inner infold shallow leaving the posterior loop and first triangle broadly confluent, the third outer salient angle obsolete.

Fur long and soft; eyes small; ears moderately large, not concealed; hands with enormous claws, those of the three central digits especially lengthened, slender, and recurved; feet with large claws but these only about half as long as those of fingers; palms and soles naked between the pads; plantar tubercles 5; tail short and thick, densely haired. Mammæ 2 — 2 = 8.

#### Prometheomys.

- B. Skull of extreme "fossorial" form, with straightened and far-protruding incisors, shallow and slender rostrum and slightly inclined occiput; interorbital region broad, not sharply constricted off from braincase; post-orbital crests of squamosals weak; infraorbital canal wider above than usual, but lacking the lower fissure-like portion seen in *Prometheomys* and normal voles; anterior palatine foramina very small; palate essentially as in *Microtus*. Auditory bullæ small, their walls strengthened by numerous stout perpendicular trabeculæ; external meatus very small; stapedia artery enclosed in a bony tube.

Mandible with nearly vertical coronoid process and much reduced angular process; alveolar protuberance of incisor rising to the level of the condyle.

Incisors with white enamel; upper incisors unusually long, slender, and straight ("proödont"), their tips protruding far in front of the nasals, their alveolar



portions extending backwards between the molars to terminate near the palatal surface of the hinder part of the maxilla opposite the hinder end of  $m^1$ .

Cheek-teeth essentially as in *Prometheomys*, but  $m^3$  with its first outer infold still more reduced;  $m_3$  with the first inner infold less reduced;  $m_1$  in some species less reduced, the fourth and fifth triangles in such forms being more clearly separated from the anterior loop.

Fur fine, short, dense, and mole-like; eyes small; ears vestigial and concealed; hands and feet of moderate size; claws very small; palms and soles naked; plantar pads 6. Tail very short, with a long terminal pencil.

Mammæ 2 - 2 = 8 . . . . . **Ellobius.**

### f. SPECIAL NOTES.

#### 1. *The Evolution of the Incisor Teeth.*

Gnawing, as is well known, is the most characteristic of all rodent habits. It is the habit which from the first has exerted the greatest and most continuous influence upon the structure of these mammals. By degrees it has produced all those essential modifications of the incisor teeth, of the jaws, of the jaw muscles, and of the bones to which those muscles are attached, which now distinguish the order Rodentia so sharply from all others. But, if this be so, gnawing must be regarded as the primitive rodent habit, and departures from that habit, whether great or small, are specializations, progressive or retrograde according to the point of view. In turn this gives rise to the reflection that incisor teeth, that by their form and curvature are perfectly adapted for gnawing are, among living rodents, more primitive than those which have lost something of this form and curvature in becoming adapted to other uses.<sup>1</sup>

In rodents with typical gnawing propensities the exact form and curvature of the incisors, no doubt, depend very largely upon the nature of the substance to be gnawn; the hard shells of nuts, the trunks of trees, and the stems of grasses make very different demands upon the teeth. But in all such typical rodents the upper incisors are strongly curved, "orthodont"<sup>2</sup> at least, and

<sup>1</sup> Lest this view appear far-fetched I will add that no one looking at the essential characters of a rodent incisor, namely, its life-long growth and the restricted distribution of its thick enamel, can doubt that it is primarily the product of the gnawing habit. All rodents, whatever their present habits, have descended from ancestors that gnawed vigorously. A good parallel to some of the retrogressive specializations observable among Rodentia is afforded among Carnivora by *Proteles*; no one can fail to recognize the stamp of its predatory ancestors in its incisors and canines; but no one would attribute predatory habits to *Proteles* itself after inspection of its vestigial cheek-teeth.

<sup>2</sup> THOMAS, Ann. Mag. N.H., [9], 1, p. 35, 1918; *ibid.*, [9], 4, p. 289, 1919.

sometimes recurved or "opisthodont." Such strongly curved upper incisors are better adapted mechanically to resist the powerful thrust of the lower incisors, by which the chief part of the work of gnawing is performed. Where the upper incisors have become more or less straightened and protruding (*i.e.*, "proödont"), forming smaller segments of larger circles, their possessor has abandoned to a greater or less extent the gnawing habit; such "proödont" incisors are used sometimes as forceps, for picking out small seeds of grasses, etc.; but more often proödonty is one of the chief expressions of fossorial specialization, the proödont species using the upper incisors for digging burrows.

Some very interesting correlations of minor features with the curvature of the upper incisors are worthy of note. Many facts, observable in such widely different orders as the Primates (Man himself, amongst others), Chiroptera, Insectivora, Carnivora, Ungulata, and Marsupialia, as well as in Rodentia, make it probable that the incisor teeth of mammals were originally multicuspidate or multitubercular. The advanced position of these teeth in the jaws, far in front of the point where the jaw muscles can drive complex teeth with advantage, together with the mammalian need for anterior trenchant teeth, has led to their simplification; but traces of an ancient primitive complexity are to be seen, either as normal features or as atavistic variations, in all the orders above named.

In rodents traces of coronal tubercles and of the valleys between them may be seen sometimes on the tips of quite unworn incisors; the unworn incisor of *Trogotherium* is an example.<sup>1</sup> Usually such features are quite ephemeral; but in certain groups (*e.g.*, Lagomorpha), or certain genera (*e.g.*, *Synaptomys*, *Proedromys*, and *Prometheomys* among Microtinæ) grooves which may be regarded as the external vestiges of the primitive valleys of the incisor occur, usually on the anterior heavily enamelled face of the tooth, but sometimes, though less clearly marked, upon its weaker posterior surface as well. In many genera (*e.g.*, *Lemmus* and *Myopus*) in which the upper incisors cannot be described as grooved, feeble traces of such a structure can be seen by reflected light on holding the tooth at an appropriate angle. In the molars of certain voles (*e.g.*, the  $m_1$  of *Mimomys*) the true significance of such grooves is shown most clearly (see p. 115); wherever it occurs either in the incisors or in the molars, such a groove may be taken to represent the mouth of a primitive valley of the tooth-crown; usually all other trace of the valley (except at the summits of quite unworn teeth) has vanished, but at the mouth a mere notch in the periphery of the tooth has stamped itself upon the enamel organ and dentinal pulp of the ever-growing incisor, and so persists, partaking in the general progress towards hypsodonty, though it is often, or usually, quite devoid of functional importance. In so far as it represents the last, though

<sup>1</sup> HINTON, Ann. Mag. N.H., [5], 8, p. 189, 1914.

highly modified, vestige of the primitive complication of the incisor crown, the presence of a groove may be regarded as primitive, and the absence of such a groove as a specialized feature of the rodent incisor. It is interesting to note that grooved incisors are always strongly curved incisors; proödont incisors with grooves are unknown to me among Myomorpha. On the other hand, strongly curved incisors may show no trace of grooves; so that it would seem that the minor primitive feature (a groove) disappears before the major primitive feature (strong curvature).

Another minor character, very widely distributed among rodents, seems also to be directly correlated, as a general rule, with the more primitive strong curvature of the upper incisors. This is the pigmentation of the enamel, the colour of which, from genus to genus, ranges from deep reddish brown to very pale yellow and even to pure white; the significance of the colour when present, and of the similar pigmentation of enamel seen in the red-toothed shrews, is not known. Its wide distribution in all families of Simplicidentate Rodentia, its high antiquity, dating at least back to Oligocene times, the circumstances that the most strongly curved incisors are the most deeply pigmented and that highly specialized "proödont" incisors are almost invariably pure white, or if tinted are always very pale, are facts which lead me to believe that pigmentation of the enamel is, as opposed to non-pigmentation, a primitive character.

Many years ago Ryder<sup>1</sup> pointed out that when the incisors are wider than thick, the gnawing habit is feebly developed (*e.g.*, Microtinæ), and that when the incisors are thicker than wide, the gnawing habit is greatly developed (*e.g.*, Murinæ). In Microtinæ and in many other rodents the upper incisors, as they become straighter and more proödont, become rounder in section and less truly chisel-like towards the cutting edge, a further proof, if one were needed, that in the group under consideration "proödonty" is the result of specialization for habits inconsistent with ordinary gnawing.

The use of the incisors as digging instruments imposes upon them the burden of unusually rapid waste; to repair this their pulps, in response to the stimulus of extra work, have become larger and more active, pushing their way back to points in the jaws considerably behind those reached by the pulp cavities of the incisors of genera that are less fossorial. In *Ellobius*, the most specialized of the Microtinæ in this respect, the upper incisor has pushed back between the molars to the hinder border of the maxilla, often causing a fenestration in the palatal surface of this bone; and the lower incisor terminates behind level with the condyle. In all other Microtine genera the upper tooth terminates posteriorly in front of  $m^1$ , the lower well below the condyle.

<sup>1</sup> RYDER, Proc. Acad. Nat. Sc. Philadelphia, 1877, p. 314.

## 2. *The Evolution of the Cheek-Teeth.*

The problems relating to the evolution of the cheek-teeth of the Microtinæ are fascinating but difficult. In all members of the subfamily the molars are hypsodont and prismatic, and the worn surfaces of these teeth are always flat and even. In the highest genera the molars are persistently growing teeth implanted in the jaws by their crowns and not by fangs; the re-entrant folds of the crowns are partly filled by cement, which gives attachment to the alveolar periosteum; the crowns show a double system of curvatures, one more or less transverse, the other longitudinal. By means of the alveolar periosteum and the curvatures of their crowns in combination, the teeth are kept tightly "keyed-up" together at the grinding surface, and the delicate dentinal pulps and enamel organs at the bases of the crowns are protected from the injurious effects of pressure and other stresses and strains when the teeth are in use. In the highest Microtinæ the structure of the crown itself shows an important peculiarity. The enamel, which in primitive Muridæ is rather thick, continuous, and at almost all points of the periphery of uniform thickness, is in these highly developed teeth thinner generally and differentiated in a peculiar way; on the concave sides of the prisms or salient angles, *i.e.*, on the posterior sides of the prisms in upper, the anterior sides in lower molars, the enamel is relatively thick, whereas on the convex sides it is very thin, and at certain points it may be lacking altogether. When the molars are at work the lower jaw moves forwards so that the opposed plates of thick enamel, curved in opposite directions, backwards above, forwards below, shear past each other like scissor blades; thus the tough vegetable matter upon which the higher voles feed is sliced and cut to pieces by the cheek-teeth.

It is generally recognized that the Microtinæ have descended from the same ancestors as the rest of the Muridæ; therefore it is admitted that the highly specialized cheek-teeth of the Microtinæ have been evolved gradually from the primitive brachydont and tuberculate molars which characterize all lowly Muridæ. The hypsodont cheek-teeth of the Microtinæ are adapted, as already stated, for the shearing and slicing of coarse, tough vegetable substances; but the brachydont tubercular molars of lowly Muridæ, with their crowns of limited growth, uneven wearing surfaces, and undifferentiated enamel are fitted merely for the purpose of bruising and crushing the relatively soft and succulent materials which form a mixed diet. Microtinæ owe directly or indirectly their special characters and, having regard to the severe competition which they have had to face with the Murinæ in the Old World and with the Cricetinæ in the New World, probably their continued existence, to the circumstance that they have acquired the power of subsisting upon food which is despised for the most part by their rivals.

Direct evidence that such has been the general course of molar evolution within the group is afforded by the vestiges of a tubercular cap which occur, more or less well preserved, upon the summits of the unworn cheek-teeth of *Microtinæ*, and also by the existence of certain *Microtine* genera in which the cheek-teeth are, in one respect or another, noticeably less specialized than are those of the highest forms alluded to above.

A survey of the cheek-teeth of *Microtinæ* shows that the molars differ considerably in complexity in different genera. Before we can form any idea of the history and relationships of the various genera and before we can arrive at any more definite notion than that outlined above of the dental characters of the ancestor common to the whole group, we must determine the direction of general progress within the group. Have the molars tended to increase in complexity? Have they tended to become simpler by the reduction and atrophy of useless parts? Or have they tended to become more complex in some parts or directions, and simpler in others? In attempting to find answers to these questions, we leave the ground which is common to nearly all workers and enter upon a field which has been in dispute for many years. In this place it would, of course, be improper to attempt a full discussion of the points at issue; but it is necessary to give a brief outline of my own opinion in order that the point of view, from which the relationships of the *Microtinæ* have been discussed above may be appreciated.

In the cheek-teeth of *Microtinæ*, as in those of other mammals, the apical portions of the crown are developed first. Growth takes place at the base of the tooth, so that in descending through the successive levels of the crown from the apex or wearing surface to the pulp-cavities below we pass continuously from older to newer horizons. These deeper and newer horizons are exposed successively by wear upon the grinding surfaces of the teeth; and if we study a series of specimens illustrating a given tooth in successive stages of wear, beginning with the unworn germ and ending with the senile stump (when such exists), we find that the characters of the grinding surface change from stage to stage more or less conspicuously, according to the particular tooth and to the particular genus or species chosen for examination. From such a study it becomes apparent that more or less well-marked differences of form and structure characterize successive levels of the crown, and that each succeeding deeper horizon of the tooth is the more or less modified descendant of the one immediately above it. The apical parts of the crown are therefore not only the oldest portions of the individual tooth, but they tend to be the most conservative and primitive portions, the parts likely to retain vestiges of structures which, although no longer of functional importance, may have been inherited from ancestors in which they were of functional importance. That this is a sound view of the matter is immediately proved by the fact that in all rodents

with tall-crowned, prismatic cheek-teeth, those teeth possess when quite unworn more or less well-developed tubercular caps, readily explicable as heritages from brachyodont ancestors, but apparently admitting of no other explanation.<sup>1</sup>

The tubercular cap of the unworn tooth is thus of great interest.<sup>2</sup> It is found more or less clearly developed on the molars of various hypsodont genera, representing between them all three of the great tribes of Simplicidentate rodents; in all three wherever the cap occurs in a well-developed form it shows the tubercles arranged in three longitudinal rows, a circumstance which by itself would almost suffice to prove that such a triserial arrangement, similar to that so familiar in brachyodont Murinæ, represents the primitive arrangement of cusps or tubercles in the molars of this order. In certain Microtine genera, e.g., *Dicrostonyx* and *Arvicola*, some of the coronal tubercles remain clearly recognizable individually, so that we are able to institute a comparison between them and the tubercles occurring normally in the molars of less specialized Muridæ; but in most Microtines the tubercles have lost their individual distinctness, and such a comparison is therefore not possible. Speaking generally (if one may be permitted to anticipate the answers to be given to the questions raised on p. 103), in the present subfamily the transverse simplification of the teeth has progressed very far; so that, although we frequently find traces of some of the tubercles of the median row in this group and evidence that those tubercles in a much modified form build up an important share of the tooth-crown, the triserial arrangement is masked to a greater extent than it is in other groups of Muridæ, where nevertheless the molars are more reduced longitudinally than they are in Microtinæ. But when we consider that such wholly ephemeral structures as these coronal tubercles have had no serious functional importance in Microtinæ since at least Middle Tertiary times, it is not surprising that they have atrophied

<sup>1</sup> A contrary view is expressed by Ameghino in his remarkable "Recherches de Morphologie Phylogénétique sur les molaires supérieures des Ongulés," Buenos Aires, 1904, pp. 32-36. In this very interesting section of his work at p. 34 he says:—

"Nous avons donc sur les molaires nouvelles déjà calcifiées mais qui ne sont pas encore sorties de leurs alvéoles, des caractères morphologiques de deux catégories d'une signification bien distincte.

"1°. Ceux qui sont limités au sommet de la couronne; de ceux-ci, quelques-uns persistent jusqu'à l'âge adulte et sont ceux propres de l'espèce ou du genre, tandis que les autres disparaissent presque immédiatement et sont les caractères précurseurs ou prophétiques destinés à acquérir un plus grand développement et à devenir persistants chez les successeurs.

"2°. Ceux qui distinguent l'ensemble de la molaire, surtout ceux qui se trouvent près de la base et du col; ceux-ci reproduisent à grands traits les caractères qui étaient propres aux ancêtres immédiats, mais qui n'existent plus dans l'espèce." That there is truth in this second paragraph will become evident at a later stage (see p. 118).

<sup>2</sup> Good figures of the tubercular cap of the molars of *Spalax* have been given by Méhely, "Species generis *Spalax*," pp. 296 and 305, 1913; of *Heterogeomys* by Merriam, N. Amer. Fauna, No. 8, pp. 84, 85, and Pl. 16.

in many genera; it is indeed surprising that any of them, in their primitive form, should have lingered to the present time in any *Microtine* genus at all.

It is not possible at present to give a full account of the unworn cheek-teeth of *Microtinæ*, since material suitable for the treatment of all the genera does not exist in collections. Nevertheless, we have enough to show the general direction of progress and we can form a fairly clear notion of what has been the course of dental evolution within the group. It is not my intention now to describe all the instances known to me, but merely to give an account of some selected examples illustrating the general argument, premissing, of course, that I am not acquainted with anything that is incompatible with the views here advanced. But before turning to this task it is necessary to say a word about the homologies of tooth cusps. As has long been recognized the inner and outer sides of upper molars correspond respectively with the outer and inner sides of lower molars. Fleischmann<sup>1</sup> went a step further and asserted that the anterior and posterior ends of upper molars are respectively homologous with the posterior and anterior ends of lower molars; so that in his view a lower molar is the completely inverted image of an upper one. Such a conception of the molars if well founded demolishes the homologies of cusps recognized by the supporters of the Tritubercular Theory, and it has been contested by Osborn.<sup>2</sup> Forsyth Major<sup>3</sup> said, however, in reply to Osborn: "There can be no doubt as to the correctness of Fleischmann's statement, which is easy to verify. A left upper anterior milk tooth of *Didelphys*, for instance, is at first sight very difficult to distinguish from one of the right lower series. Even in such specialized molars as those of modern Ruminants, in holding side by side a right upper and a left lower molar, or *vice versa*, what appear to be the mutual homologies are to be traced out even to very small details." Personally I have not the slightest doubt that lower molars are the completely inverted images of upper ones; and Fleischmann's conception, inconvenient as it may be to workers who have investigated the molars of so many other orders from a different standpoint, has proved to be of the utmost service in working out the evolution of rodent molars. It removes those contradictions which confront us whenever we compare lower molars with upper molars on the basis of the ordinary view of the homologies; it gives a meaning to many characters otherwise unintelligible, and it enables us to carry analysis of the crown structure to a point beyond the reach of the more generally accepted theory.

The most instructive and at the same time the most complex tooth in *Microtinæ* is  $m_1$ , and it is better to begin with this tooth, reserving the discussion of the other molars for a later page.

<sup>1</sup> Sitzungsab. Preuss. Akad. Wiss. Berlin, 1891, 2, p. 891.

<sup>2</sup> Bull. Amer. Mus. Nat. Hist., 1892, p. 84.

<sup>3</sup> P.Z.S., 1893, p. 201.

The unworn  $m_1$  of *Dicrostonyx* (Fig. 57) shows no fewer than seventeen more or less distinct tubercles arranged in three longitudinal rows. Although these tubercles are but feebly salient, they are clearly recognizable upon careful microscopic examination; those capping the five posterior closed triangles are the best developed, but those capping the anterior loop can scarcely be

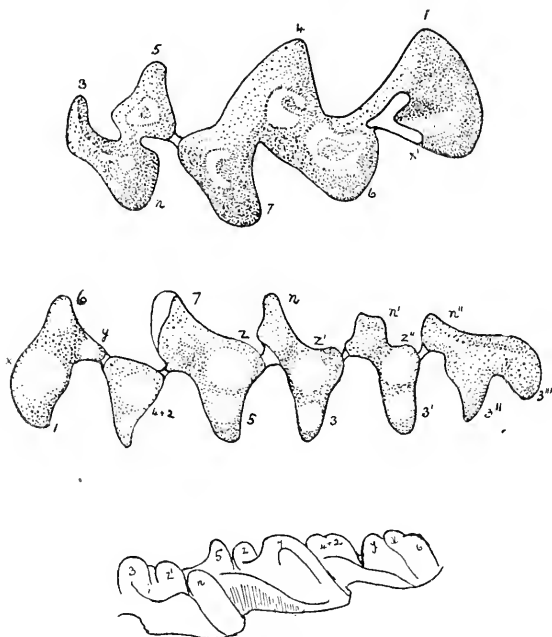


FIG. 57.—*Dicrostonyx grænlandicus* Traill.

Right  $m^1$  and left  $m_1$  of a new-born individual, unworn. The sketch at the bottom is a camera lucida drawing of part of the  $m_1$  viewed obliquely from the outer side and shows the tubercles capping the posterior loop and five posterior triangles (B.M., No. 78.5.13.1, Floeberg Beach, Grinnell Land; lat.  $82^\circ 27' N.$ , July 1876, Capt. Feilden).

said to be differentiated from each other. The tubercles of the median row are relatively large; each of them crowns fully half of one of the inner triangles together with the corresponding central portion of the tooth; the extremity of each inner triangle is crowned by an inner tubercle; an outer tubercle caps each outer triangle. The posterior loop is capped by three tubercles, namely, a small outer (cusp 6), a large inner (1), which is probably a compound of several distinct elements, and a small antero-



median tubercle (*y*), which caps the isthmus connecting the posterior loop with the first inner triangle. This young tooth thus shows that the posterior loop, closed triangles, and anterior loop of the worn  $m_1$  of adult *Dicrostonyx* are direct derivatives from the bases of the coronal tubercles, a median and an inner tubercle forming together the foundation of each inner triangle, an outer tubercle that of each outer triangle.

The unworn  $m_1$  of *Arvicola* is of great interest. As long ago as 1872, Forsyth Major called attention to the occurrence of "accessory prisms" in very young and but slightly worn examples of this tooth;<sup>1</sup> and in 1877 he gave a detailed account and excellent figures of two of his specimens.<sup>2</sup> Although various persons, including Winge, who accepted the characters of the young  $m_1$  as evidence that *Arvicola* had descended from a form that possessed a more complex dentition,<sup>3</sup> have commented upon Forsyth Major's observations, no one hitherto seems to have studied the quite unworn tooth. Such extremely young teeth are rare in collections, but I have managed during the past twenty-five years to bring together a considerable number, from widely separated localities in Europe and Asia, representing various late Pleistocene and recent species. My material includes two or three uncut germs and suffices to show that the complications noted by Forsyth Major are constantly present in the early stages of growth in this genus.

When entirely unworn the  $m_1$  of *Arvicola* (Fig. 58*b, c*) consists of a posterior transverse loop, five alternating substantially closed triangles, and a small but exceedingly complex anterior loop. The enamel is seen in optical section as a thin sheet bounding the greater part of the periphery of the tooth; whether it extends

<sup>1</sup> FORSYTH MAJOR, *Atti della Soc. Ital. Sci. Nat.*, 15, p. 122, 1872, Tav. 2, fig. 12.

<sup>2</sup> FORSYTH MAJOR, *Atti Soc. Tosc. Sc. Nat.*, 3, p. 117, Tav. ix, figs. 25 and 26. He says that in these figures "sono rappresentati due primi denti inferiori di giovane *Arvicola amphibius*, da me raccolti nella . . . Buca delle Fate sopra Molina di Quosa, nei quali si vede un piccolo prisma accessorio tanto dal lato interno che dal lato esterno nella parte anteriore del dente, di modo che il numero totale di prismi in questo dente è di cinque all' esterno e di sei all' interno, come nella maggior parte delle Arvicole [= Microti], mentre che nell' *A. amphibius*, come anche nell' *A. nivalis* e *glareolus*, questo dente ha quattro prismi esterni e cinque interni.

"Il paio di prismi accessori però è separato dal resto del dente soltanto da un solco poco profondo, che per il logoramento presto sparisce. La medesima conformazione l' ho trovato in giovani primi denti inferiori dell' *A. nivalis*; però mai nell' *A. glareolus*."

<sup>3</sup> WINGE, *Danmarks Pattedyr*, 1908, p. 73, "Tilsyneladende er forreste nedre Kindtand hos Vandrotten oprindeligere formet, med færre Slynngninger paa Tyggefladen end hos de andre; men i Virkeligheden er den det ikke; dens simple Form er fremkommen ved en Sammensmeltning og Udviskning af Slynger, der hos Ungen endnu ere tydelige," and on p. 75 he says that  $m_1$  "har hos det voxne Dyr kun 7 Emailleslynger; men hos Unger kan der vare tydelige Tegn paa en Deling af den forreste Slynge i flere." It is interesting to find Winge recognizing the validity of the principle maintained so ably and for so long by Forsyth Major.

over the actual summits of the posterior loop and five closed triangles or not is difficult to say. If enamel does occur on the apices of these parts it must be very thin indeed; personally I am inclined to think that it is absent and that the teeth of *Arvicola* (and of many other voles) afford a parallel to the Murinæ, in which Hensel<sup>1</sup> long ago observed that apical enamel is lacking. The reduction of the apical enamel is a specialization, the significance of which will become apparent a little later. With the apical enamel in such a reduced condition one could hardly expect to find any of the coronal tubercles very clearly differentiated, and those of the middle row have indeed become intimately blended with those of the outer and inner rows, so that no obviously independent and therefore readily recognizable tubercles of the middle row remain. Nevertheless, traces of this row are to be seen in the form of the closed triangles and it would appear that the bases of both the inner and the outer triangles are formed by the median tubercles; the junction of the median tubercle with either the outer or the inner tubercle which forms the peripheral part of each salient angle is marked by a slight constriction; that constriction in the unworn or slightly worn  $m_1$  affects both the posterior and anterior sides of each salient angle, forming on each a vertical furrow; the furrow dies out rapidly on the anterior surface, but on the posterior surface it frequently persists through all stages of growth until the animal becomes aged (Fig. 59). A much clearer, less disputable memorial of the primitive brachyodont and tubercular crown is afforded, however, by a series of four transverse notches or passes, crossing the isthmuses that connect the posterior loop and the first four triangles one with another, thus putting the outer and the inner re-entrant folds in open though narrow connection with each other. These passes stand in relation to the rest of the tooth exactly as "wind gaps" or "hanging-valleys" do to a mountain range.

The summit of the anterior loop is formed by a large irregular postero-median tubercular eminence from which a number of furrows or little valleys radiate, descending obliquely to the outer, anterior, and inner borders of the loop. Three of these valleys, one external, one internal, and one median and longitudinal, are comparatively large and are very constantly present; of them the median valley is the largest and most persistent, wearing down to form an ephemeral enamel islet which is shown in Forsyth Major's figures. The valleys are separated from each other by crests or digitations, which appear as peripheral prolongations from the posterior tubercular mass. As one would expect, these vanishing elements of the tooth show, as regards their details, a not inconsiderable amount of variation in different individuals or species. Thus in an unworn  $m_1$  of the Pleistocene *A. abbotti* (Fig. 58c) the whole tubercular cap of the loop is cut up by the three valleys into four elevated crests, whereas in a recent *Arvicola*

<sup>1</sup> HENSEL, Zeitschr. deutsch. geol. Ges., 8, p. 283, 1856.

(Fig. 58*b*) the valleys do not extend so far back, and so the postero-medial tubercle appears to be much larger than in the

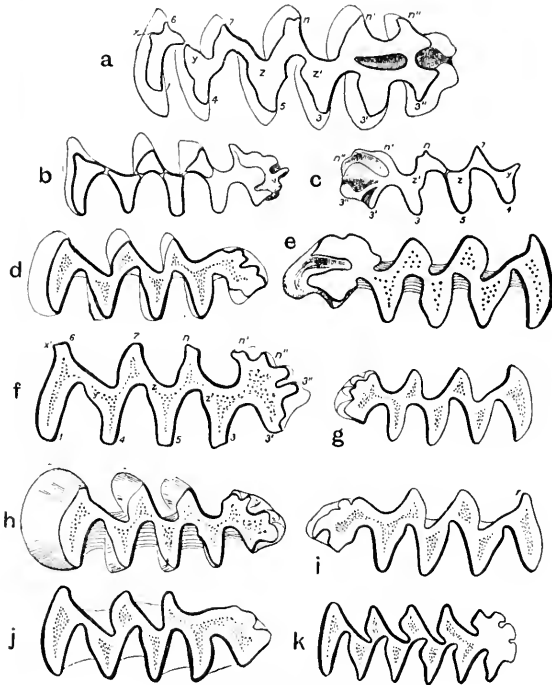


FIG. 58.—*Ondatra* and *Arvicola*.

Crown views of unworn or little worn specimens of the  $m_1$ .

- a. *Ondatra zibethica*. Left  $m_1$ , unworn.
- b. *Arvicola amphibius*. Left  $m_1$ , unworn.
- c. *A. abbotti*. Right  $m_1$ , unworn (Pleistocene).
- d. *A. sapidus*. Left  $m_1$ , slightly worn.
- e. *A. abbotti*. Right  $m_1$ , slightly worn (Pleistocene).
- f. *A. terrestris*. Left  $m_1$ , slightly worn (*B.M.*, No. 3.9.25.7).
- g. *A. scherman exitus*. Right  $m_1$ , slightly worn (*B.M.*, No. 5.11.18.23).
- h. *A. abbotti*. Left  $m_1$ , slightly worn (Pleistocene).
- i. *A. sapidus*. Right  $m_1$ , slightly worn (*B.M.*, No. 8.2.9.201).
- j. *A. sapidus*. Left  $m_1$ , slightly worn (*B.M.*, No. 8.9.1.71).
- k. *Ondatra zibethica*. Left  $m_1$ , slightly worn; drawn to about half scale of other figures (*B.M.*, No. 94.5.9.39).

fossil. Each of the crests between the principal valleys, two on each side, is equivalent to a salient angle, so that in the unworn tooth five outer and six inner salient angles are represented; and

like the more normally shaped salient angles behind, each crest consists of two intimately connected elements more or less distinctly separated from each other by a little oblique furrow. The two elements are, as in the other salient angles, the representatives of two of the primitive tubercles, one belonging to the median row, the other to one of the lateral (inner or outer) rows. The homologies, as I understand them, of these parts are indicated by the lettering to the figures.

It will be seen from the figures that the salient angles and re-entrant folds have a very different general appearance in these young teeth from that which characterizes them in the adult stages of wear. The salient angles or dentinal spaces are small and narrow, the re-entrant folds or cement spaces are wide and open, broadly U-shaped. These are characters common to the teeth of all young voles, and they persist in the adult teeth of some genera (e.g. *Ellobius*, Fig. 56).

As the  $m_1$  of *Arvicola* wears down its crown-pattern undergoes a rapid transformation. The remnants of the crown tubercles are quickly worn away, the ephemeral enamel islet representing the worn-down median valley of the anterior loop being about the last of these ephemeral features to disappear. The salient angles and re-entrant folds acquire their adult form, the anterior sides of the prisms becoming regularly concave, their posterior walls convex. The two posterior outer and the three posterior inner re-entrant folds persist as deep infolds which substantially close the dentinal spaces; but the third outer and fourth inner folds gradually diminish in depth so that the fourth triangle becomes broadly confluent with the fifth, and their common dentinal core becoming broadly continuous with that of the anterior loop, these two triangles are in the fully adult tooth part and parcel of the anterior loop. The manner in which the third outer fold is reduced is very instructive when compared with what happens in certain species of *Mimomys* discussed below. Here and there in adult teeth, long after all ordinary trace of youthful complication has disappeared, more or less well-developed vertical furrows may be seen descending the posterior walls of the prisms or the sides of the anterior loop (Fig. 59); traced upwards in younger stages of wear these furrows are seen to meet the mouths of the ephemeral valleys of the tubercular cap of the crown, and, as is clearly shown in the genus *Mimomys*, such furrows are to be interpreted as the functionless but persistent last vestiges of the primitive tubercular cap.

The late Pliocene and early Pleistocene genus *Mimomys* comprised, no doubt, the species which was the direct ancestor of the late Pleistocene and recent species of *Arvicola*. To it, therefore, we naturally look for further information as to the composition of the primitive tubercular cap of the  $m_1$ . Unfortunately, however, no unworn teeth of *Mimomys* have as yet been discovered; nevertheless, as *Mimomys* is a far more primitive genus than

*Arvicola*, we do glean some additional information from the less-worn teeth that are available, for certain of the highly ephemeral complications seen in the young *Arvicola* are more strongly developed and persist to a far later stage of wear in some of the species (and particularly the geologically older species) of *Mimomys*.

The oldest known form is *Mimomys pliocænicus* from the Norwich Crag, and in Fig. 60a-c, the  $m_1$  of this species is shown in different stages of wear. In this genus the molars develop roots in adult life and by comparing the degrees to which the roots are developed we are able to form an idea of the relative ages of the teeth before us. In Fig. 60, a represents a right  $m_1$  in the youngest stage of wear yet seen; but the lateral view, a', shows that the tooth belonged to a subadult individual, since the cement spaces are already closing below, the first step towards the

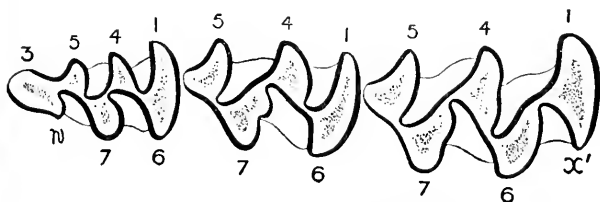


FIG. 59.—Right upper molars of *Arvicola amphibius* Linnaeus, lettered to show the homologies of the cusps.

In this specimen  $m^2$  shows a well-marked vestige of cusp z (or "metaconule") between 4 and 7; a weaker trace of the same structure and traces of other median tubercles are seen in  $m^1$ .

development of roots; b and b' represent a slightly older tooth in which the cement spaces are completely closed below; c and d represent two teeth which belonged to individuals in the prime of life; lastly, e represents a very old specimen provided with very long fangs, its crown being almost worn away.

If we compare the youngest though considerably worn tooth of *M. pliocænicus* (Fig. 60a) with the unworn  $m_1$  of *Arvicola* (Fig. 58c) we see, on making due allowance for the difference in individual age, a very striking resemblance. In each the posterior loop is followed by five substantially closed triangles and a small anterior loop; in each the third outer fold is deep and is directed backwards instead of forwards. The third outer prism in each is cleft by a vertical "prism-fold," very shallow and superficial, it is true, in the tooth of modern *Arvicola* (in which it rarely occurs), deep and persistent throughout life in *M. pliocænicus*; this "prism-fold" incompletely separates the outer tubercle, which forms the tip of the salient angle, from the median tubercle (very conspicuous in *Mimomys*, less so in *Arvicola*) which lies in front

complicating the anterior border of the prism. It is interesting to note that this particular median tubercle (always, of course, associated with the third outer angle) crops up again and again as an atavism in many widely separated Microtine genera (cf. Fig. 67, 3). The anterior loop proper is too far worn in the

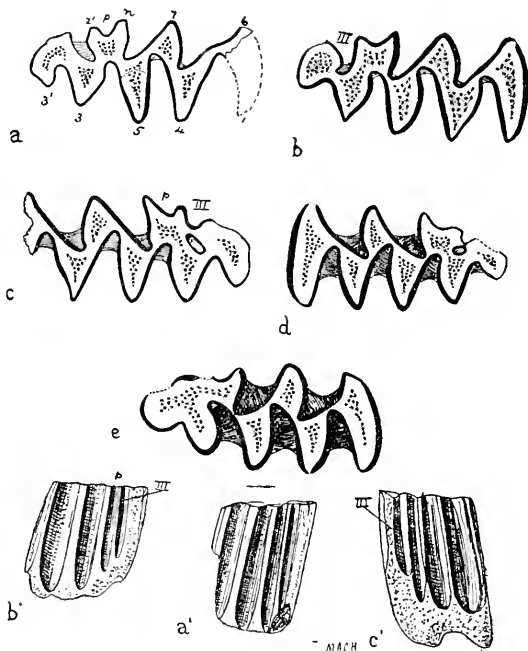


FIG. 60.—*Mimomys pliocænicus* Forsyth Major.

Crown and external views of the  $m_1$  in different stages of wear (Norwich Crag).

- a, a'*. Right  $m_1$ , cement spaces closing.  
*b, b'*. Right  $m_1$ , cement spaces closed.  
*c, c'*. Left  $m_1$ , with short roots.  
*d*. Left  $m_1$ , with moderately long roots (for outer and inner views see Pl. XIII, figs. 1, 1a).  
*e*. Right  $m_1$ , old, with very long roots.

subject of Fig. 60a to show any clear trace of complications, although a certain waviness of its antero-external border suggests that these were present in a slightly earlier stage of wear. One other feature deserves notice, namely, the peculiar outward convexity of the isthmus connecting the posterior loop with the

first closed triangle; this little feature is seen again and again in the young teeth of many members of the subfamily, and, as the young  $m_1$  of *Dicrostonyx* (Fig. 57) shows, it is the last trace of one of the median tubercles.

In the succeeding stage (Fig. 60*b*) the third outer fold has acquired a normal form and direction and the fourth and fifth triangles have become broadly confluent, their common dentinal core being, however, shut off from that of the anterior loop. In middle age, as Figs. 60*c* and *d* show, an interesting change, without a parallel in modern *Arvicola*, takes place on the grinding surface of the  $m_1$  of *M. pliocenicus*. The third outer valley is reduced by insulation, its inner portion being converted into an enamel islet which persists as a conspicuous feature of the grinding surface for a very long time. Gradually that islet wears out; in old age (Fig. 60*e*) it disappears; and thus the tooth, in its last stages of wear, acquires substantially the appearance that it has through all the adult stages of wear in *Arvicola*. After the insulation of its internal portion, the outer part of the third outer valley is represented by a vertical groove on the side of the crown; this groove dies out below above the level of the base of the "prism-fold" and of the bases of the hinder outer cement spaces; this feature is clearly shown in Figs. 60*a'*, *b'* and *c'* as well as in Pl. XIII, fig. 1. From the latter illustration it will be seen that some trace of this external vestige is sometimes continued downwards beyond the limits of the enamelled crown on to the surface of the dentine forming the anterior fang, a circumstance which shows how such groove-like vestiges of ancient valleys tend to persist long after they have ceased to be of any functional importance.

The progressive reduction of the  $m_1$  in a later species, *M. intermedius*, is illustrated in Figs. 61*a-f*, which are arranged in order of age beginning with the youngest. It will be seen from these drawings that towards its summit the crown of  $m_1$  in *M. intermedius* agrees closely in structure and form with that of the younger specimens of *M. pliocenicus*, possessing exactly the same complications. As revealed by the successive stages of wear this initial complexity is got rid of in deeper levels of the crown in exactly the same way in both species. But in *M. intermedius* the complexity is wholly ephemeral instead of being almost life-long, and the adult simplified pattern, corresponding closely with that which first appears in *M. pliocenicus* in old age, appears on the grinding surface of the tooth long before the cement spaces show the least signs of closure below. The anterior costa of the "prism-fold" is, however, weak in *M. intermedius*, and therefore, after the insulation of the third outer fold, no feature can be seen on the outer surface of the crown to distinguish the external vestige of the reduced valley from the concavity of the "prism-fold." But in a closely allied and associated form, *M. savini* (Fig. 99, 13-16; Fig. 101, 1-14), the costa is distinct, and an adult pattern and structure precisely

similar to that seen in the  $m_1$  of *M. plioccenicus*, after the disappearance of the islet, is speedily brought to the surface by wear. The youngest tooth of *M. intermedius* at present known (Fig. 61a) shows two of the lowest crown tubercles

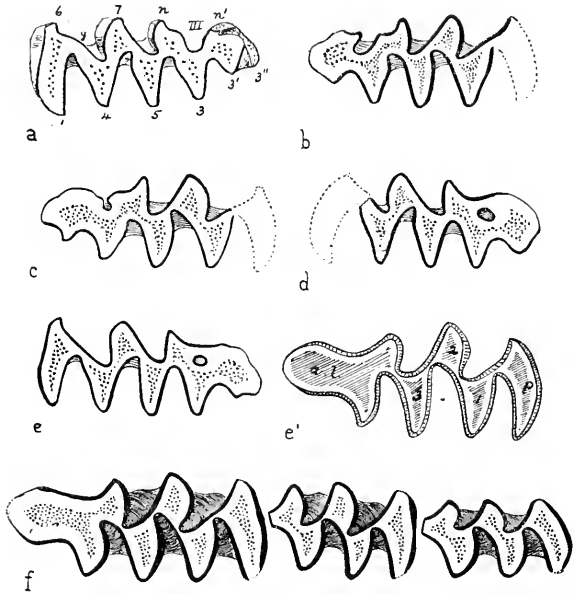


FIG. 61.—*Mimomys intermedius* Newton.

Crown views of young specimens of the  $m_1$  and of the lower molars of the type specimen; all from the Upper Freshwater Bed at West Runton.

- a. Left  $m_1$ , very young, with third outer fold intact, and other youthful features.
- b. Right  $m_1$ , slightly older than a.
- c. Right  $m_1$ , with third outer fold undergoing insulation.
- d and e. Two examples of the left  $m_1$  with the third outer fold represented by an ephemerally formed enamel islet; e', basal pattern of e for comparison with the adult crown pattern shown in the type specimen f. (In e' the dentinal spaces are lettered to illustrate the terminology usually employed in descriptions of Microtine molars: p = posterior loop; 1, 2, 3 closed triangles; a.l. anterior loop.)

surmounting the fore-part of the anterior loop; but wear has proceeded too far to enable us to say whether a median valley was originally present in the fore-part of the anterior loop, as in *Arvicola*, or not.

In the species of *Mimomys* so far mentioned the third outer fold



of  $m_1$  is reduced by insulation; but although some early Pleistocene species of *Arvicola* appear to agree with these species of *Mimomys* in this respect, others, including all the known later Pleistocene and recent species, do not, for in these later forms, as described above, the fold in question is reduced merely by a gradual weakening or transverse shallowing. Side by side, however, there occur in the same deposits with those of *M. pliocenicus*, *M. intermedius* and *M. savini* the remains of other species of *Mimomys* which seem to stand nearer to the ancestor of the existing species of *Arvicola*. In these (*M. newtoni* and *M. majori*) the third outer fold of  $m_1$ , although often reduced in depth as in modern *Arvicola*, never suffers reduction by insulation. The material representing the older species, *M. newtoni*, is still too scanty for satisfactory discussion, but remains of the later form, *M. majori*, are more abundant in collections. The youngest specimen I have seen is represented in Fig. 104*b*, and in Pl. XV, fig. 1, and it is a tooth of considerable interest. It shows that confluency of the dentinal spaces which commonly appears in the teeth of young voles shortly after the removal of the tubercular cap by wear. There is no trace of the "prism-fold"; but the third outer valley, already containing a little cement, is persistent. In front of this fold and obliquely placed upon the outer margin of the anterior loop is a small enamel islet which represents the inner part of a highly reduced fourth outer fold. Just below the swollen outer lip of the islet there commences a shallow furrow which passes vertically down the outer side of the crown. If the islet had not been present it would have been difficult to interpret the meaning of the furrow, and before the discovery of this young tooth the furrow, observed in many adult examples of the  $m_1$  of *M. majori*, puzzled me considerably. But the relation of the furrow to the islet shows quite clearly that the former must be regarded as the external vestige of the reduced fourth outer valley. This vestige is often present and is long persistent in *M. majori* as shown by the figures in Pl. XV; on the grinding surface, the only feature that it makes is a minute curl in the enamel of the outer border of the anterior loop (cf. Fig. 105, 14).

Attention may be called also to the young tooth shown in Fig. 104*a* and *a'*; this specimen, referred to typical *M. majori*, closely resembles the young  $m_1$  of *M. intermedius* (Fig. 61*a*) in general form; it shows not only a persistent third outer fold and a persistent external vestige of the fourth outer fold, but very clear traces of the median tubercles *y* and *z*.

A very young  $m^1$  of *M. intermedius* (Fig. 101, 16) shows that transverse passes across the summit of the crown, described above as occurring in unworn teeth of *Arvicola*, occur also in *Mimomys*; the last trace of one is seen crossing the isthmus between the two posterior triangles.

The unworn  $m_1$  of *Ondatra* (Fig. 58*a*) shows clearly that in this genus the enamel does not extend across the summit of the

tooth, the dentine being already exposed in each of the dental spaces; therefore no coronal tubercles linger in the  $m_1$  of *Ondatra*. But the form of the prisms is most suggestive, indicating that the derivatives of the outer row of tubercles are reduced almost to disappearance, this series contributing no more than the mere tips to the outer salient angles, including that of the posterior loop. The derivatives of the inner tubercles are larger, each forming about half of one of the inner salient angles as in *Dicrostonyx*. The central or basal portions of the inner salient angles, the greater part of each outer triangle, and the isthmuses connecting the inner and outer triangles are formed evidently by derivatives of the median row. A narrow pass, quite similar to those described in young *Arvicola*, separates the posterior loop from the first inner triangle; but all the closed triangles and the anterior loop are already connected with each other by narrow isthmuses of dentine bounded by enamel. Between the posterior and anterior loops there are five alternating and substantially closed triangles. The third outer angle shows a minute prism-fold. The anterior loop is of very great interest, closely resembling in all essentials that of the unworn  $m_1$  of *Arvicola*. It is cleft from before backwards by a median longitudinal valley, which extends from the front margin of the tooth to the isthmus connecting the anterior loop with the fifth closed triangle. The valley is divided into two portions, an anterior and a posterior, by a little isthmus of enamel and dentine; its posterior and central portion is confined to the summit of the crown, where it forms a large elliptical enamel-lined lake or islet; the anterior portion is a deep furrow notching the anterior border of the tooth and descending its front surface for a considerable distance. On either side of this median valley there are two salient angles as in *Arvicola*, but the posterior one on each side is normally formed and persists in adult stages of wear instead of being ephemeral as in the latter genus. The anterior salient angle on each side is complicated by traces of a prism-fold and is probably a compound of several originally distinct but now highly reduced and ephemeral elements.

In Fig. 58k a slightly worn  $m_1$  of *Ondatra* is shown. In this tooth also we see distinct traces of some of the ephemeral parts just described; the last trace of the median valley and remnants of the other complications of the anterior loop are particularly noteworthy.

It would be tedious to describe the young specimens of  $m_1$  for every genus in which I have observed ephemeral complications; such features occur normally in the young of many widely separated genera, e.g., *Synaptomys*, *Dolomys*, some species of *Evotomys* and *Microtus*, and in the figures accompanying this work various examples are shown to which it is unnecessary to make any special reference. Among voles *Prometheomys* and *Ellobius* have the  $m_1$  simpler, in a longitudinal sense, in adult stages of wear than in

other genera; in these two genera the molars (Figs. 55 and 56) retain many primitive characters, *e.g.*, extreme brachyodonty (for *Microtinae*), confluent dentinal spaces, U-shaped re-entrant folds, undifferentiated enamel, and absence of cement; therefore the simplicity of  $m_1$  might not unnaturally be regarded as a primitive feature too. But the unworn  $m_1$  of *Prometheomys* (Fig. 62) is a relatively complex tooth with a large anterior loop, which is sharply de-limited from the fourth and fifth triangles behind by the well-developed third outer and fourth inner infolds; the cap of the loop is tubercular and shows traces of an islet and a groove, similar to, though far weaker than, those present in the unworn  $m_1$  of *Ondatra*. In the posterior loop cusp  $x$  is large and distinct; in  $m_2$ ,  $m^1$  and  $m^2$  not only  $x$  but the other median ubercles are conspicuous features of the unworn crown. In

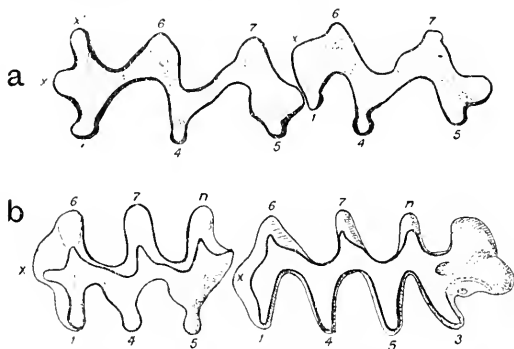


FIG. 62.—Unworn molars of *Prometheomys schaposchnikowi* Satunin.

Crown views: a. right  $m_1$  and  $m_2$ , b. left  $m_1$  and  $m_2$  arranged and lettered to show the homologies of the cusps.

*Prometheomys*  $m_1$ , when unworn, is almost as complex as that of *Arvicola* and owes its adult simplicity to a process of reduction. In *Lemmus* and its allies  $m_1$  is similarly simple; but in these forms the simplification is of such ancient standing and the teeth are in other ways so highly specialized that unworn examples of the  $m_1$  no longer show any trace of a greater complexity in front, and only some traces of the three primitive rows of tubercles.

Not much need be said about the unworn crowns of the remaining cheek-teeth. In general they show similar traces of the three longitudinal rows of tubercles, and these traces indicate that in each tooth a great part of the crown is derived from the median row.

The homologies of the cusps are most easily seen on comparing a left  $m^3$  with a right  $m_1$  or *vice versa*<sup>1</sup>; the posterior loops of all

<sup>1</sup> Drawings of upper and lower molars are arranged and lettered for such a comparison in Figs. 62, 63 and 77.

the lower molars are the homologues of the anterior loops of  $m^2$  and  $m^3$ . In  $m^1$  the anterior part of the tooth is more complex; cusp  $x^1$ , owing partly to the terminal position of the tooth in the tooth-row, partly to the fact that the cusp is the opponent of the complex anterior loop of  $m_1$ , is large and persists as an essential element of the crown. In the other teeth this cusp has been suppressed; but small complications of the anterior loop in  $m^2$  and  $m^3$  and of the posterior loops of the lower molars may be seen, at all events occasionally, in all genera. These features when present always occur, as will be seen from the figures, in definite situations, and on the view of the homologies here adopted they are easily interpreted as being vestiges of the cusps  $x^1$  and  $x$ ; but if any other view of the homologies be taken they are meaningless. In the unworn  $m^1$  of *Dicrostonyx* cusp  $x^1$  is separated from cusp 1 by a little V-shaped median and longitudinal valley which furrows the anterior surface of the tooth (Fig. 57). More or less clear traces of the separation of those two cusps may be seen in many genera from time to time. Of the median tubercles persistent traces of  $y$  and  $z$ , representing respectively the "protoconule" and "metaconule" of Trituberculy, frequently occur in the upper molars of Microtinæ; such a vestige of  $y$  is one of the normal features in the upper molars of the genus *Lagurus* (Fig. 43).

In  $m^3$  we find a striking parallel to  $m_1$ . The posterior part of the tooth, corresponding with the anterior part of  $m_1$  (and no doubt owing to the fact that it, like the latter, develops freely, unhampered by the presence of any neighbour), shows a great range in complexity. In many genera as in *Antelionomys* (Fig. 88) some species of *Evotomys* (Fig. 78) and *Alticola* (Fig. 91, 1a), it is very complex; but from that most complicated condition a continuous gradation of forms leading down to the most reduced and simplified condition, found in *Prometheomys* and *Ellobius*, may be traced (Figs. 55, 56, 91, 1-16, 95). In some genera as in *Arvicola*, *Evotomys* and some species of *Microtus* (e.g., *M. nivalis*) where the adult  $m^3$  is more or less extensively simplified longitudinally, young or unworn specimens of this tooth show more or less ephemeral additional salient angles on one or both sides behind.

In species in which the cheek-teeth develop roots in old age the changes seen in the enamel pattern as the teeth are worn down are most instructive. In *Evotomys rufocanus* (Figs. 10, 1, 2, 11; 81, 82)  $m_1$  and  $m^3$  are characterized by their greater complexity in youthful stages of wear; by middle life the patterns of these teeth are much simplified and the dentinal spaces in all the molars are tightly closed, the teeth having a form recalling *Microtus* rather than *Evotomys*; but after the roots are developed, in extreme old age, the re-entrant folds become shallow, the salient angles rounded, and the teeth acquire a form which resembles that seen in any ordinary and more primitive species of *Evotomys*. Here we have an illustration of the truth contained in that second paragraph quoted from Ameghino on p. 104.

At this point, before proceeding to a more general comparison, it will be useful to sum up the results obtained from a study of the molars of the Microtinæ alone.

Firstly, there is evidence that the cheek-teeth above and below have been evolved from teeth in which there were three longitudinal rows of tubercles. Of these rows the median has retained, in its modernized form, its full functional importance; but the outer row in the lower and the inner row in the upper molars have suffered reduction.

Secondly, there is evidence that all the molars have to a greater or less extent suffered reduction in a longitudinal direction. This reduction has affected the ends of the teeth; it has been most far-reaching in  $m_2^2$  and  $m_3$ ; the anterior ends of  $m_1^1$  and the posterior end of  $m^3$ , free from contact with neighbouring teeth, have suffered least. Apart from cusp  $x^1$ , normally lost by all the teeth except  $m^1$ , reduction has chiefly affected the posterior ends of the upper and the anterior ends of the lower molars; in other words simplification has proceeded from behind forwards in upper molars, from before backwards in lower molars. The parts, which according to Fleischmann's theory are homologous in the two series are equally liable to reduction above and below; whereas, as is familiar to all upholders of the tritubercular theory, what are generally supposed to be the homologous cusps have very different fortunes in the two jaws.

Lastly there is no evidence at all of any progressive complication of the molars within the group. On these various grounds we may reject the theories of the progressive complication of the teeth of Microtinæ advanced or supported by many authors.<sup>1</sup>

As the result of my work I conceive the molars of the ancestor of the Microtinæ to have been low-crowned, rooted, multituberculate teeth, each tooth, above and below, having three longitudinal rows of tubercles. In this primitive form  $m^1$ ,  $m_2^2$  and  $m_3$  possessed at least twelve,  $m^3$  not fewer than fifteen, and  $m_1$  from eighteen to twenty-one tubercles.

We now proceed to a comparison of the cheek-teeth of Microtinæ with those of other Muridæ. The oldest Muridæ at present known are the Cricetodonts of early and middle Tertiary age. In the most primitive of these (*i.e.*, those in which the cheek-teeth retain more of the primitive complexity), such as *Cricetodon cardurcense* Schlosser,<sup>2</sup> described from the Miocene of France, the outer sides of the upper molars and the inner sides of the lower molars are nearly as complex as in any Microtinæ, showing representatives of the cusps 1, 4, 2 (never present in Microtinæ), 5, and 3 with  $x^1$  in  $m^1$ . On the other hand, the median tubercles are much reduced as in modern Cricetinæ, and the inner cusps of the upper,

<sup>1</sup> TULLBERG, Ueber das System der Nagetiere, 1899, pp. 229, 232, 235, 237, 239, 442-443.

MILLER and GIDLEY, Journ. Washington Acad. Sci., 8, pp. 436-437, 1918.

<sup>2</sup> SCHLOSSER, Die Nager des europäischen Tertiärs, Palæontographica, 31, p. 90, Taf. viii, figs. 28 and 35, 1884.

and corresponding outer cusps of the lower molars are reduced to two (6 and 7). Cusps 4, 5, 6, and 7 have become dominant and the teeth make a close approach to that form, with two large cusps (6 and 7) on one side and the remains of five cusps separated by three enamel islands or folds on the other, which is seen in so many rodents in all the three great tribes of Simplicidentata. *Cricetodon* has thus specialized in a direction quite different from that followed by the Microtinæ; although some of its dental characters point back to the same common source, it cannot be considered as in any way ancestral to the group with which we are dealing.

The Nesomyinæ now restricted to Madagascar are of especial interest, inasmuch as one of the genera, *Brachytarsomys*, has developed in such a way that Forsyth Major was able to describe it as "a forerunner of the Microtinæ."<sup>1</sup> The most primitive genus is *Nesomys*. Its cheek-teeth are brachyodont, rooted, and complex. Like those of *Cricetodon*, they show cusps 1, 4, 2, 5, and 3 well developed, with a trace of  $x^1$  in  $m^1$ , and cusps 6 and 7 are the chief elements on the opposite sides of the teeth. But all the cusps are about equally developed and, what is more important, the median row is well represented, not specially reduced as in *Cricetodon*. In this one respect *Nesomys* makes a nearer approach to the voles. The vole-like *Brachytarsomys* is generally regarded as a fossorial modification of the Nesomyinæ in which the cheek-teeth (Fig. 63) have acquired a strikingly Microtine general appearance, although they are far more brachyodont than in any known vole. The molars agree further with those of Microtinæ in lacking any trace of an independent cusp 2. The skull (Fig. 18) under the influence of fossorial habits and of jaw muscles, which have developed exactly as in some of the higher voles, has become almost the counterpart of that of *Arvicola* or *Microtus* in the advanced position of the orbit, the structure of the infraorbital canal, the zygomatic arch, the form and course of the temporal ridges (which fuse in front to form an interorbital crest), and the flattening of the braincase. In other respects, correlated chiefly with the extreme brachyodonty, the skull of *Brachytarsomys* is very primitive. Although in both respects modified in much the same manner as in the higher voles, the cheek-teeth are already too reduced and the skull is too highly specialized for the genus to be considered as representing the ancestor common to all Microtinæ; but that it may descended from that ancestor there can be little doubt and it has perhaps be necessary later on to transfer *Brachytarsomys* from the Nesomyinæ to the Microtinæ. Pending the examination of spirit material and unworn teeth it is not advisable to make such a change.

Probably on account of the close superficial resemblance which exists between the adult cheek-teeth of Microtinæ and those of

<sup>1</sup> FORSYTH MAJOR, Proc. Zool. Soc., 1897, p. 719.

such highly specialized Cricetines as *Neotoma*, it is very generally, but in my opinion quite erroneously, believed that the Microtinae are more closely related to the Cricetinae than they are to the Murinae. Miller and Gidley<sup>1</sup> indeed form a family Cricetidae

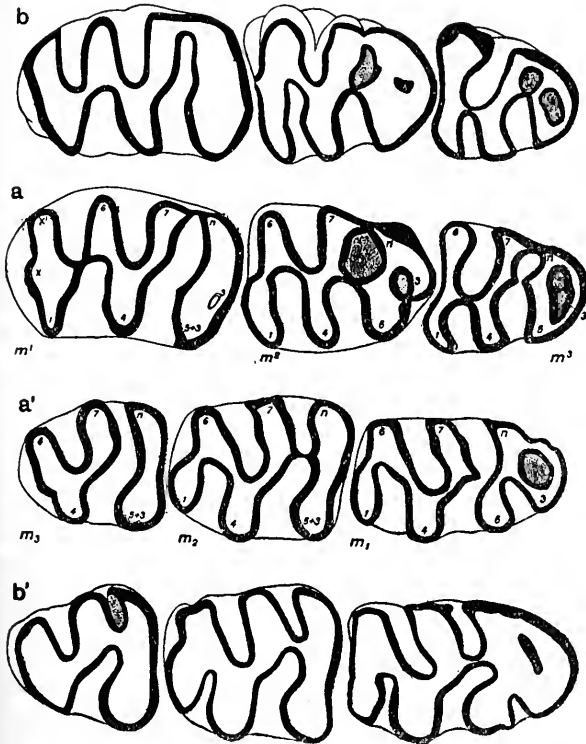


FIG. 63.—Cheek-teeth of *Brachytarsomys albicauda* Gunther.

Crown views enlarged: *a*, *b*, right upper, *a'*, *b'*, left lower molars arranged and lettered to show the homologies of the cusps. *a*, *a'*, younger and less worn; *b*, *b'*, older and more worn.

(containing the Cricetinae (including the Nesomyinae), Gerbillinae, Microtinae, and Lophiomyinae) which they distinguish from the Muridae (containing the Dendromyinae, Murinae, Phloeomyinae, Otomyinae, and Hydromyinae) by the structure of the upper molars. According to them the tubercles of these teeth in Cricetidae

<sup>1</sup> MILLER and GIDLEY, Journ. Washington Acad. Sci., 8, pp. 436, 439, 1918.

"always present a longitudinally biserial arrangement and never develop a functional third series on lingual side of crown"; whereas in Muridæ, as they define the family, the upper teeth have "a functional row of tubercles on lingual side of crown internal to the protocone and hypocone, these tubercles entering conspicuously into the plan of modification of the crowns." This classification is based, in my opinion, on a misconception; all three rows of tubercles are present in Cricetinaë, Nesomyinaë, and Microtinaë as well as in the "Muridæ" of Miller and Gidley. The inner series (cusps 6 and 7, etc.) are present in all; it is the median row and not the inner row that fluctuates in development. The median tubercles, as we have seen, are well developed in primitive Nesomyinaë; and in their transformed, modernized state they contribute largely to the crown of the Microtine molar. But in Cricetinaë, as in the still older Cricetodonts, the median tubercles suffer reduction and eventually disappear. In the beautiful figures of South American forms, published long ago by Hensel,<sup>1</sup> clear traces of these median tubercles are visible (cf. Hensel's figs. 23a and b, 25a and b, and 26a and b); and in unworn or but very slightly worn upper molars of *Neotoma* small vestiges of these median tubercles occur.

In Murinaë the median tubercles are excessively developed, more or less at the expense of their neighbours, as was recognized by Osborn.<sup>2</sup> The cusps which Miller and Gidley refer to as "protocone" and "hypocone," in the passage quoted, are in reality the "protoconule" and "metaconule," cusps *y* and *z* of the notation used by me. Clear trace of such an excessive development of the median row, transformed as it is, is met with in many Microtines, as for example, in the unworn  $m_1$  of *Ondatra* described above. Among Murinaë forms like *Apodemus epimelas* and *Chiruromys (Pogonomys)* present the most primitive, least-reduced molars met with in the subfamily; but in all, the longitudinal simplification of the molar crowns has proceeded further than in the lowest Microtinaë.

The enamel in the unworn teeth of some of the more highly specialized Murinaë, as was first pointed out by Hensel,<sup>3</sup> does not extend over the summits of the tubercles. In Microtinaë a similar condition is frequently seen in unworn teeth. Atrophy of apical enamel is clearly a specialization effected in order to render the teeth serviceable for the particular task before them from the first moment that they cut the gum, a very important adaptation in such precocious animals as young mice.

Summing up, there is in my opinion ample evidence to prove that all the Muridæ (and indeed all the Simplicidentate Rodents)

<sup>1</sup> HENSEL, Abhandl. Königl. Akad. Wiss., Berlin, 1872, Taf. i-iii.

<sup>2</sup> OSBORN, "The Rise of the Mammalia in North America," Address Boston, 1893, p. 19.

<sup>3</sup> HENSEL, Zeitschr. deutsch. geol. Ges., 8, p. 283, 1856.

SCHLOSSER, Die Nager des europäischen Tertiärs, p. 111, 1884.



have descended from ancestors with brachyodont multituberculate molars, in which the tubercles both in upper and lower molars were triserially arranged. In the most primitive Nesomyinæ and Murinæ, the transverse complication, occasioned by the triserial arrangement of the tubercles, is more completely preserved than in the other subfamilies; in the most primitive Microtinæ, on the other hand, the no less archaic longitudinal complexity of the teeth is preserved to an unusually large extent, although in all other respects the teeth of some of these primitive Microtinæ have reached the highest possible level of specialization. This association of archaic and progressive features in one and the same form, often in one and the same organ, is a familiar one to the student of mammals; over and over again we find that what is fundamentally a lowly type has preserved itself and prospered in competition with more highly organized forms, by adapting all its plastic characters to the needs of some special environment.

But if the views expressed above be sound, then those brilliant generalizations constituting the famous Tritubercular Theory, which has stimulated so much productive palæontological research, do not apply to the Simplicidentate Rodents. Equally inapplicable is the still more brilliant though less known theory of Winge. In the teeth of these mammals, whatever may be the case elsewhere, we have nowhere to deal with increasing complication of the molar crown; on the contrary in every family molar evolution resolves itself into a tale of reduction. There is throughout this great group a general tendency for the molars to become hypsodont, and increasing hypsodonty implies, as a rule, progressive simplification.

Forsyth Major taught me many years ago two things:—(1) that a triangular tooth is not necessarily tritubercular; (2) that we are not entitled to neglect any element of a molar, no matter how small and inconspicuous it may be, if we can identify it when it occurs. He was the first<sup>1</sup> to show that the primitive rodent molar must have been a very complex thing, and the first to suggest a Multituberculate origin for the whole group. The views expressed above are merely extensions of his theory; but they have been arrived at quite independently, as the result of many years' work, upon the basis of material far richer than that at the disposal of my late friend.

In conclusion it may be stated, in order to put my meaning beyond doubt, that like Forsyth Major I regard the Allotheria of Marsh (= the Multituberculata of Cope) as the probable source of the Simplicidentate Rodents, as well as of all the other Placentals. Although as regards general characters members

<sup>1</sup> The chief papers in which Forsyth Major expressed and developed his views are: 1873, "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz," *Palæontographica*, 22; 1893, "On some Miocene Squirrels," *P.Z.S.*, 1893, p. 179; 1897, "On the Malagasy Rodent Genus *Brachyromys*," *P.Z.S.*, 1897, p. 695; 1899, "On Fossil and Recent Lagomorpha," *Trans. Linn. Soc. London*, 2nd Ser. Zool., 7, p. 433.

of some other Orders, *e.g.*, the Insectivora, are no doubt more primitive than Rodentia, the latter are in fundamental molar structure among the most primitive of living mammals. In no other group do we find such clear and such generally distributed traces of the original Multituberculate tooth structure. The molar types regarded as primitive by the supporters of the Tritubercular Theory, by Winge, and by the supporters of many other rival theories, are in my opinion secondary and not primitive types, although often very ancient; these secondary forms have been developed again and again, from Jurassic times onwards, in all Orders as the result of progressive simplification of the primitive Multituberculate tooth.

Although probably no known Multituberculate can be claimed as ancestral to Rodents, it is interesting to note that some of them, like *Polymastodon*, developed along lines which are parallel to the direction followed by the Rodentia. It is among Allotheria alone that we find molar teeth which fit the conception of the primitive Simplicidentate molar given above. The earliest Rodents known, those from the Basal Eocene, are already quite highly specialized in many ways, and the Order is evidently one of very great antiquity.

### 3. *The Dental Formula of the Muridæ.*

The question as to whether the anterior cheek-tooth above and below in the Muridæ is a true molar ( $m_1^1$ ), a premolar ( $p_4^1$ ), or a persistent milk-molar ( $mp_4^1$ ) has attracted attention from time to time.

Owen<sup>1</sup> stated that in rodents "the first or anterior of the molar series, whether the number be 2 — 2, 3 — 3, or 4 — 4, is a premolar; it has displaced a deciduous predecessor in a vertical direction." But such a replacement is entirely unknown in Muridæ, and Owen's formula,  $p_4^1 m_{1-2}^{1-2}$ , lacking the support of any positive evidence, has been abandoned for many years in favour of that now in common use, namely,  $m_{1-2-3}^{1-2-3}$ .

In 1872 Forsyth Major<sup>2</sup> was led to suspect that the anterior cheek-tooth, above and below, in Muridæ is neither a "molar" nor a "premolar" in the ordinary sense of those terms, but is the posterior milk-molar, which in this family has become persistent in each jaw, the permanent premolar ( $p_4$ ), normally replacing this tooth, having been suppressed. Long afterwards, but independently when working at Microtinæ, I arrived at a similar conclusion,<sup>3</sup> and adopting Hensel's tooth notation (which I have always preferred) both Forsyth Major and I wrote the formula

<sup>1</sup> OWEN, *Anatomy of Vertebrates*, 1868, 3, p. 300.

<sup>2</sup> FORSYTH MAJOR, *Atti Soc. Ital. Sci. Nat.*, 15, p. 112 (1872); *Palæontographica*, 22, p. 75 (1873); *Abhandl. Schweiz. palæontol. Ges.*, 4, p. 111, footnote 3 (1877).

<sup>3</sup> HINTON, *Proc. Geol. Assoc.*, 21, p. 490 (1910).

$dm_1^1 m_{1.2}^{1.2}$ , which in the more usual notation would be expressed as  $mp_4^4, m_{1.2}^{1.2}$ .

Kellogg<sup>1</sup> used the formula  $p_4^4 m_{1.2}^{1.2}$ . In his paper he cites the views of Forsyth Major and myself, but does not indicate clearly whether he intends to agree with us or not, although he seems to admit that the homologization of the front lower cheek-tooth in *Microtinæ* with  $mp_4$  would afford an explanation of its complexity.

The reasons for the suggested homologization of the teeth in question with  $mp_4^4$  have been given fairly fully by me.<sup>2</sup> Briefly they are that the lower tooth is so complex in *Microtinæ* that we are unable to derive it from any known rodent molar without postulating the addition of new parts; that there is no evidence of increasing complication at all in this tooth; and that everywhere, even when most complex, the tooth is undergoing reduction whether we trace it forwards from youth to age in one species or forwards from one species to another in successive geological horizons. Posterior milk-molars are commonly more complex than true molars; therefore the tooth in question may be a persistent milk-molar. The facts (1) that in *Mus musculus* the last molars are sometimes suppressed (in South America<sup>3</sup>), indicating that numerical reduction, when it occurs, takes place from behind; and (2) that in those rare cases in which an extra tooth is developed in *Muridæ* it appears at the posterior end of the series (*Microtus agrestis* as recorded by Winge<sup>4</sup>; *Saccostomus hildæ*, B.M.<sup>5</sup>), so that according to the current notation the extra tooth would have to be regarded as  $m_4$ ; are cited in support of this view.

If, however, the view now maintained that the molars of all *Simplicidentata* were primitively as complex at least as they are in the most primitive *Microtinæ* be correct, the argument above, in so far as it is based upon the complexity of the anterior lower tooth, loses its force. In any case I can only reiterate the opinion expressed in 1923 that no change in the commonly accepted notation of the cheek-teeth of *Muridæ* should as yet be adopted.

#### 4. *The Range in Time of the British Fossil Microtinæ.*

Fossil remains of *Microtinæ* occur abundantly in the later Pliocene and Pleistocene deposits of Britain. A study of the remains collected from the deposits of the Norfolk coast and from the terrace-deposits of the Thames shows that the individual species have short ranges in time. They thus afford help to the geologist endeavouring to correlate scattered or isolated cavern

<sup>1</sup> KELLOGG, Univ. Cal. Publ. Zool., 21, p. 245, 1922.

<sup>2</sup> HINTON, Ann. Mag. N.H., [9], 11, p. 162, 1923.

<sup>3</sup> WINGE, Jordfundne og nulevende Gnavere fra Lagoa Santa, p. 601.

<sup>4</sup> WINGE, Vidensk. Meddel. naturh. Foren. Kjöbenhavn, 1881, 1882, p. 24 (footnote).

<sup>5</sup> SCHWANN, P.Z.S., 1906, p. 110.

and fissure deposits with others to which ordinary stratigraphical methods can be applied. The succession, beginning with the oldest, would seem to be as follows :—

### UPPER PLIOCENE OR CROMERIAN.

*a. Norwich Crag, Weybourne Crag*, and a stratum unknown *in situ*, but represented by the "clay pebbles" occurring in the Lower Freshwater Bed of the Norfolk Coast.

The voles known from these deposits are all species of *Mimomys*, namely :

†*Mimomys pliocenicus* Forsyth Major.

†*Mimomys reidi* Hinton.

†*Mimomys newtoni* Forsyth Major.

*b. Shelly Crag at East Runton.* The species known from this deposit are :—

†*Mimomys pliocenicus* Forsyth Major.

†*Mimomys intermedius* Newton.

†*Mimomys savini* Hinton.

*c. Upper Freshwater Bed at West Runton.* Four genera and ten species are known from this horizon :—

†*Mimomys intermedius* Newton.

†*Mimomys savini* Hinton.

†*Mimomys majori* Hinton.

†*Evotomys* sp. (*E. glareolus* group).

†*Pitymys gregaloides* Hinton.

†*Pitymys arvaloides* Hinton.

†*Microtus arvalinus* Hinton.

†*Microtus nivaloides* Forsyth Major.

†*Microtus nivalinus* Hinton.

†*Microtus ratticepoides* Hinton.

Among other characteristic mammals of the Cromerian deposits may be mentioned *Macaca*, *Machærodus*, *Trogontherium* and *Hippopotamus*.

*Pitymys gregaloides* and *Machærodus* have both been found in Kent's Cavern, and their presence suggests that among the many deposits of that famous cave there is a stratum of Cromerian age.

### PLEISTOCENE.

*a. High Terrace of the Thames.* Remains of three species have been obtained from a small section in the High Terrace gravel at Ingress Vale, near Greenhithe, Kent. These are :—

†*Mimomys cantianus* Hinton.

†*Evotomys* sp. (*E. glareolus* group).

*Microtus* or *Pitymys* sp.

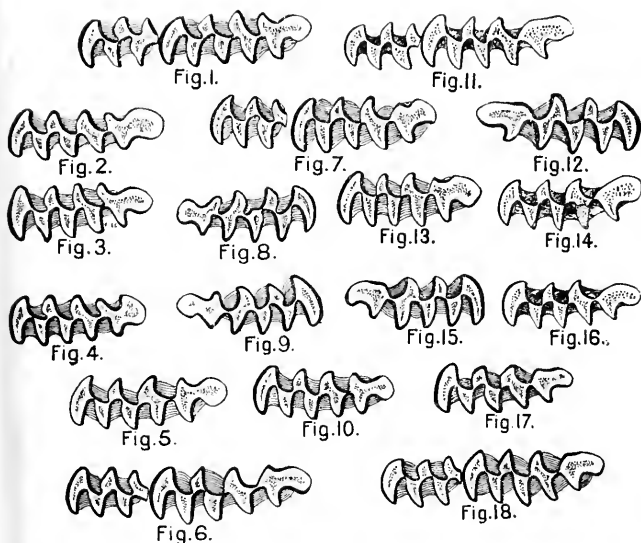


FIG. 64.—Lower molars of Cromerian species of *Pitymys*<sup>1</sup>; all from the Upper Freshwater Bed at West Runton with the exception of fig. 12.

1. *Pitymys arvaloides* Hinton. Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 656.5).
2. *P. arvaloides*. Left  $m_1$  (*Savin Coll.*, No. 8.38).
3. *P. arvaloides*. Left  $m_1$  (*Savin Coll.*, No. 8.35).
4. *P. arvaloides*. Left  $m_1$  (*Savin Coll.*, No. 8.37).
5. *P. arvaloides*. Left  $m_1$  (*Savin Coll.*, No. 656.6).
6. *P. arvaloides*. Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 491.6).
7. *P. arvaloides*. Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 8.28).
8. *P. arvaloides*. Right  $m_1$  with vestige of eusp 2 (*Savin Coll.*, No. 656.2).
9. *P. arvaloides*. Right  $m_1$  (*Savin Coll.*, No. 8.28).
10. *P. arvaloides*. Left  $m_1$ .
11. *P. gregaloides* Hinton. Left  $m_1$ ,  $m_2$ , type (*B.M.*, No. 12345; *Hinton Coll.*).
12. *P. gregaloides*. Right  $m_1$ , Kent's Cavern (*B.M.*, No. 15084a; *McEneary Coll.*).
13. *Pitymys* sp. Left  $m_1$  (*Savin Coll.*, No. 8.30).
14. *P. gregaloides*. Left  $m_1$  (*White Coll.*).
15. *P. gregaloides*. Right  $m_1$  (*Savin Coll.*, No. 8.24).
16. *P. gregaloides*. Left  $m_1$ .
17. *P. gregaloides*. Left  $m_1$  (*Savin Coll.*, No. 8.26).
18. *P. gregaloides*. Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 491.5).

<sup>1</sup> For diagnoses of these species see HINTON, *Ann. Mag. N.H.*, [9], 12, p. 541, 1923; a full account is given in Vol. II of this Monograph.

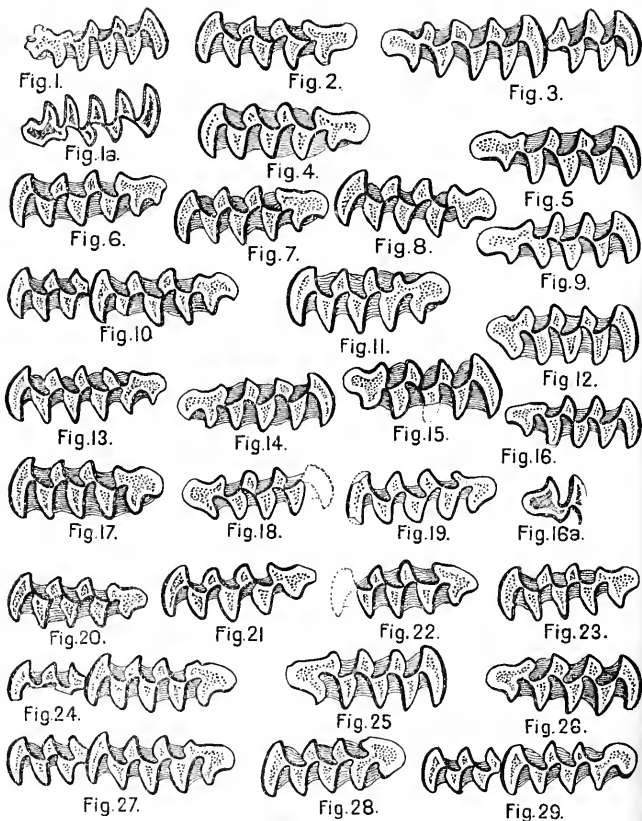


FIG. 65.—Lower molars of *Microtus* from the Upper Freshwater Bed<sup>1</sup> (Cromerian).

(For explanation see opposite page.)

<sup>1</sup> For diagnoses of these species see HINTON, Ann. Mag. N.H., [9], 12, p. 541, 1923; a full account is given in Vol. II of this Monograph.

## EXPLANATION OF FIG. 65.

All the specimens are from the Upper Freshwater Bed at West Runton.

1. *Microtus arvalinus* Hinton. Right  $m_1$ , young, with ephemeral complications; *la* basal view.
2. *M. arvalinus*. Left  $m_1$ .
3. *M. arvalinus*. Right  $m_1$  and  $m_2$  (*Savin Coll.*, No. 644.8).
4. *M. arvalinus*. Right  $m_1$  (*Savin Coll.*, No. 644.8).
5. *M. arvalinus*. Right  $m_1$  (*Savin Coll.*, No. 654.1).
6. *M. arvalinus*. Left  $m_1$ .
7. *M. arvalinus*. Left  $m_1$  (*Savin Coll.*, No. 643.10).
8. *M. arvalinus*. Left  $m_1$  (*Savin Coll.*, No. 643.9).
9. *M. arvalinus*. Right  $m_1$  (*Savin Coll.*, No. 7.25).
10. *M. arvalinus*. Left  $m_1$  (*Savin Coll.*, No. 643.1).
11. *M. arvalinus*. Left  $m_1$  (*Savin Coll.*, No. 643.2).
12. *M. arvalinus*. Right  $m_1$ .
13. *M. arvalinus*. Left  $m_1$  (*Savin Coll.*, No. 643.11).
14. *M. arvalinus*. Right  $m_1$ .
15. *M. nivaloides* Forsyth Major. Right  $m_1$  (*Savin Coll.*, No. 12.26).
16. *M. nivaloides*. Right  $m_1$  (*Savin Coll.*, No. 654.5); *16a* part of basal view.
17. *M. nivaloides*. Left  $m_1$ .
18. *M. nivaloides*. Right  $m_1$ .
19. *M. nivaloides*. Left  $m_1$  (*Savin Coll.*, No. 7.11).
20. *M. nivaloides*. Left  $m_1$  (*Savin Coll.*, No. 643.6).
21. *M. nivaloides*. Left  $m_1$ .
22. *M. nivalinus* Hinton. Left  $m_1$ .
23. *M. nivaloides*. Left  $m_1$  (*Savin Coll.*, No. 643.4).
24. *M. nivalinus*? Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 8.17).
25. *M. nivalinus*. Right  $m_1$  (*Savin Coll.*, No. 8.18).
26. *M. nivalinus*. Right  $m_1$  (*Savin Coll.*, No. 643.5).
27. *M. nivalinus*? Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 643.12).
28. *M. nivalinus*. Left  $m_1$ , type (*Savin Coll.*, No. 8.16).
29. *M. rattieepoides* Hinton. Left  $m_1$  and  $m_2$  (*Savin Coll.*, No. 653.3).

*Trogontherium* and the remains of many other species indicating a rich mammalian and molluscan fauna occur also at Ingress Vale. The whole assemblage closely resembles that known from Cromerian horizons and suggests that there is no great difference of age between the portion of the High Terrace represented at Ingress Vale and the Upper Freshwater Bed at West Runton.

**b. Early Middle Terrace of the Thames** (typical locality, Grays Thurrock, Essex). Three species are known viz. :—

- †*Arvicola praeceptor* Hinton.
- †*Evotomys* sp. (*E. glareolus* group).
- †*Microtus agrestoides* Hinton.

*Macaca*, *Hippopotamus*, *Rhinoceros megarhinus* and *Elephas antiquus* are characteristic survivals from the Upper Pliocene occurring in this horizon. The species of *Arvicola* is not closely related to modern species of that genus; it seems to be a direct descendant from one of the species of *Mimomys* occurring in the Upper Freshwater Bed. Very similar forms are found in the latest "Cromerian" horizons as in the so-called Upper Fresh-

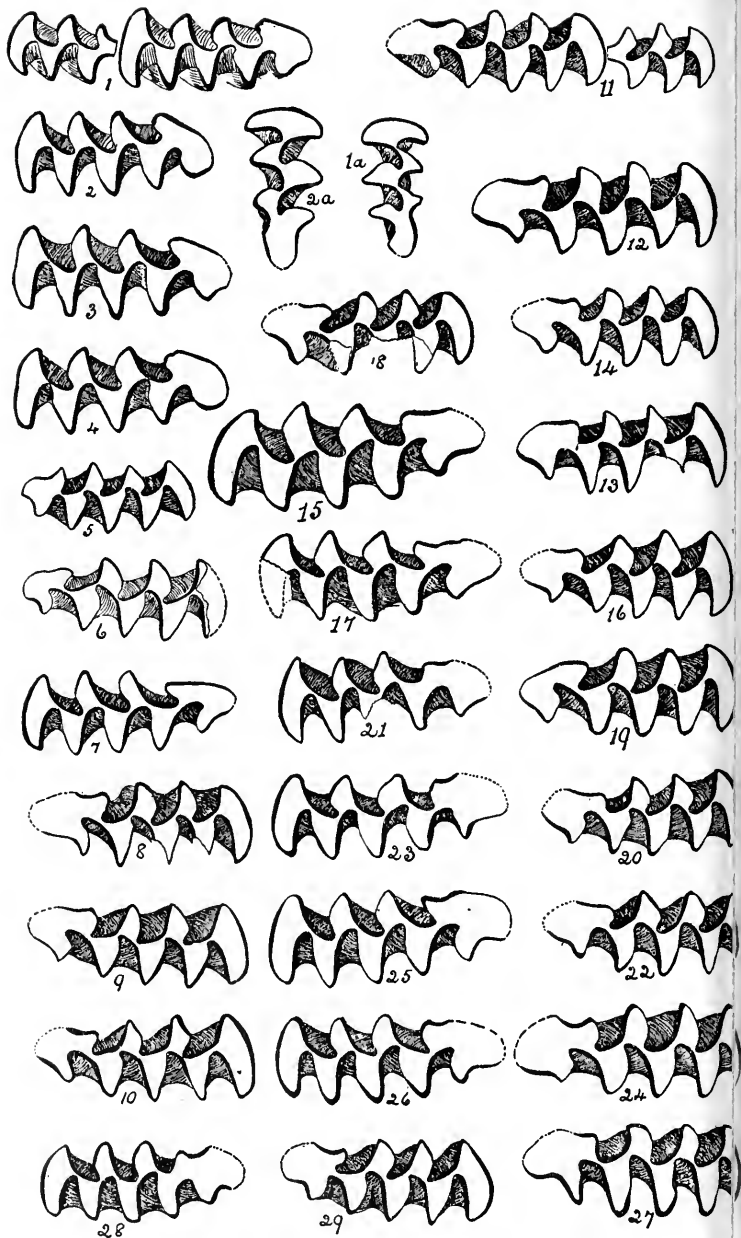


FIG. 66.—Cheek-teeth of recent and British fossil members of the *Microtus nivalis* group (Hinton, Proc. Geol. Assoc., 20, p. 39, Pl. I, 1907).  
 (For explanation see opposite page.)



## EXPLANATION OF FIG. 66.

- 1, 2, 3 and 4. *M. nivalis* Martins. Recent; Apennines, Italy (Dr. Forsyth Major).  
 5. *M. agrestoides* Hinton. Right  $m_1$ . Pleistocene; Grays.  
 6-14. *M. nivalis* group. Pleistocene; Middle Terrace deposits, Crayford.  
 15. *M. nivalis* group. Middle Terrace, Wickham.  
 16-23. *M. nivalis* group. Pleistocene; Clevedon Cave.  
 24-27. *M. malei* Hinton. Pleistocene; Clevedon Cave.  
 28. *Microtus* sp. Clevedon Cave.  
 29. *Microtus* sp. Middle Terrace, Crayford.

water Bed of Bacton. These facts and those mentioned above in connection with the High Terrace appear to show that the Cromerian beds on the one hand, and the High and early Middle Terrace deposits of the Thames on the other, are in part contemporary, and may in fact be regarded as parts of one great whole. Confirmation of this view may be found at Piltdown, where in a deposit that is evidently the stratigraphical equivalent of the High Terrace of the Thames, the remains of a fauna still more ancient than that represented at Ingress Vale have been found. *Eoanthropus*, *Mastodon*, and *Stegodon* are genera which might well carry us back to Norwich Crag times. These facts and deductions have a not unimportant bearing upon the question as to the date of the major glaciation of Britain; but that is a subject which I have discussed elsewhere.<sup>1</sup>

c. **Late Middle Terrace of the Thames** (typical locality, Crayford and Erith). The following species are known:—

- †*Dicrostonyx gulielmi* Sanford.  
 \**Lemmus lemmus* Linnæus.  
 \**Microtus nivalis* group.  
 †*Microtus malei* Hinton (and allied forms).  
 \**Microtus ratticeps* Keyserling and Blasius.

Between Early and Late Middle Terrace times the Microtinæ, together with most of the other mammals of Britain, were completely changed. Old forms, surviving in a more or less modified condition from the Pliocene period, now became extinct, and were replaced by an entirely new assemblage. Microtine remains occur

<sup>1</sup> HINTON and KENNARD, "The Relative Ages of the Stone Implements of the Lower Thames Valley," Proc. Geol. Assoc., 19, p. 76, 1905.

HINTON and KENNARD, "Contributions to the Pleistocene Geology of the Thames Valley. 1. The Grays Thurrock Area." Part II, Essex Naturalist, 15, p. 56, 1907.

HINTON, "Preliminary Account of the British Fossil Voles and Lemmings," Proc. Geol. Assoc., 21 p. 489, 1910.

HINTON, "Rivers and Lakes," London, Sheldon Press, 1924, pp. 49-177.

HINTON, "The Pleistocene Mammalia of the British Isles and their bearing upon the date of the Glacial Period," British Association, Southampton, 1925. (In the press. Yorkshire Geological Society's Proceedings.)

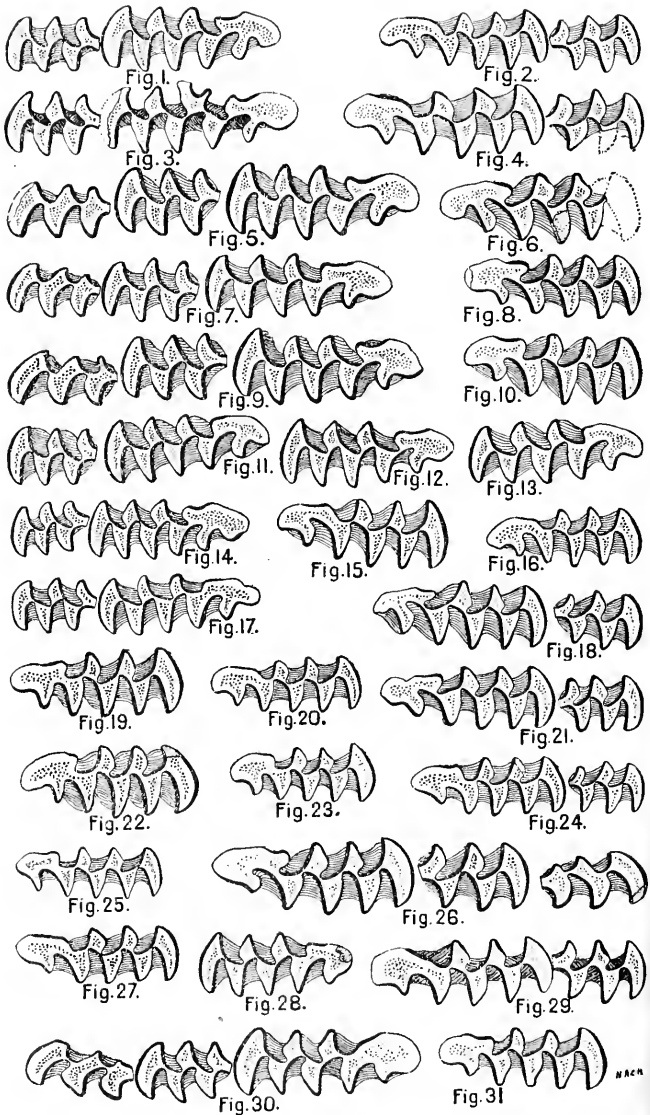


FIG. 67.—Lower molars of British Pleistocene species of *Microtus* (Later Middle Terrace forms).

(For explanation see opposite page.)

## EXPLANATION OF FIG. 67.

*Microtus* sp. (allied to *M. malei*).

Figs. 1, 3, 4, 5, 7, 8, 9, 12, 14, 21, 26, from the Clevedon Cave.

Figs. 2, 6, 10, 11, 13, 15-20, 22, 25, 27, 28 and 31, from the Later Middle Terrace deposits of Crayford.

*Microtus ratticeps* K. and Blasius. Clevedon Cave. (Fig. 29.)

*M. ratticeps*. Ightham Fissures. (Fig. 30.)

abundantly in later Middle Terrace horizons, not only at Crayford and Erith but in other deposits which I regard as contemporary (e.g., the Clevedon Cave and Banwell Cave). Just how many species should be recognized among the voles listed above as members of the "*M. nivalis* group" and "*M. malci* and allies" is difficult to say; but these forms are strongly marked and especially characteristic of this horizon. I have examined many thousands of Microtine fossils from a great many British deposits, but have never found these peculiar late Middle Terrace forms in association with any species other than those mentioned in the list above.

**d. Ightham Fissure Stage.** The species are:—

†*Dicrostonyx henseli* Hinton.

\**Lemmus lemmus* Linnæus.

†*Evotomys harrisoni* Hinton.

†*Evotomys kennardi* Hinton.

†*Arvicola abbotti* Hinton.

\**Microtus ratticeps* Keyserling and Blasius.

†*Microtus anglicus* Hinton.

\**Microtus arvalis* Pallas.

†*Microtus corneri* Hinton.

*Microtus agrestis* Linnæus.

In deposits of this age *Dicrostonyx henseli*, *Microtus anglicus*, *M. arvalis*, and *M. corneri* are especially abundant, whereas *Lemmus lemmus* and *Microtus ratticeps* are rare.

Most of the cavern deposits of Britain are intermediate in age between Late Middle Terrace and the Ightham Fissure stages. In these caves one finds *Lemmus lemmus* and *Microtus ratticeps* to be more abundant than at Ightham, and *Dicrostonyx henseli* is frequently replaced by the older form *D. guilelmi*. Rarely, as at Merlin's Cave, in the Wye Valley, and at the Langwith Cave in Derbyshire, the two species of *Dicrostonyx* are associated. Of the two species of *Evotomys* found at Ightham, one (*E. harrisoni*) is a representative of the living *E. glareolus*, the other (*E. kennardi*) is a member of the *E. nageri* group and therefore probably the forerunner of the peculiar forms which now inhabit some of the smaller islands around the British coast (*E. skomerensis*, *E. cæsarius*, *E. alstoni* and *E. erica*). *Arvicola abbotti* is a widely

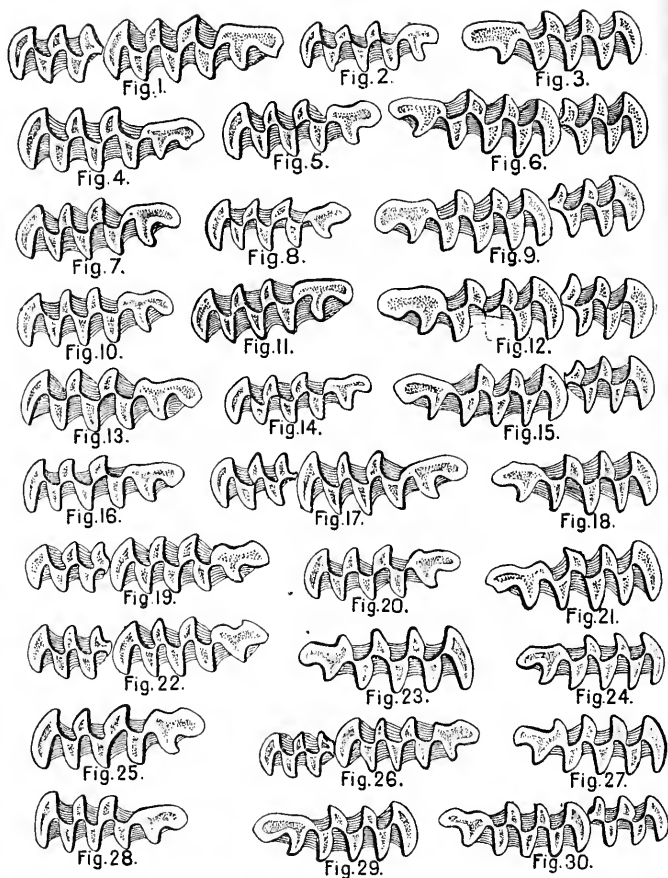


FIG. 68.—Lower molars of fossil and living species of the subgenus *Stenocranius*.

*Microtus (Stenocranius) anglicus* Hinton.

Figs. 1-7, 9, 10, 12-22, 25, 26, 28-30 from the Ightham Fissures (Late Pleistocene).

Fig. 11. Uphill Cave, Weston-super-Mare.

*M. (S.) tianshanicus* Büchner. Recent. (Figs. 8 and 24.)

*M. (Stenocranius)* sp. Recent; Mongolia. (Fig. 23.)

*M. (S.) angustus* Thomas. Recent. (Fig. 27.)

distributed and characteristic Late Pleistocene form; it is specialised for fossorial habits, and is no doubt nearly related to the living members of the *A. scherman* group. Of the species of *Microtus*, *M. corneri* is of special interest as being the forerunner of the peculiar *M. orcadensis* and its representative in the Channel Islands, *M. sarnius*.

**e. Third Terrace of the Thames** and its tributaries (typical development in the Lea Valley at Ponder's End and Angel Road. Three species are at present known to occur :—

†*Dicrostonyx henseli* Hinton.

†*Microtus anglicus* Hinton.

\**Microtus arvalis* group.

In deposits of this stage remains of *Dicrostonyx henseli* occur in great abundance, all other species being extremely rare or absent. Since the publication of Mr. S. Hazzledine Warren's accounts of the Third Terrace in the Lea Valley<sup>1</sup> it has been generally recognized that the terrace in question represents a cold period. The discovery of a cold fauna and flora at that horizon was predicted by me<sup>2</sup>; and in my opinion the Third Terrace marks the opening of the major glaciation of this country. In surveying the Pliocene and Pleistocene succession in Britain it is not until we reach late Pleistocene times that we find any evidence at all of a "cold fauna or flora" or any real evidence of glaciation; it is not possible to frame a glacial theory that will fit all the facts, be they physiographical, stratigraphical, or palæontological, unless we are prepared to place the "major glaciation" at this comparatively late moment.

Many deductions as to former climatic conditions have been and no doubt will continue to be made from the presence or absence of particular species or groups of species in successive geological horizons. Such deductions should, however, be made with the greatest caution. In my opinion no reliable evidence of changes of climate is afforded by the fossil mammals of countries now temperate. Very few species are unable to exist in temperate conditions; their presence or absence depends upon access, food, shelter, and competition, rather than upon climate. Among Microtinæ, *Microtus nivalis*, the Snow Vole, buried for ten months in a year under Alpine snows, and *Dicrostonyx*, the "warmth-hater" of Hensel, have been favourite subjects for geological comment and speculation. The presence of their remains in abundance on the plains of temperate Europe has been regarded again and again as a strong proof of former severe climatic conditions. But *M. nivalis* still lingers on in the hot lowlands of southern France, and *Dicrostonyx* lives in the by no means Arctic

<sup>1</sup> S. HAZZLEDINE WARREN, Q.J.G.S., 68, p. 213, 1912; and 71, p. 164, 1916.

<sup>2</sup> HINTON, Proc. Geol. Assoc., 21, p. 503, 1910.

climate of Unalaska. It may be worth mentioning that a specimen of *D. hudsonius* from Labrador lived in the Museum rather close to a radiator from early September to Christmas, that far from hating warmth it took the utmost care to keep warm, and that its death was due not to the subtropical atmosphere of the Upper Mammal gallery, but to a surfeit of Christmas dainties provided by mistaken kindness.

N.B.—In the lists of species given above, as elsewhere in this Monograph, a dagger (†) precedes the name of each extinct species; an asterisk (\*) indicates that the species is extinct in Britain though living elsewhere.

## II. SYSTEMATIC REVISION OF THE MICROTINÆ

### GROUP : LEMMI.

Lower incisor short, its alveolus not extending backwards beyond  $m_3$ , lingual to molars throughout.

#### Genus : 1. DICROSTONYX Gloger.

1779. *Mus* Pallas, Nov. Spec. Quadr. Glires Ord., p. 77 (in part).  
1795. *Lemmus* Link, Beytr. Naturgesch., 1, pt. 2, p. 74 (in part).  
1808. *Sphalax* (misprint for *Spalax*) Tiedemann, Zoologie, p. 476.  
Not of Gueldenstaedt, 1770.  
1811. *Myodes* Pallas, Zoogr. Rosso-Asiat., 1, p. 173 (in part).  
1813. *Brachyurus* Fischer, Zoognosia, ed. 3, 1, pp. 14, 24; 3, 1814,  
p. 55 (in part).  
1817. *Arvicola* Cuvier, Règne Anim., 1, p. 207 (in part). Not of  
Lacépède, 1801.  
1817. *Georychus* Cuvier, Règne Anim., 1, p. 207; Richardson, 1829.  
Not of Illiger, 1811.  
1827. *Hypudæus* Lesson, Man. Mamm., p. 277 (in part).  
1829. *Hypudæus* Fischer, Synopsis Mamm., p. 299 (misquoting  
Lesson).  
1830. *Cuniculus* Wagler, Nat. Syst. Amphib., p. 21. Not of Brisson,  
1762.  
1841. *Dicrostonyx* Gloger, Hand- und Hilfsbuch Naturgesch., 1,  
pp. xxxi, 97.  
1845. *Lemmus* Schinz, Synopsis Mamm., 2, p. 255 (in part; misprint  
for *Lemmus*).  
1845. *Hypudæus* Schinz, Synopsis Mamm., p. 250. Not of Illiger,  
1811.  
1854. *Myolemmus* Pomel, Catal. Méthod., p. 27; based upon an  
unidentifiable species, "*Arvicola ambiguus*" Pomel, occurring in  
the Pleistocene of France.  
1855. *Misothermus* Hensel, Zeitschr. deutsch geol. Gesellsch., 7,  
p. 492; based upon *Myodes torquatus* Pallas.  
1881. *Borioikon* Poljakov, Mém. Acad. Imp. Sci. St. Petersburg, 39,  
Supplement, p. 34; type *Myodes torquatus* Pallas.  
1887. *Cuniculatus* Nelson, Report Nat. Hist. Coll. Alaska, p. 278  
(misprint for *Cuniculus*).  
1897. *Tylonyx* Schulze, Mamm. Europæa in Helios, Abhandl. u.  
Vorträge Gesamtgeb. Naturw. Berlin, 14, p. 83.

*Genotype*.—An American species, probably *Mus hudsonius*  
Pallas.

*Distribution and Range in time.*—Circumpolar. In the Old World it is not known to occur in Lapland, but from the eastern shore of the White Sea its range extends more or less continuously eastwards to the Behring Strait. In this region apparently it does not now come south of latitude  $68^{\circ}$  N.; northwards it is known to reach  $82^{\circ}$  N. latitude, inhabiting Spitzbergen,<sup>1</sup> Novaya Zemlya and the New Siberian Islands. Fossil remains of at least two species occur abundantly in the late Pleistocene deposits of Western and Central Europe, indicating that the range of the genus was formerly far more extensive in the Old World than at present, extending southwards and westwards to Ireland, southern England, southern France and the Swiss Alps. Remains of the genus are also known from the late Pleistocene of Central Asia, indicating that its range in that continent formerly extended southwards at least to the Altai Mountains.

In America the genus ranges through the Labrador Peninsula, the whole of Arctic America from the western shore of Hudson's Bay to Alaska and the islands of St. Lawrence and Unalaska, the Arctic Archipelago, and northern and eastern Greenland. No fossil remains have, as yet, been found in the New World.

*Characters.*—Medium-sized Microtinæ, sharply distinguished from all other genera by their highly modified external characters, remarkable seasonal changes in the pelage, colour, and fore-claws, peculiar skulls and characteristic cheek-teeth.

Size medium, hind-foot 15–20 mm., condylo-basal length of skull 29–32 mm. Fur dense, long, very soft and silky. Eyes moderate, larger than in *Lemmus*. Ears very small, each reduced to a low fold of naked integument encircling the meatus and entirely concealed beneath the fur; pre-auricular ear-tufts, formed by hairs arising from the region immediately in front of the meatus, well marked, capable of motion independently of the rest of the fur and serving completely to close the meatus when laid back by muscular contraction.<sup>2</sup> Tail short and cylindrical, its vertebræ about equal to the hind-foot in length, densely clothed with long adpressed bristles, forming a true terminal pencil which often somewhat exceeds the vertebral

<sup>1</sup> No material has been seen from Spitzbergen, but Arctic Lemmings are said by Heuglin to be carried there occasionally by drift ice. Parry found the skeleton of one upon an ice-floe to the north of Spitzbergen in lat.  $81^{\circ} \frac{3}{4}$  N. (Appendix to "Narrative," 1828, p. 190.)

Heuglin says: "In der Advent-Bai im Is-fjord stieß ich übrigens an günstigen, sommerlich gelegenen Oertlichkeiten öfter auf Lemmingbaue und unser Harpunier versicherte mich, in derselben Gegend diese Thiere ausgegraben zu haben" (Reisen n. d. Nordpolarmeer, 1870–1871, Theil 3, p. 8, 1874).

<sup>2</sup> The character and independent motion of these ear-tufts have been described by Heuglin (Reisen n. d. Nordpolarmeer, 1870–1871, Theil 3, p. 10, 1874), who had opportunities of examining living examples of *D. torquatus*. Recently, thanks to the generosity of Mr. E. Else, I have been able to observe a living specimen of *D. hudsonius* from Labrador, and I am able to confirm Heuglin's statements.



portion of the tail in length. Hands and feet short and broad, each with five digits, the palms and soles densely furred. In the hand, the thumb is reduced to a small vestige which bears, however, a minute, flattened nail; on the palmar side of the thumb is a large pollical tubercle, two or three times as large as the thumb, covered with horny integument; the four outer digits are very short and subequal in length, digits II and V being but slightly shorter than digits III and IV. The lateral fingers (II and V) bear long, slender, laterally compressed claws which, apart from their great size and somewhat unusual vertical thickness, do not differ much from those of ordinary lemmings. The claws of the two central digits (III and IV) are extraordinary structures subject to a remarkable seasonal change; in young specimens and in adults in full summer pelage, they do not differ greatly from those of other lemmings; but in winter they are very large, sometimes exceeding half an inch in length, and have the appearance of being double, each of the two fingers seeming to bear two enormous claws, one on top of the other, which are separated at their tips by a more or less deep notch. When these differences in the claws first attracted attention, Pallas and other early observers, working with scanty material, were not unnaturally inclined to attribute them to sex; but Middendorff's researches in Taimyrland and in the museums of London and Munich showed that the difference was not sexual, and he was led to suspect that in some way the variation in the form and size of the claws was correlated with the seasonal pelage changes, of which he gave an excellent account.<sup>1</sup> Coues in 1879 was the first to demonstrate exactly what takes place, and he described the process as follows<sup>2</sup>:—

"In spring and early summer, these claws [III and IV] do not appear very different from those of *Myodes* [*Lemmus*], though averaging larger, more bulbous at base underneath, with the terminal portion slenderer, straighter, and sharper. This bulbous portion underneath grows out simultaneously with increase in length and amount of curvature of the main portion of the claw, until it equals or even exceeds the length of the latter, and is quite as stout, or even stouter, being somewhat broad and pad-like. At this period, it runs the whole length of the claw, from which it is separated by a groove along the sides, and by a notch at the end, both of varying depth. The claw then looks like nearly two claws, one underneath the other. The pad would then seem to gradually sever its connection with the main claw by progressive increase of the constriction marked by the lateral groove and terminal notch, as well as by loosening from the base, when it appears like an excrescence; it is finally lost. Thus the process appears to be a periodical one, like the shedding of the horns of ruminants, and not continually progressive with age; and would seem to be connected with the particularly fossorial habits of the quasi-hibernating animal that digs galleries underground in which to

<sup>1</sup> MIDDENDORFF, *Sibirische Reise*, 2, Th. 2, p. 93, 1853.

<sup>2</sup> COUES, *Monographs N. Amer. Rodentia, Murida*, 1879, p. 248.

reside during the cold season, as compared with its freer and more active mode of life in summer.<sup>31</sup>

Hind-feet remarkably broad, the width across the bases of the digits equal to about one-half the length, all the toes being rather short; hallux well developed, scarcely shorter than digit V; digits II, III and IV longer and subequal, III being, however, slightly longer than its neighbours; all, including the hallux, bear long, slender, curved, and sharply pointed claws, which equal or surpass their digits in length.

In both hands and feet the claws are covered and protected by long hair growing from the dorsum and sides of each paw and its digits; these hairs always project beyond the claw tips, the shorter summer hairs being replaced by a longer growth in the winter, which keeps pace with the increasing length of the claws. Palms and especially the soles densely clad with long crisp hair, which on each sole forms a stiff curling brush quite comparable with that developed upon the foot of a hare. When the hairy covering is clipped away the palms are seen to be quite smooth, bearing, apart from the great pollical tubercle, no trace of the pads present in normal Microtinæ. Normally too, judging from a specimen from Discovery Bay specially examined by me and from two studied by Tullberg,<sup>1</sup> no trace of the pads remains upon the sole; but Miller<sup>2</sup> states that he found "several minute, faintly developed tubercles near the base of the toes." Mammæ, in adult females, 2 - 2 = 8.

Colour in *summer* brownish or greyish above, whitish or yellowish below; often with brilliant rufous suffusions upon the fore-quarters and throat. In *winter* pure white above and below, *Dicrostonyx* being the only genus among Simplicidentata that shows the phenomenon of winter whitening completely developed.<sup>3</sup> *Young* like adults in summer pelage, but duller, and with a dark stripe along the spine. This stripe, in some forms, persists also in the adult summer pelage.

Hair, with the exception of the special hairs (which are whitish throughout) clothing the tail and feet, everywhere with slaty bases, the colour, both in summer and in winter pelage, being produced by the terminal parts of the hairs. In the summer coat the hairs are shorter, 15-18 mm. long on the back, and their terminal portions have from one to three diversely coloured annulations, which vary both in number and hue with the species or subspecies and with their precise situation upon the body. In winter the hairs are longer, about 25 mm. on the back, with pure white tips. The change is made by two moults, one in autumn, the other in spring; it is brought about by the rapid growth of new hairs and the more gradual shedding

<sup>1</sup> TULLBERG, Ueber das System der Nagetiere, p. 257, 1899.

<sup>2</sup> MILLER, N. Amer. Fauna, No. 12, 1896, p. 37.

<sup>3</sup> In *Lemmus obensis novosibiricus* winter whitening takes place also (see p. 203).

of the old ones. In the autumn moult the whitening usually starts low down on the flanks and extends gradually upwards and forwards to the crown of the head, whereas in the spring moult the coloured coat of summer first appears upon the head and shoulders and gradually extends backwards and downwards. The process is nevertheless subject to a great deal of individual variation.<sup>1</sup>

*Skull* (Fig. 69) rather strongly built, moderately broad and but little depressed. Rostrum, in correlation with the rather weak upper incisors, light and slender, the anterior palatal foramina rather large, the diastema and nasals rather long. Nasals extending backwards about as far as the ascending branches of the premaxillaries, ending at a point usually a little in front of a line connecting the anterior margins of the orbits. Zygomatic arches given off squarely from the sides of the rostrum, the greatest zygomatic breadth falling in the anterior or maxillary parts of the arches and amounting to between 62 and 70% of the condylo-basal length. Upper border of jugal raised into a moderately high convex crest for the insertion of the temporal fascia. Temporal ridges salient throughout; in the moderately constricted interorbital region they are usually persistently separated by a longitudinal sulcus, which becomes, however, narrower and deeper with age until, in some exceptional individuals, the groove may be interrupted at one point by the ridges coming into actual contact with each other. Posteriorly the temporal ridges traverse the parietals and squamosals, but their course is slightly below the level of the lateral borders of the interparietal. Anteriorly the parietals are widely and shallowly emarginated by the intertemporal portion of the coronal suture.

<sup>1</sup> An interesting experiment made by Ross,\* in arctic seas, nearly a century ago is worthy of notice. He kept an individual in its summer coat alive in his cabin through the winter months, and on February 1 it still retained the summer pelage. On that date Ross removed the animal from the cabin to the deck and there exposed it to the rigours of the arctic winter. Within a week, when the experiment was terminated by the death of the captive, the coat turned wholly white except in a relatively small area over the spine. By clipping off the white hair-tips Ross found that he could restore to the animal the appearance it possessed while in summer pelage, and he therefore thought that the change had taken place by a bleaching of the tips of the hairs. The true interpretation is doubtless, however, that given by Middendorff,† viz., that the hairs of the winter coat were all present though concealed under the tips of the summer hairs while the animal remained in the cabin, the unnatural warmth of that place retarding their growth and so delaying the shedding of the old hairs; that the sudden exposure accelerated the growth of the new hairs which rapidly attained their full length and concealed the far shorter hairs of the old coat; and that finally sufficient time did not elapse between the exposure to cold and the death of the animal to permit of the old coat being cast, and therefore Ross was able to bring that old coat once more to the surface by cutting off the ends of the newer and longer hairs.

\* Ross, App. Narr. Second Voyage, 1835, Nat. Hist., p. xiii.

† MIDDENDORFF, Sibirische Reise, 2, Th. 2, p. 91, 1853.

In the newborn animal the distance between the squamosals in front is roughly equal to twice the interorbital breadth; in the adult the space between these bones is diminished, being no greater and often less than the interorbital breadth. In the

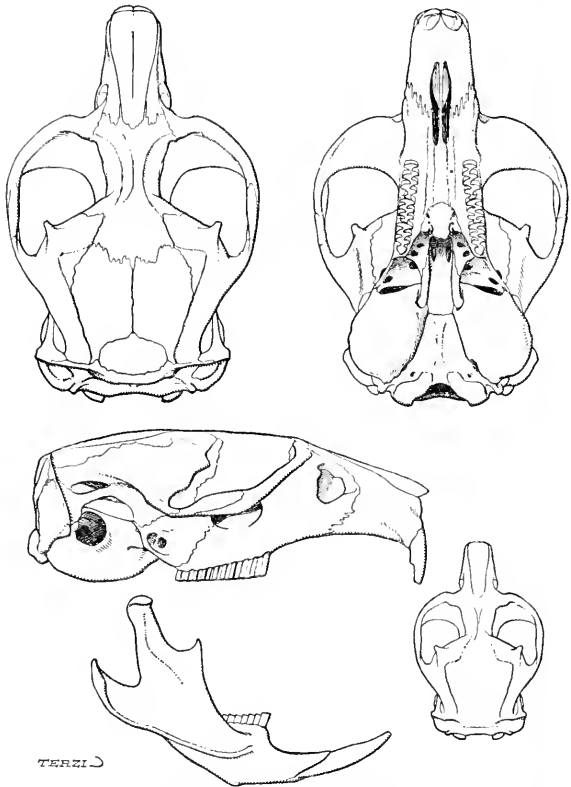


FIG. 69.—*Dicrostonyx granlandicus* Traill.

Dorsal, ventral, and lateral views (enlarged) of the skull. The small outline is a natural-sized representation of the skull in dorsal view.

adult each squamosal develops a strong, prominent, peg-like post-orbital process, which gives origin to a tendinous portion of the temporal muscle. Posterior portions of squamosals very broad, forming practically the whole of the large supratympanic fossæ; supratympanic fenestra very small. Inferior portions of lambdoid crest, *i.e.*, all below the supratympanic fenestra

on each side, formed by the squamosals alone, the lateral processes of the supraoccipital being short. Interparietal of normal shape, wider than long; in some forms it articulates with the squamosals, but in others it is separated from those bones by narrow tongues of the parietals which pass back on either side to articulate with the supraoccipital. The cheek-tooth rows diverge slightly behind;

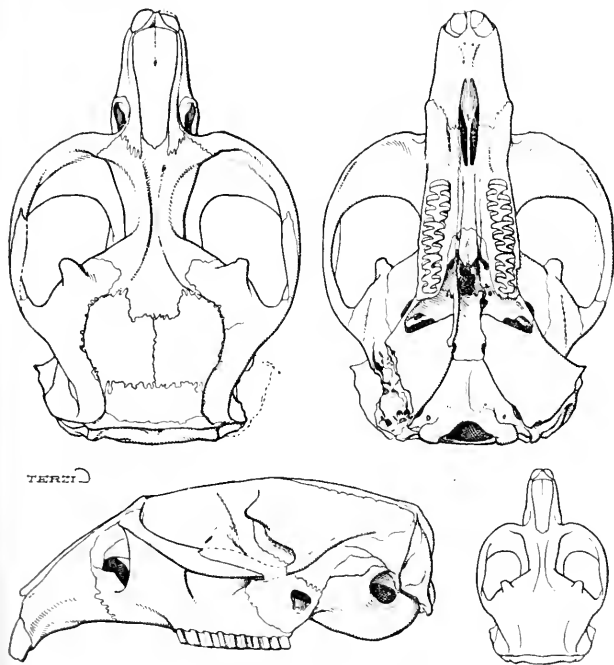


FIG. 70.—*Dicrostonyx henseli* Hinton.

Dorsal, ventral, and lateral views (enlarged) of the type skull from the late Pleistocene fissure deposit at Ightham, near Sevenoaks, Kent (B.M., No. M.11,803, Geol. Dept.). The small outline is a natural-sized representation of the skull in dorsal view.

the alveolar capsules, in consequence of the great height of the teeth, rise up in the floor of the orbit and in the sphenorbital fissure; in correlation with this and with the breadth of the teeth, the presphenoid is reduced in most species to a slender bar. Palatal structure differing from that of *Microtus* chiefly in the extension further forwards of the mesopterygoid fossa and in the shortness and free termination of the post-palatal median septum, which is here represented merely by a short median

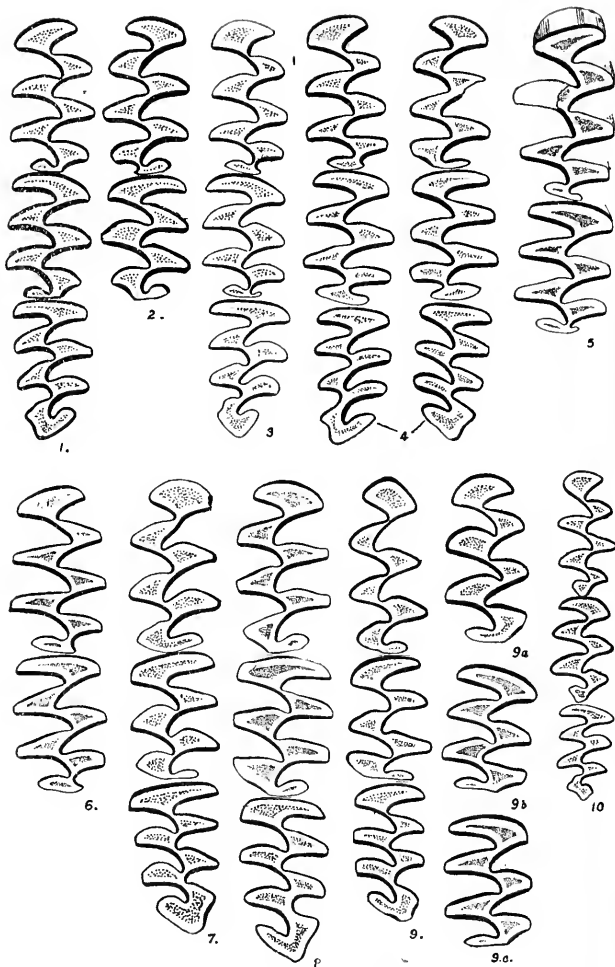


FIG. 71.—*Dicrostonyx*.

Crown views of upper molars:

1. *Dicrostonyx torquatus* Pallas (Miller Coll., B.M., No. 7.7.7.3621). Right  $m^1$ ,  $m^2$ , and  $m^3$ .
2. Same specimen. Left  $m^1$  and  $m^2$ .
3. *Dicrostonyx greenlandicus* Traill. Discovery Bay (B.M., No. 77.8.6.5a). Right  $m^1$ ,  $m^2$ , and  $m^3$ .
4. *Dicrostonyx guillemi* Sanford. Pleistocene; Hutton Cave, Somersetshire. Upper molars, right and left, of the typical skull (Taunton Museum).
5. *Dicrostonyx guillemi* Sanford. Pleistocene; Kesh Caves, Co. Sligo. Right  $m^1$  and  $m^2$  (Dublin Museum, C.K. 12).
6. *Dicrostonyx guillemi* Sanford. Pleistocene; Dog Holes, Warton Crag, Lancashire. Right  $m^1$  and  $m^2$  (B.M.; presented by J. Wilfrid Jackson).
7. *Dicrostonyx hudsonius* Pallas. Labrador. Left  $m^1$ ,  $m^2$ , and  $m^3$  (B.M., No. 61.2.4.1).
8. *Dicrostonyx henseli* Hinton. Pleistocene; Ightham Fissures, Kent. Left  $m^1$ ,  $m^2$ , and  $m^3$ .
9. *Dicrostonyx henseli* Hinton. Pleistocene; Doneraile Caves. 9. Left  $m^1$ ,  $m^2$ , and  $m^3$ ; a, right  $m^1$ ; b, and c. right  $m^2$  (Dublin Museum).
10. *Dicrostonyx torquatus unguatus* v. Baer. Novaya Zemlya. Right  $m^1$ ,  $m^2$ , and  $m^3$  of a young individual (B.M., No. 80.3.29.2).

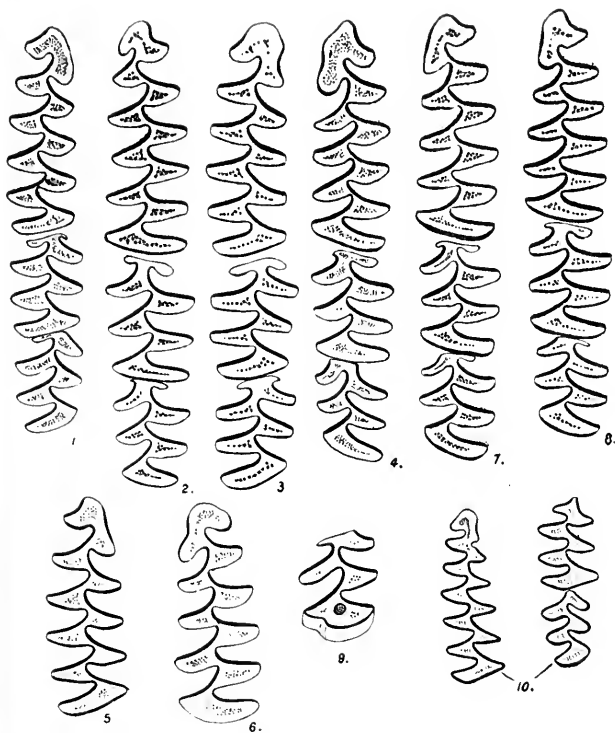


FIG. 72.—*Dicrostonyx*.

Crown views of lower molars :—

1. *Dicrostonyx grœnlandicus*. Discovery Bay. Right  $m_1$ ,  $m_2$ , and  $m_3$  (*B.M.*, No. 77.8.6.5a).
2. *Dicrostonyx gulielmi* Sanford. Pleistocene; Langwith Cave, Derbyshire. Left  $m_1$ ,  $m_2$ , and  $m_3$ .
3. *Dicrostonyx gulielmi* Sanford. Pleistocene; Edenvale Caves, Co. Cork. Right  $m_1$ ,  $m_2$ , and  $m_3$  (*Dublin Museum*).
4. *Dicrostonyx hudsonius* Pallas. Labrador. Left  $m_1$ ,  $m_2$ , and  $m_3$  (*B.M.*, No. 61.2.4.1).
5. *Dicrostonyx hudsonius* Pallas. Labrador. Right  $m_1$  (*B.M.*, No. 61.2.4.2).
6. *Dicrostonyx gulielmi* Sanford. Pleistocene; Kesh Caves, Co. Sligo, Ireland. Left  $m_1$  (*Dublin Museum*).
7. *Dicrostonyx henseli* Hinton. Pleistocene; Ightham Fissures, Kent. Left  $m_1$ ,  $m_2$ , and  $m_3$ .
8. *Dicrostonyx henseli* Hinton. Pleistocene; Doneraile Caves, Co. Clare, Ireland. Left  $m_1$ ,  $m_2$ , and  $m_3$  (*Dublin Museum*).
9. *Dicrostonyx* sp. Pleistocene; England. Right  $m_3$  showing abnormal reduction by insulation of the first inner infold.
10. *Dicrostonyx torquatus unguilatus* v. Baer. Novaya Zemlya. Right  $m_1$ ,  $m_2$ , and  $m_3$  of young individual (*B.M.*, No. 80.3.29.2).

spine. Pterygoid fossæ deep, their floors distinctly dorsal to the ventral surface of the basisphenoid. Auditory bullæ of small or medium size; middle ear filled with a rather dense sponge of bone; canaliculus tympanicus completely ossified; tegmen tympani articulating as usual with the squamosal; mastoid portion slightly but noticeably inflated. Basisoccipital moderately broad in front.

In consequence of the shortness and wholly lingual course of the lower incisors, the *mandible*, like that of other lemmings, differs from that of the voles in the stoutness of its horizontal, and slenderness of its ascending rami. In adults the lower incisor on each side terminates near the hinder edge of  $m_3$ ; but in the newborn it does not pass  $m_2$ . In each ramus the anterior border of the coronoid process rises above the molar level at a point opposite the middle of  $m_3$ . Angular processes large and of normal form.

*Dentition*.—Upper incisors without grooves, and with normal cutting edges. Lower incisors short, traversing the lower jaw on the lingual side of the molars to terminate opposite  $m_3$ .

*Cheek-teeth* rootless and persistently growing, with their re-entrant folds destitute of cement. When unworn with tubercular caps; when worn displaying a normal prismatic pattern. In adult stages of wear (Figs. 71, 72) all the triangles are substantially closed, of somewhat peculiar, transversely elongated form, the inner and outer salient angles being subequal in size in each tooth. Enamel conspicuously differentiated into thick and thin portions, forming respectively the concave and convex sides of the salient angles as in the higher members of the genus *Microtus*, becoming very thin at, or lacking altogether from, the tips of the salient angles. The patterns of the upper teeth (Fig. 71) are as follows:— $m^1$  with an anterior loop, followed by six alternating triangles, of which the postero-external one is much reduced, and with four salient angles on each side;  $m^2$  with an anterior loop and five triangles (three external, two internal), of which the postero-external one is reduced, and with four outer and three inner salient angles;  $m^3$  with an anterior loop, four closed triangles, a posterior loop formed by two confluent and more or less reduced triangles, and with four salient angles on each side. In most of the known species a vestigial fifth inner angle is developed at the hinder end of  $m^1$  and a similar vestigial fourth inner angle at the hinder end of  $m^2$ ; but in two species, the living *D. hudsonius* and the extinct *D. henseli*, these vestiges are absent (cf. Figs. 71, 4 and 71, 7) and the posterior wall of the triangle immediately in front (fourth inner angle in  $m^1$ , third inner in  $m^2$ ) is reduced, losing its concave form and a great deal of its thick enamel. This distinction, first pointed out by Hensel<sup>1</sup> in 1858 and Forsyth Major<sup>2</sup> in 1872,

<sup>1</sup> HENSEL, Zeitschr. deutsch geol. Gesellsch., 8, p. 280.

<sup>2</sup> FORSYTH MAJOR, Atti Soc. Ital. Sc. Nat., 15, p. 125.



has been used by G. M. Allen<sup>1</sup> recently to divide the genus into two subgenera, viz., *Dicrostonyx* containing the only living species that lacks the vestigial angles, and *Misothermus* comprising all the others which retain, or, as Allen thinks, have acquired them. In the mandible,  $m_1$  consists of a posterior loop, seven closed triangles (of which four are internal, three external), and an anterior loop compounded out of at least four more or less reduced and confluent triangles (Fig. 72, 1-8, 10); occasionally the postero-external triangle, normally blended in the anterior loop, is shut off as an eighth closed triangle; this tooth has never less than nine dentinal spaces, and five outer and six inner salient angles; but occasionally one of the usually ephemeral elements of the anterior loop maintains its independence and persists, forming an additional outer or inner salient angle (Fig. 72, 2);  $m_2$  has a posterior loop, four alternating triangles, and a pair of vestigial angles in front; of the latter the outer vestige is the more reduced, and the dentine of the vestigial pair is confluent with that of the fourth triangle; not counting the vestiges this tooth has three well-developed salient angles on each side;  $m_3$  is like  $m_2$ , but a little more reduced; its third or antero-internal triangle is sometimes partially confluent with the fourth; of the vestigial angles in front, the outer one is lost in many species, while in *D. hudsonius* both the inner and the outer vestiges are lacking.

Owing to the want of material from the Old World it is impossible to say how many species of *Dicrostonyx* exist and to determine what status should be accorded to several of the forms currently recognized. We are indebted to G. M. Allen for a revision of the American members of the genus, and free use has been made of his work in preparing the accounts of the described forms given below.

Allen arranges the species, as indicated above, in two subgenera, *Dicrostonyx* and *Misothermus*, distinguished by the presence or absence of the postero-internal vestigial angles in  $m^1$  and  $m^2$ . But this difference, although useful for discriminating between species and very constant in American and in European fossil species, is to my mind altogether too slight a foundation for subgenera, particularly in view of the fact that in the Old World *D. torquatus* the characters of  $m^1$  and  $m^2$  appear to be rather inconstant (Figs. 71, 1 and 71, 2). Whether we regard the minute postero-internal angle so frequently present in these two teeth as an ancient vestigial structure (my view) or as a rudiment of a new complication (Allen's view), it seems to be just such a character as may from time to time vanish or appear quite independently in any member of the genus; no conclusion as to the special interrelationships of the known forms, fossil or recent, can be based upon the mere presence or absence of such a structure.

<sup>1</sup> G. M. ALLEN, Bull. Mus. Comp. Zool. Harvard Coll., Cambridge, Mass., 62, p. 513.

1. *Dicrostonyx torquatus* Pallas.

(Synonymy under the subspecies.)

*Range*.—Arctic regions of the Old World from the eastern shore of the White Sea through Russia and boreal Asia; eastward limits of range unknown. Inhabiting Spitzbergen, Novaya Zemlya, and the New Siberian Islands. Not ranging south of lat. 68° N.

*Characters*.—Size medium; head and body about 130 mm.; hind-foot 20; condylo-basal length of skull 30. Essential external characters as described under the genus.

Colour, in summer, brown or grey above according to the subspecies; the brown or typical form without a spinal stripe; the grey form (*D. t. unguatus*) with a definite dorsal stripe.

Skull normal, but available material not sufficient to enable us to appreciate specific peculiarities. Upper incisors moderately heavy and much more strongly curved than in *D. grænlandicus* ("orthodont" instead of "proödont"); those of *D. rubricatus* being apparently intermediate. Cheek-teeth of the more complex type;  $m^1$  and  $m^2$  usually with postero-internal vestigial angles, but these are sometimes absent (Fig. 71, 1); hinder wall of the postero-internal triangle in each of the two teeth named retaining its thick enamel and usually its concave shape.

*Remarks*.—The material before me is totally inadequate for the purpose of determining the characters of this species and its relationship to the American *D. rubricatus*.

1a. *Dicrostonyx torquatus torquatus* Pallas.

1779. *Mus torquatus* Pallas, Nov. Spec. Quadr. Glirium Ord., pp. 77, 205, taf. xi, B.
1779. *Mus lenensis* Pallas, Nov. Spec. Quadr. Gilr. Ord., p. 199.
1808. *Spalax torquatus* Tiedemann, Zoologie, 1, p. 47.
1811. *Myodes torquatus* Pallas, Zoogr. Rosso-Asiat., 1, p. 173; Middendorff, Sibir. Reise, 2, Th. 2, p. 87, 1853.
1817. *Arvicola (Georychus) torquatus* Cuvier, Règne Anim., 1, p. 207.
1820. *Lemmus torquatus* Desmarest, Mammalogie, p. 289.
1827. *Hypudæus torquatus* Lesson, Man. Mamm., p. 277.
1829. *Hypudæus torquatus* Fischer, Synopsis Mamm., p. 298 (misquoting Lesson).
1844. *Myodes hudsonius* Middendorff, Bull. Cl. physmath. Acad. Imp. Sci. St. Petersburg, 3, p. 291. Not of Pallas, 1779.
1874. *Cuniculus hudsonius* Coues, Proc. Acad. Nat. Sci. Philadelphia, p. 196 (part).
1877. *Cuniculus torquatus* Coues, Monogr. N. Amer. Rodentia, Muridæ, p. 246 (part).
1896. *Dicrostonyx torquatus* Miller, N. Amer. Fauna, No. 12, pp. 38–40 (part).
- 1922.† *Dicrostonyx torquatus altaicus* Vinogradov, Ann. Mus. Zool. Acad. Sc. Russ., 23, p. 372; *Co-types*:—High Mining School Collection, No. 248/11 A. Leningrad (Gtorny Institute); seven left and five right mandibular rami; described from the Caverns of Tsharysch and Khankara Rivers, N. W. Altai, 180 kilometres from Bijsk.

*Type*.—Unknown.

*Type locality*.—Region around the mouth of the River Obi, N.W. Siberia.

*Range*.—That of the species, excepting the island of Novaya Zemlya.

*Characters*.—Essential characters those of the species.

*General colour of adults in summer pelage*.—Brownish black above, more or less brightened by the rufous and yellowish sub-terminal bands of the hairs, darkest along the spine, paling to ashy grey on the sides of the head, towards the rump and lower flanks, and upon the outer and lower parts of the limbs. No distinct dorsal stripe; but a more or less distinct dusky streak upon the top of the head from the tip of the nose to the crown. Ear-tufts, shoulders and humeral regions, together with the foremost parts of the flanks, bright brownish-red, this colour being continued ventrally to form a more or less complete and extensive collar; the red tint more or less distinctly interrupted by a pallid streak passing upwards from the throat on each side to the region behind the ears. Under parts, apart from the pectoral collar but including the inner surfaces of the limbs, yellowish or dirty white. Feet and tail hairs white.

For *external and cranial measurements*, see tables at end of volume.

*D. t. altaicus* Vinogradov, described from the Pleistocene cavern deposits of N.W. Altai, is said to be distinguished from the typical subspecies by the structure of  $m_1$ , which possesses eight instead of seven closed triangles; but this character is wholly unreliable. Vinogradov himself finds it "not quite constant" in either the fossil or the recent material before him, and if he had been able to examine the enormous amount of fossil material before me he would never have attributed systematic importance to such a detail.

### 1b. *Dicrostonyx torquatus ungulatus* v. Baer.

1841. *Lemmus ungulatus* von Baer, von Baer and Helmersen, Beiträge, 4, p. 283.

1853. *Myodes torquatus* var. *pallida* Middendorff, Sibir. Reise, 2, Th. 2, p. 93; Heuglin, Reisen nach dem Nordpolarmeer, Theil, 2, frontispiece, 1873, Theil, 3, p. 6, 1874.

*Type*.—Unknown.

*Type locality*.—Novaya Zemlya.

*Range*.—Known only from the type locality.

*Characters*.—Essential characters as in the species.

*General colour of adults in summer pelage*.—Upper parts ashy-grey in general colour; with a distinct blackish spinal stripe, running from the root of the tail to the occiput, and continued forwards to the nose by a less definite blackish streak. Ear-tufts, shoulders, foremost parts of flanks, and breast heavily

washed with a bright reddish-chestnut brown, much as in *D. t. torquatus*. Under parts, feet and tail whitish.

For *external and cranial measurements* see tables at end of volume.

*Remarks.*—The descriptions of this animal, given by von Baer, Middendorff and Heuglin, and the figure published by the latter, seem sufficient to prove its distinctness from *D. t. torquatus*. Pending the acquisition of modern material it may be regarded as a subspecies of *D. torquatus*, but its precise status is doubtful.

## 2. *Dicrostonyx chionopæ* Allen.

1914. *Dicrostonyx chionopæ* G. M. Allen, Proc. New England Zool. Cl., 5, p. 62.

*Type.*—Museum of Comparative Zoology, Harvard Coll.

*Type locality.*—Nijni [Nischne] Kolymsk, near the mouth of the Kolyma River, N.E. Siberia.

*Range.*—Known only from the type locality.

*Characters.*—Smaller than *D. torquatus* (total length only 116 mm.), but with a relatively large skull (condylo-basal length 27.5 mm.).

Head and body length unusually small, scarcely exceeding 100 mm. Hind-foot relatively very large, 20 mm. Summer pelage imperfectly known; winter pelage pure white as usual.

The type and only known specimen, is an adult male collected October 15, 1911, which has nearly completed its change into the winter dress. The only remnants of the summer coat remaining are a small patch of hazel on the top of the head and nape, another on the centre of the chest, and a concealed substratum of russet-tipped hairs with a few black hairs intermixed in the mid-dorsal region. Middle fore-claws already much enlarged.

*Skull.*—The skull is described as "quite adult with the basioccipital suture solidly fused and ridged." In relation to the size of the animal it is very large; only slightly smaller in all respects than the skull of *D. torquatus* from the Taimyr Peninsula figured by Middendorff. Interparietal nearly rectangular, without an anterior median projecting point. Cheek-teeth not described, but presumably as in *D. torquatus*.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—It is to be hoped that further material will be obtained. The hind-foot measurement is so large in proportion to the total length that one is almost tempted to believe that an adult skull has by some error been allocated to an immature skin. Assuming that no such mistake can have been made, this is a form of extraordinary interest.

Baird (Mamm. N. America, p. 559, 1857) says: "The N. P. Exploring Expedition, under Captain Rogers, collected specimens

[of '*Myodes torquatus*'] on the island of Arikamtchichi, in Behring's Straits, near the Asiatic shore."

### 3. *Dicrostonyx rubricatus* Richardson.

(Synonymy under subspecies.)

*Range*.—Arctic America from the Alaskan Peninsula eastwards along the Arctic coast to the western shores of Hudson's Bay. Represented by a subspecies upon the island of Unalaska; and probably inhabiting the more westerly islands of the Arctic Archipelago.

*Characters*.—Essential characters closely resembling those of *D. torquatus*, of which *D. rubricatus* is clearly the New World representative. Characters, if any, differentiating the skull from that of *D. torquatus* not at present satisfactorily known. Cheek-teeth of the more complex type;  $m^1$  and  $m^2$  usually with well-developed postero-internal vestigial angles, the hind walls of their postero-internal triangles always retaining their thick enamel and concave form;  $m_3$  usually with a pair of anterior vestigial angles. Outward appearance, in summer, variable with the subspecies; the typical form from Alaska making rather a near approach in coloration to *D. torquatus*, while the western subspecies has a peculiarly uniform reddish-grey pelage with a sharply defined black spinal stripe extending from the head to the root of the tail.

*Remarks*.—*D. rubricatus* is undoubtedly very closely related to the Old World *D. torquatus*, and until more material representing the latter is available, the status of *D. rubricatus* will remain doubtful. Three well-marked subspecies are currently recognized, two inhabiting the mainland of N. America and a third confined to the island of Unalaska.

#### 3a. *Dicrostonyx rubricatus rubricatus* Richardson.

1839. *Arvicola rubricatus* Richardson, Zool. Capt. Beechey's Voyage, 1839, p. 7.  
 1845. *Hypudæus rubricatus* Schinz, Synopsis Mamm., 2, p. 250.  
 1877. *Cuniculus torquatus* Coues, Monogr. N. Amer. Rodentia, Muridæ, p. 246 (part). Not of Pallas.  
 1896. *Dicrostonyx torquatus* Miller, N. Amer. Fauna, No. 12, p. 38 (part).  
 1900. *Dicrostonyx nelsoni* Merriam, Proc. Washington Acad. Sci., 2, p. 25; Miller, "List," 1912, p. 207.<sup>1</sup>  
 1900. *Dicrostonyx hudsonius ulascensis* Stone, Proc. Acad. Sci. Philadelphia, 1900, p. 37; Miller, "List," 1912, p. 207.

<sup>1</sup> Throughout this work these abbreviations are used for:—

1. MILLER, List of North American Land Mammals in the United States National Museum, 1911. Smithsonian Inst. U.S. Nat. Mus. Bull., 79, 1912, pp. 1-455.
2. MILLER, List of North American Recent Mammals. Smithsonian Inst. U.S. Nat. Mus. Bull., 128, 1924, pp. 1-673.

1901. *Dicrostonyx hudsonius nelsoni* Elliot, Field Columbian Mus. Publ., Zool. Ser. 2, p. 210, fig. 48.  
 1905. *Dicrostonyx richardsoni* Macfarlane, Proc. U.S. Nat. Mus., 28, p. 736. Not of Merriam.  
 1919. *Dicrostonyx rubricatus* G. M. Allen, Bull. Mus. Comp. Zool., Harvard Coll., Cambridge, 62, p. 518.  
 1914: *Dicrostonyx rubricatus rubricatus* Miller, "List," 1924, p. 397.<sup>1</sup>

*Type*.—Unknown; none specified, the description based upon Collie's notes.

*Type locality*.—Shore of Behring Strait, Alaska.

*Range*.—Alaskan peninsula and coastal islands, eastwards in the neighbourhood of the Arctic coast of Mackenzie to Coronation Gulf.

*Characters*.—Closely resembling the Old World *D. torquatus* in all essential respects; but adults in summer pelage rather more brilliantly coloured and with a somewhat indistinct black spinal stripe extending from the nose to the tail.

*Colour of adults in summer*.—"Sides of the muzzle and an area about the eyes gray, due to a mixture of short hairs, some whitish, others black-tipped. Forehead from nose to the nape, black, sometimes grizzled with a few gray hairs. This mark is continued as a narrow black median stripe to the root of the tail. Ears marked by a tuft of rusty hairs. Shoulders nearly clear chestnut, about morocco-red of Ridgway (1912) mixed with whitish, this colour extending back along the sides of the thorax, and blending dorsally with the grizzled whitish and blackish of the back; hips grayish. Lower surfaces usually washed with orange buff, but in some specimens whitish. Tail and feet whitish" (G. M. Allen, 1919, p. 519).

*Young* in first pelage resemble adults in summer coat, but lack the brilliant colours of the adults; general colour of upper parts uniform cinnamon buff, with black dorsal stripe from the forehead to the tail. Ear-tufts black. A clear tawny patch at the shoulder. Sides and under surface washed with ochraceous buff.

*Skull*.—Closely resembling that of *D. torquatus*; differing from that of *D. hudsonius* in the relatively shorter nasals and slightly more squarely spreading zygomatic arches. Interparietal separated laterally from the squamosal on each side by a narrow tongue sent backwards by the parietal to articulate with the supra-occipital.

*Cheek-teeth*.—Essentially as in *D. torquatus*; a postero-internal vestigial angle constantly present in  $m^1$  and  $m^2$ .

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Mr. G. M. Allen deserves great credit for identifying the Alaskan Collared Lemming with Richardson's "*Arvicola rubricatus*." Richardson's brief diagnosis, based upon Surgeon Collie's manuscript notes of a mouse that "burrows in the turfy

<sup>1</sup> See footnote on p. 151.

soil on the shores of Behring's Straits,"—once the connection is pointed out—is, as Mr. Allen says, "unmistakable and describes the highly coloured adult Alaskan Lemming sufficiently well."

This animal is undoubtedly very closely related to *D. torquatus* and it is not improbable that when satisfactory material representing the Old World form is acquired, it will be necessary to treat *D. rubricatus* as a subspecies of *D. torquatus*.

### 3b. *Dicrostonyx rubricatus richardsoni* Merriam.

1825. *Arvicola grœnlandica* Richardson, Parry's Second Voyage, App., 1825, p. 304 (part). Not of Traill.
1835. *Arvicola hudsonia* J. C. Ross, J. Ross's Narrative Second Voyage, App., 1835, p. xii.
1848. *Myodes hudsonicus* Gray, P.Z.S., 1848, p. 43.
1850. *Myodes grœnlandicus*, Gray, App. to Rae's Narrative, Exped. Arctic Sea, 1846-1847, 1850, p. 200.
1854. *Georychus hudsonius*, Audubon and Bachman, Quad. N. Amer., 1854, 3, p. 81 (in part), pl. 119. Not of Pallas.
1874. *Cuniculus hudsonius* Coues, Proc. Acad. Nat. Sci. Philadelphia, 1874, p. 196 (part).
1877. *Cuniculus torquatus* Coues, Monogr. N. Amer. Rodentia, Muridæ, p. 246 (part).
1896. *Dicrostonyx torquatus* Miller, N. Amer. Fauna, No. 12, pp. 38-40 (part).
1900. *Dicrostonyx richardsoni*, Merriam, Proc. Washington Acad. Sci., 2, p. 26; Miller, "List," 1912, p. 207.
1901. *Dicrostonyx hudsonius richardsoni* Elliot, Field Columbian Mus. Publ., Zool. Ser. 2, p. 211.
1919. *Dicrostonyx rubricatus richardsoni* G. M. Allen, Bull. Mus. Comp. Zool., Cambridge, 62, p. 525; Miller, "List," 1924, p. 398.

*Type*.—U.S. Nat. Mus., No.  $\frac{5489}{6164}$ , Merriam Coll.; adult male, skin and skull, collected July 1859, by W. MacTavish.

*Type locality*.—Fort Churchill, Keewatin, west coast of Hudson's Bay.

*Range*.—From the western shore of Hudson's Bay, westwards through Arctic America, meeting and intergrading with *D. r. rubricatus* in the neighbourhood of Coronation Gulf.

*Characters*.—Adults, in summer, of a nearly uniform ruddy grey above, with a black dorsal stripe from nose to tail. Skull with rostrum relatively longer and nasals less tapering than in *D. r. rubricatus*. Bullæ rather larger.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—As Mr. G. M. Allen remarks this "is a very strongly marked subspecies and though closely related to the Alaskan *rubricatus*, with which it intergrades to the north-westward, it parallels *hudsonius* of Labrador in its dull uniform coloration, though it is not so gray as the latter." Specimens from near the type locality are widely different in external appearance from true *D. rubricatus* and from *D. torquatus* as may be gathered

from the fact that Middendorff, thoroughly acquainted with the Old World species, thought Audubon's very fair figure of a specimen of *D. richardsoni* in summer pelage to be "completely erroneous" and "not at all to be recognized."

### 3c. *Dicrostonyx rubricatus unalascensis* Merriam.

1853. *Myodes torquatus* Middendorff, Sibir. Reise, 2, Th. 2, p. 92. Not of Pallas, 1779.  
 1900. *Dicrostonyx unalascensis* Merriam, Proc. Washington Acad. Sci., 2, p. 25; Miller, "List," 1912, p. 208.  
 1901. *Dicrostonyx hudsonius unalascensis* Elliot, Field Columbian Mus. Publ., Zool. Ser. 2, p. 210.  
 1919. *Dicrostonyx rubricatus unalascensis* G. M. Allen, Bull. Mus. Comp. Zool., Cambridge, 62, p. 530; Miller, "List," 1924, p. 398.

*Type*.—U.S. Nat. Mus., No. 99,622 (Biol. Surv. Coll.); skull lacking occiput, found in an owl pellet, July 8, 1899, by C. H. Merriam.

*Type locality*.—Island of Unalaska, Alaska.

*Range*.—Known only from the type locality.

*Characters*.—"Closely related to *rubricatus*, from which it differs in its relatively longer and more slender rostrum, its weaker, less broadly rounded zygomata, and slightly more protruding incisors. External characters unknown" (G. M. Allen, 1919, p. 531).

For *cranial measurements*, see table at end of volume.

*Remarks*.—This lemming was first discovered by Wosnessensky about 1850. He obtained a specimen which was examined by Middendorff, who says of it:—"Es ist ein halbwuchsiges Weibchen in der Tracht der Jungen von Taimyr, von denen es ununterscheidbar ist. Am 11ten Mai gefangen, zeigt es an der zweiten Zehe der Vorderpfote (von innen gerechnet) die hufartige Entwicklung des Nagels." Unalaska, situated as it is in the Pacific off the extremity of the Alaskan Peninsula in lat. 54° N., has a mild climate; and the presence upon it of a member of a genus otherwise restricted, so far as its living representatives are concerned, to the desolate Arctic tundra is a fact of very great interest and one which should inspire caution in the geologist drawing inferences as to past climatic conditions from the occurrence of remains of *Dicrostonyx* in the Pleistocene deposits of Western Europe. For many years Wosnessensky's discovery, recorded by Middendorff and by Hensel, was doubted (Nehring, Ueber Tundren und Steppen, 1890, p. 23); but it has now been fully confirmed by the U.S. Biological Survey. Curiously, although twenty-nine skulls, collected from owls' pellets, have now been obtained from the island, the survey has not succeeded in procuring a specimen in the flesh; and our knowledge of the outward appearance of the animal is limited to the statement of Middendorff cited above.



4. *Dicrostonyx exsul* G. M. Allen.

1887. *Cuniculatus torquatus* Nelson, Rept. Nat. Hist. Collect. Alaska, 1887, p. 278 (part).  
 1919. *Dicrostonyx exsul* G. M. Allen, Bull. Mus. Comp. Zool., Cambridge, 62, p. 532; Miller, "List," 1924, p. 398.

*Type*.—Mus. Comp. Zool., Harvard College, No. 11,885; adult male, skin and skull, collected June 24, 1913, by J. Dixon.

*Type locality*.—St. Lawrence Island, Behring Sea.

*Range*.—Only known from the type locality.

*Characters*.—"Similar to *rubricatus*, but coloring much less intense, more grayish throughout. Skull with more abruptly narrowed nasals, their proximal ends bevelled sharply to a median point instead of tapering gradually; interparietal more nearly square in general outline" (G. M. Allen, 1919, p. 532).

*Colour of adults in summer pelage*.—Pinkish grey above, blacker on the rump, with an indistinct blackish dorsal line. Each ear-patch a mixture of ochraceous buff and tawny. Throat heavily washed with tawny.

For *external and cranial measurements*, see tables at end of volume.

5. *Dicrostonyx grœnlandicus* Traill.

1823. *Mus grœnlandicus* Traill, Scoresby's Journ. Voyage Northern Whale-fishery, p. 416.  
 1824. *Lemmus hudsonius* Sabine, Parry's Voyage, Suppl. to App., p. clxxxviii. Not of Pallas.  
 1843. *Myodes grœnlandicus* Wagner, Schreber's Säugethiere, Suppl., 3, p. 606.  
 1845. *Lemmus* [sic] *grœnlandicus* Schinz, Synopsis Mamm., 2, p. 256.  
 1850. *Myodes hudsonius* Gray, App. to Rae's Narr. Exped. Arctic Sea, 1846-1847, p. 200.  
 1857. *Hypudæus grœnlandicus* Reinhardt, Rink's Grönl. geogr. stat. beskriv., p. 8.  
 1868. *Myodes torquatus* var. *grœnlandicus* Brown, Proc. Zool. Soc., 1868, p. 350.  
 1877. *Myodes torquatus* Feilden, Zoologist [3], 1, p. 320; Winge, Medd. om Grønland, 21, 1902, p. 382. Not of Pallas, 1778.  
 1886. *Cuniculus torquatus* Greely, Three Years of Arctic Service, 2, p. 363 (part).  
 1896. *Dicrostonyx torquatus* Miller, N. Amer. Fauna, No. 12, pp. 38-40 (part).  
 1901. *Dicrostonyx hudsonius* Elliot, Field Columbian Mus. Publ., Zool. Ser. 2, p. 209. Not of Pallas, 1778.  
 1911. *Dicrostonyx hudsonius grœnlandicus* Jacobi, Abh. u. Ber. k. zool. anthrop.-ethnogr. Mus. Dresden, 12, No. 4, p. 8; Miller "List," 1912, p. 207.  
 1919. *Dicrostonyx grœnlandicus* G. M. Allen, Bull. Mus. Comp. Zool., Cambridge, 62, p. 533; Miller, "List," 1924, p. 398.

*Type*.—Unknown.

*Type locality*.—Jameson's Land, East Greenland, in lat. 71° N.

*Range*.—This species inhabits the maritime districts of northern and eastern Greenland, ranging from about Cape Dalton on the east coast in lat. 69° N., northwards to the limit of land (Mary Murray and Lockwood Islands in lat. 83° N.), and thence westwards along the northern coast to the Kane Basin and Robeson Channel, and southwards to the margin of the Humboldt Glacier. It also inhabits the countries westwards of Robeson Channel, ranging from about 83° N. lat. southwards through Grant Land, Grinnell Land, Ellesmere Land and Baffin Land, reaching its southern limits at Cape Mercy in the Cumberland Peninsula and on the northern shore of Hudson's Straits. Its western limits of range are imperfectly known, but it probably extends to the eastern shore of the Gulf of Boothia in Cockburn Land and the Melville Peninsula; for some of the specimens obtained by Dr. Rae, in 1847, during his expedition to the region north of Repulse Bay appear to belong to this species and not to *D. rubricatus*.

*Characters*.—A rather small species (hind-foot to 16.5 mm.; condylo-basal length of skull to 29.6 mm.). Skull and teeth essentially as in *D. torquatus*; but rostrum slender and upper incisors weak and somewhat straightened. Adults in summer with grey upper parts resembling *D. hudsonius* in appearance; spinal stripe represented only by a dusky streak on top of the head. Essential characters as in other members of the genus, but hind-foot unusually short, varying between 13 and 16.5 mm. in six adults from Discovery Bay.

*Colour of adults in summer pelage*.—Upper parts with a fine grizzle of grey, black and ochraceous the general effect approaching the "mouse-gray" of Ridgway; more or less brightened by ochraceous at the ears, on the nape, shoulders, rump, and on the flanks. The prevailing grey colour is produced by hairs which have their middle thirds white, very narrow subterminal ochraceous bands, and dusky tips. The colour is locally brightened by broadening of the subterminal ochraceous bands and at the ear-tufts by the entire elimination of dusky tips. Spinal stripe almost obsolete; usually represented only by a dark streak between the nose and the withers, but in one specimen from Discovery Bay traceable as a narrow ill-defined streak from the rostrum almost to the rump. Under parts washed with ochraceous-orange. Tail and feet white or cream-coloured.

Skull rather small and lightly built, with the rostrum slender. Parietals articulating with the supraoccipital. Auditory bullæ rather large and anteriorly inflated.

*Dentition*.—Upper incisors weak, noticeably narrower than in *D. rubricatus*, less strongly curved and somewhat protruding ("proödont"). Cheek-teeth essentially as in *D. torquatus*, but rather light; postero-internal vestigial angles in  $m^1$  and  $m^2$  present, but usually weakly developed;  $m_3$  lacking an antero-external vestigial angle.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—This is a well-marked form, sharply differentiated from *D. rubricatus* and *D. torquatus* by its small size, grey colour and to some extent by its cranial and dental peculiarities. It is possible, as Mr. G. M. Allen has suggested, that it intergrades with *D. rubricatus richardsoni* somewhere to the north of Hudson's Bay, and some of Dr. Rae's specimens, probably those obtained in the neighbourhood of the Gulf of Boothia, seem to lend some slight support to this suggestion; but pending definite proof of such intergradation, it is better to accord *D. grænelandicus* full specific rank. Outwardly the Greenland Lemming rather closely resembles *D. hudsonius*, which, however, is distinguished by its larger size, and more importantly by its peculiar cheek-teeth.

### 6. *Dicrostonyx hudsonius* Pallas.

1779. *Mus hudsonius* Pallas, Nov. Spec. Quad. Glires Ord., p. 208, taf. 26, fig. A, B, C.  
 1808. *Spalax hudsonius* Tiedemann, Zoologie, 1, p. 478.  
 1817. *Arvicola (Georychus) hudsonius* Cuvier, Règne Anim., 1, p. 207.  
 1820. *Lemmus hudsonius* Desmarest, Mammalogie, p. 289.  
 1827. *Hipudæus hudsonius* Lesson, Man. Mamm., p. 277.  
 1829. *Hypydæus hudsonius* Fischer, Synopsis Mamm., p. 299.  
 1843. *Myodes hudsonius* Wagner, Schreber's Säugethiere, Suppl., 3, p. 604.  
 1845. *Lemmus hudsonius* Schinz, Synopsis Mamm., 2, p. 255.  
 1854. *Georychus hudsonius* Audubon and Bachman, Quad. N. Amer., 3, p. 81 (part).  
 1872. *Myodes torquatus* var. *hudsonius* Forsyth Major, Atti Soc. Ital. sci. nat. Milano, 15, p. 122.  
 1874. *Cuniculus hudsonius* Coues, Proc. Acad. Nat. Sci. Philadelphia, p. 196 (part).  
 1877. *Cuniculus torquatus* Coues, Monogr. N. Amer. Rodentia, Muridæ, p. 246 (part).  
 1896. *Dicrostonyx torquatus* Miller, N. Amer. Fauna, No. 12, pp. 38-40 (part).  
 1897. *Dicrostonyx hudsonius* Bangs, Proc. Biol. Soc. Washington, 11, p. 237; Miller, "List," 1912, p. 207; G. M. Allen, Bull. Mus. Comp. Zool., Cambridge, 62, 1919, p. 514; Miller, "List," 1924, p. 398.

*Type.*—Unknown.

*Type locality.*—Labrador; probably the east coast.

*Range.*—This species inhabits the barren-ground area of the Labrador Peninsula, northwards from the Straits of Belle Isle on the south-east and from about the Great Whale River (in lat. 55° N.) on the west coast. It is also found on some of the small islands along the eastern side of Hudson's Bay. According to G. M. Allen it is completely isolated from *D. rubricatus*, the species inhabiting the western shore of Hudson's Bay, by the wooded region around James Bay.

*Characters.*—Size rather large; hind-foot to 24 mm.; condylo-basal length of skull to 32 mm. Variable cheek-teeth ( $m^1$ ,  $m^2$ , and  $m_3$ ) somewhat simplified;  $m^1$  and  $m^2$  each lacking a postero-internal vestigial angle and with the posterior wall of the hinder inner triangle more or less reduced;  $m_3$  without anterior vestigial angles. Upper parts of adults in summer pelage nearly uniform buffy grey; with a median blackish line from the nape to the tail, not sharply defined; ear-tufts, sides of body and throat buff; belly grey.

*Colour of adults in summer.*—General tone of upper parts, including the head, varying between buffy grey and clear grey, produced by the mixture of three kinds of hairs, some grey-tipped, others with dusky tips and yellowish subterminal bands, and still others longer and entirely black, the precise hue depending largely upon the development of the yellowish subterminal ring in the second sort of hairs. A black spinal line extends from the nape to the tail, but is not sharply defined. Ear on each side surrounded by an indistinct greyish patch; while each ear-tuft is composed of tawny hairs. Throat collar represented by a wash of tawny connecting the axillæ and sometimes continued backwards on the chest in the middle line. A paler tinge of tawny along the flanks and about the anus. A buffy spot on each side of the nose and around the eye. Tail like the back, or with a tuft of long grey hairs. The *young* in summer are like the adults but darker; the spinal stripe extends to the point of the nose and is more sharply defined; the throat collar is very indistinct.

*Skull.*—With dorsal contour rather more convex and less flattened from before backwards than in other recent species; nasals relatively long; interparietal frequently articulating laterally with the squamosals; presphenoid rather broad.

*Cheek-teeth.*— $m^1$  and  $m^2$  with the hinder wall of the postero-internal triangle in each tooth reduced, straight or convex instead of being concavely curved, its thick enamel more or less atrophied; no postero-internal vestigial angles.  $m_3$  without any trace of the anterior vestigial angles present in all other known species (Fig. 72, 4).

For *external and cranial measurements*, see tables at end of volume.

### FOSSIL SPECIES.

Fossil remains of *Dierostonyx* occur abundantly in the late Pleistocene deposits of Europe, and have been found in deposits of a similar age in northern and central Asia; but hitherto none have been detected in North America.

Pomel was the first to pay attention to these remains in Europe, and his excellent description<sup>1</sup> of some lower jaws, from the Brèche de Coudes, in the Auvergne, upon which he based his

<sup>1</sup> POMEL, Catalogue Méthodique, 1853, p. 27.

*Arvicola (Myolemmus) ambiguus*, leaves no room for doubting that *Myolemmus* is a synonym of *Dicrostonyx*. Unfortunately the lower jaw, in this genus, yields little that is diagnostic of species, and Pomel's description contains nothing that will enable us to determine which of the fossil species should bear the name *ambiguus*. The description of the lower jaws is followed by an account of a skull which Pomel referred also to *A. (M.) ambiguus*; but from the characters mentioned it is evident that this skull belonged to some other genus—probably *Lemmus*. Pomel's species "*ambiguus*" therefore cannot now be identified and the name must be dropped.

In 1855 Hensel<sup>1</sup> described a fragmentary skull from a Pleistocene deposit at Quedlinburg, Saxony. Possessing at that time no recent material and knowing the skull of the recent animal only from the poor figures given by Middendorff, Hensel recognized the close affinity of the fossil species with the living *D. torquatus*. He also appreciated the great differences which exist between the skull and teeth of the Arctic Lemming and those of the Norwegian Lemming and its allies, and he separated the former as a distinct genus *Misothermus* from the latter, which he left in the genus *Myodes* (= *Lemmus*). A little later Hensel procured a skull of *D. torquatus* from the Taimyrland, and found that the two anterior upper molars ( $m^1$  and  $m^2$ ) had each a minute postero-internal angle which was not present in the teeth of the Quedlinburg fossil.<sup>2</sup> But reasoning from his experience of the variability of the posterior ends of the upper molars in voles generally, Hensel justly remarked that this minute difference must be held to be a mere individual peculiarity until such time as one could examine a sufficiently large number of dentitions to prove the contrary.

In 1870 Sanford<sup>3</sup> referred a skull from the Hutton Cave, in Somersetshire, to *Lemmus torquatus*; but he based a new species of *Arvicola* (*A. gulielmi*) upon the lower jaws of the same form from the same cave. The name *gulielmi* is thus available and tenable for one of the British fossil species of *Dicrostonyx*. In 1872 Forsyth Major<sup>4</sup> found that the  $m^1$  and  $m^2$  in a skull of *D. hudsonius* from Labrador agreed with those of the Quedlinburg skull in lacking the postero-internal vestigial angle found in each of those teeth in *D. torquatus* and (according to Sanford's figure) in the skull from Somersetshire too. Forsyth Major was thus led to suggest that two species of *Dicrostonyx*, one agreeing in dentition with *D. hudsonius*, the other with *D. torquatus*, might have inhabited Europe during the Pleistocene period. Between 1872 and 1910 a large number of occurrences of fossil remains of *Dicrostonyx* in the European Pleistocene were recorded, but no

<sup>1</sup> HENSEL, Zeitschr. deutsch. geol. Ges., 7, p. 492.

<sup>2</sup> *Ibid.*, 8, 1856, p. 279.

<sup>3</sup> SANFORD, Q.J.G.S., 26, 1870, p. 125, pl. viii, figs. 2 and 4.

<sup>4</sup> FORSYTH MAJOR, Atti Soc. Ital. Sci. Nat. Milano, 15, p. 125.

one seems to have paid any attention to Forsyth Major's suggestion. In the latter year the present writer,<sup>1</sup> with the aid of excellent material, established the fact that two species have left their remains in European Pleistocene deposits and showed that neither could be identified with any of the living forms now recognized.

7. † **Dicrostonyx gulielmi** Sanford.

1870. *Arvicola gulielmi* Sanford, Q.J.G.S., 26, p. 125, pl. viii, fig. 2.  
 1870. *Lemmus torquatus*, var. Sanford, *loc. cit.*, pl. viii, fig. 4. Not of Pallas, 1779.  
 1872. *Myodes torquatus* Forsyth Major, Atti Soc. Ital. Sci. Nat. Milan, 15, p. 124.  
 1880. ?*Myodes torquatus major* Woldrich, Sitzungsber. d. k. Akad. d. Wien, math. nat. Cl. 82, Abth. 2, p. 25; based on fossil remains from a fissure deposit at Zuzlawitz, near Winterberg, Bohemia.  
 1901. *Dicrostonyx torquatus* Bate, Geol. Mag., [4], 8, p. 105.  
 1910. *Dicrostonyx gulielmi* Hinton, Ann. Mag. Nat. Hist., [8], 6, p. 38.

*Co-types*.—Taunton Museum.

*Type locality and Horizon*.—Hutton Cave, Somersetshire. Late Pleistocene.

*Nomenclature*.—Sanford's "*Arvicola gulielmi*," based upon five lower jaws of *Dicrostonyx* from the late Pleistocene deposit in Hutton Cave, would be specifically as indeterminable as Pomel's "*Arvicola (Myolemmus) ambiguus*" were it not for the fact that, under the name of "*Lemmus torquatus*, var.," Sanford described and figured, at the same time and from the same cave, a fragmentary skull which evidently belongs to the same species. No more precise information as to the provenance of the skull and lower jaws than that contained in the words "from a Somersetshire cave" is given by Sanford in his paper; but the labels in his handwriting still preserved in Taunton Museum indicate that all came from Hutton Cave. The skull in question clearly belongs to the larger European Pleistocene species with cheek-teeth of the *D. torquatus* type, and it is convenient to treat it as though it were the type of the species, although the specifically indeterminable mandibular rami are the actual co-types.

*Characters*.—Size large (dental length in adults up to 20 mm.). Cheek-teeth essentially as in *D. torquatus*.

Skull large; the nasals much expanded in front, their combined width equal to half the nasal length; zygomatic arches very heavy; anterior palatal foramina short and broad; palate boldly sculptured, with the postero-lateral bridges usually incomplete; presphenoid reduced to a slender bar; teeth very heavy.

Cheek-teeth (Fig. 71, 4) essentially as in *D. torquatus*, but larger and broader. In  $m^1$  and  $m^2$  the posterior walls of the hinder inner triangles are not reduced, but retain their thick enamel and primitive concave curvature; and there is in each

<sup>1</sup> HINTON, Ann. Mag. N.H., [8], 6, p. 37.

tooth a more or less well-marked postero-internal vestigial angle;  $m_3$  with its third or antero-external triangle less reduced than in *D. henseli* and frequently with a more or less well-marked minute fourth outer vestigial angle.

For *measurements*, see table at end of volume.

*Remarks*.—Sanford's name for this species was revived by me in 1910 after a careful comparison of the fossil material then available with the fine series of recent skulls from Discovery Bay. At that time the Discovery Bay animal was believed to be identical with *D. torquatus* Pallas, and the comparison left and leaves no room for doubting that it is distinct from *D. guillemi*. But further work has shown that the Discovery Bay Lemming is in turn specifically distinct from *D. torquatus* and has now to bear the name *D. grænlandicus* Traill. To judge from the scanty material representing *D. torquatus* as now understood, the latter species makes a nearer approach to the fossil form; but the recent material is inadequate to enable us to appreciate the specific characters of *D. torquatus*. The fossils are larger and have heavier teeth, and in  $m^1$  and  $m^2$  the postero-external triangles are relatively large, that of  $m^2$  exceeding that of  $m^1$  in size, whereas in recent *D. torquatus* they are smaller, subequal in size in  $m^1$  and  $m^2$  or else slightly larger in the former tooth than in the latter. On these grounds, pending the acquisition of further recent material, *D. guillemi* may be maintained as a distinct species. It would at present be unwise and misleading to identify the fossils in question with what is in fact the least known of all the recent species.

The following is a list of the deposits and localities in which remains have been found with short descriptions of the material upon which the records are based. In all cases, unless otherwise stated, the material has been studied and determined by the writer.

## A. GREAT BRITAIN.

### SOMERSETSHIRE. *Hutton Cave*.

Five mandibular rami (co-types of the species) and two fragmentary skulls originally described by Sanford (Q.J.G.S., 26, 1870, p. 125, pl. viii, figs. 2 and 4). Re-examined by me (Fig. 71, 4 and Plate V).

*Taunton Museum.*

### SOMERSETSHIRE. *Aveline's Hole, Burrington Coombe*.

Lower jaws at first referred doubtfully to *D. henseli*; but much more extensive material collected later proves the species to be *D. guillemi* (Hinton, Proc. Bristol Univ. Spelæol. Soc., 1, p. 75, 1922, and 2, p. 34, 1924).

*Bristol Univ. Spelæological Society's Museum.*

### DEVONSHIRE. *Chudleigh Fissure*.

Two palatal fragments showing between them  $m^1$ - $m^3$ ; and part of a mandibular ramus.

*A. S. Kennard, F.G.S.*

HEREFORDSHIRE. *Cave near River Wye, Forest of Dean.*

Part of a skull and twelve mandibular rami; collected, described and figured by Miss D. M. A. Bate (Geol. Mag., [4], 8, 1901, p. 104, figs. 2-6).

*British Museum.*

HEREFORDSHIRE. *Merlin's Cave, Wye Valley, near Symond's Yat* (possibly the cave previously worked by Miss Bate).

Parts of twenty-two skulls and five hundred and twenty-three mandibular rami representing at least two hundred and seventy individuals (Hinton, Proc. Bristol Univ. Spelæol. Soc., 2, p. 157, 1925). Many more not yet reported upon were obtained last autumn.

*Bristol University Spelæological Society's Museum.*

WILTSHIRE. *Brickearth of Fisherton, near Salisbury.*

Remains originally determined by Blackmore and Alston as *Myodes torquatus* (P.Z.S., 1874, p. 470). Dr. Blackmore has kindly lent two mandibular rami from this deposit; they are difficult to determine, but I think both are referable to *D. gulielmi*.

*Blackmore Museum, Salisbury.*

KENT. *Erith. Middle Terrace brickearth of the Thames.*

Part of a skull and mandible collected by Mr. F. C. J. Spurrell; described and figured, under the name *Myodes torquatus*, by Mr. E. T. Newton (Geol. Mag., [3], 7, 1890, p. 454, figs. 3-6). Re-examined and determined as *D. gulielmi* by the writer; this record supports the opinion that the Fisherton remains are to be referred to *D. gulielmi*, because in other respects the fauna of the Fisherton brickearth is closely similar to that obtained at Erith.

*Museum of Practical Geology.*

DERBYSHIRE. *Langwith Cave, near Mansfield.*

Part of a skull, several mandibular rami and detached maxillary molars; collected by the Rev. E. H. Mullins (Derbyshire Archæol. and N.H. Soc. Journ., 1913, p. 15 of separate).

LANCASHIRE. *Dog Holes, Warton Crag.*

Part of a right maxilla with  $m^1$  in place; a detached right  $m^1$  and six mandibular rami in British Museum presented by the collector, Mr. J. Wilfrid Jackson. Other material in Mr. Jackson's collection at Manchester not seen by me (see Lancashire Nat., 1909, p. 227).

*British Museum; Manchester.*

## B. IRELAND.

CO. SLIGO. *Kesh Caves.*CO. CORK. *Edenvale Caves.*

Numerous mandibular rami, a few fragmentary maxillæ and detached upper molars.

*Dublin Museum.*

## C. CONTINENTAL EUROPE.

SOUTHERN FRANCE. *Neschers.*

A fragmentary palate with  $m^1$  in place and some other remains probably referable to this species.

*British Museum.*



8. †*Dicrostonyx henseli* Hinton.

1855. *Misothermus torquatus* Hensel, Zeitschr. deutsch. geol. Gesellsch., 7, p. 493, taf. xxv, figs. 12 and 13. Not of Pallas, 1779.  
 1872. *Myodes torquatus* Forsyth Major, Atti Soc. Ital. Sci. Nat. Milano, 15, p. 123; Newton, Q.J.G.S., 50, 1894, p. 196.  
 1910. *Dicrostonyx henseli* Hinton, Ann. Mag. Nat. Hist., [8], 6, p. 37.

*Type*.—B.M., No. M.11,803, Geol. Dept.; Abbott Collection; presented by Sir H. H. Howorth, K.C.I.E., F.R.S.

*Type locality and Horizon*.—Ightham, Kent. Late Pleistocene; from a deposit filling fissures in the "Kentish Rag."

*Characters*.—Size rather small (dental length in adults up to 19 mm., condylo-basal length not exceeding 29 mm.). Cheek-teeth relatively broad, but essentially like those of *D. hudsonius* in pattern.

Skull (Fig. 70) in general form most nearly resembling that of *D. hudsonius* but smaller; its dorsal contour gently convex from before backwards, as in *D. hudsonius*, but with smaller and less expanded nasals, and relatively shorter diastema; palate feebly sculptured, with complete postero-lateral bridges; presphenoid reduced to a slender rod, in correlation with the relatively broader and heavier cheek-teeth; auditory bullæ very small, egg-shaped and not inflated anteriorly, their general form much as in *D. hudsonius* but their position a little different, lying with their long axes more convergent anteriorly and less nearly parallel with the long axis of the skull.

Cheek-teeth (Figs. 71, 8; 72, 7) relatively broad, but essentially like those of *D. hudsonius* in pattern. In  $m^1$  and  $m^2$  the posterior walls of the hinder inner triangles are reduced, losing their primitive concave curvature and tending to lose their thick enamel; a postero-internal vestigial angle never developed;  $m_3$  with a small antero-internal vestigial angle, but no corresponding outer vestige, the third outer triangle more or less reduced.

Other parts of *skeleton* not essentially different from those of the living members of the genus.

For *measurements*, see table at end of volume.

The following is a list of deposits and localities in which remains of *D. henseli* have been found. In all cases, unless otherwise stated, the material has been determined by the writer.

## A. GREAT BRITAIN.

KENT. Ightham, near Sevenoaks; fissure deposit.

A nearly complete skull (the type); an incomplete skull and several mandibular rami.

British Museum and Museum of Practical Geology (ex W. J. Lewis Abbott Collection); and in collection of Dr. Frank Corner.

MIDDLESEX. Lea Valley; Third Terrace deposits at Ponder's End and Angel Road.

Abundant remains, including a nearly complete skeleton, and

quantities of the dung preserved in peaty silt (Hinton, Q.J.G.S., 68, 1912, p. 249; Warren, *ibid.*, p. 213, and 71, p. 175, 1916).

DERBYSHIRE. *Langwith Cave, near Mansfield.*

Two or three examples of  $m^1$  and  $m^2$  were referred by me to *D. henseli* (Mullins, Derbyshire Archæol. and N.H. Soc. Journ., 1913, p. 15 of reprint).

HEREFORDSHIRE. *Merlin's Cave, Wye Valley, near Symond's Yat.*

Four skull fragments with  $m^1$  and  $m^2$  in place seem to be referable to this species and not to *D. guielmi*, which occurs so abundantly in this cave (Hinton, Proc. Bristol. Univ. Spelæol. Soc., 2, p. 157, 1925).

*Bristol University Spelæological Society's Museum.*

A fragmentary right mandibular ramus from a Pleistocene deposit at Corstorphine, west of Edinburgh, determined by E. T. Newton as *Dicrostonyx* sp., has been recorded by W. Evans (Scott. Nat., 1913, p. 97).

## B. IRELAND.

Co. CLARE. *Doneraile Cave.*

Several fragmentary palates and numerous mandibular rami.

*Dublin Museum.*

## C. CHANNEL ISLANDS.

JERSEY. *La Cotte de St. Brelade.*

A palate and a number of mandibular rami indicating at least fifteen individuals (Hinton, Société Jersiaise Bull. Ann., 43, 1918, p. 355).

## D. CONTINENTAL EUROPE.

NORTHERN FRANCE. *Manbeuge; fissure deposit.*

Fragmentary skulls and lower jaws described and figured, under the name *Myodes torquatus*, by G. Dubois (Ann. Soc. Géolog. du Nord, 44, p. 69, 1919). The figures of the upper molars indicate that the species represented by these remains is *D. henseli*.

*Cambrai; "dans un sable situé à la base de l'ergeron."* Remains described by G. Dubois (Ann. Soc. Géolog. du Nord, 44, p. 95, 1919); probably referable to *D. henseli*.

SOUTH GERMANY. *Wurtemberg, Kleine Scheuer.*

Numerous palates and several mandibular rami; lent by Dr. Frank Corner.

*Saxony, Quedlinburg.*

The skull and other remains described by Hensel (Zeitschr. deutsch. geol. Gesellsch., 7, p. 493).

Remains of *Dicrostonyx* have been recorded chiefly by Nehring and Woldrich from a great many late Pleistocene deposits on the Continent, but in the absence of material I am unable to determine the species. A nearly perfect skull from Eppelsheim, near Darmstadt, mentioned by Blackmore and Alston (P.Z.S., 1874, p. 470) as being in the British Museum was accidentally destroyed many years ago; the mandibulæ which remain are insufficient for specific determination.

Genus : **2. SYNAPTOMYS** Baird.

1857. *Synaptomys* Baird, Mamm. N. America, p. 558.

*Genotype*.—*Synaptomys cooperi* Baird.

*Range*.—North America, from the northern edge of the Lower Austral zone in Virginia (Dismal Swamp) and Kansas (Woodson County) northwards to Alaska, Mackenzie, and Labrador.

*Characters*.—General external form nearly as in normal voles. Fur soft and moderately long. Colour dull; brownish above, paler below. External ears well developed, slightly evident above the fur; in form like those of *Evotomys*. Hands and feet of normal size and form; thumb small, provided with a large flattened nail; five palmar and six plantar tubercles; palms clothed between wrist and pads with long white hairs which conceal the pollical tubercle; soles clad with shorter and thinner hairs between the heel and pads. Tail terete, slightly longer than the hind-foot; rather thinly clothed with long stiff hairs which do not completely conceal the scaly annulations. Mammæ,  $2 - 2 = 8$  or  $1 - 2 = 6$ .

Skull relatively narrower, more lightly built, and in general less modified than in *Lemmus*. Rostrum noticeably deflected, short and broad. Nasals ending anteriorly slightly but distinctly in advance of the strongly curved "opisthodont" upper incisors; terminating posteriorly in line with the premaxillaries and slightly in front of the orbits. Zygomatic arches lighter and less widely spreading than in *Lemmus*, though more expanded than is usual in voles; the greatest zygomatic breadth falls on the maxillary or fore-parts of the arches and is equal to 61–65% of the condylo-basal length, instead of to about 68% as in *Lemmus* or to 55–60% as in most voles. Jugals slender, with slightly convex upper borders, their outer surfaces forming nearly vertical planes instead of being abruptly convergent dorsally as in *Lemmus*. Braincase longer and narrower than in *Lemmus*, the post-glenoid region less noticeably shortened. Temporal ridges fusing<sup>1</sup> in old age to form a median interorbital crest; their posterior course over the braincase essentially as in *Lemmus*, though they are perhaps slightly less salient than in equal-aged skulls of *L. lemmus*. Squamosals very large, essentially as in *Lemmus*, though relatively a little more widely separated in front than in the latter genus, with long post-orbital crests, which bound the square shoulders of the braincase, and forming the entire floors of the posterior or supratympanic

<sup>1</sup> In two only (*S. wrangeli*, Metlakatla, British Columbia, B.M., Nos. 11.10.2.1 and 13.10.1.1) of the small series of skulls of *Synaptomys* before me, are the ridges actually fused into an interorbital crest; but in several of the other specimens the ridges are closely approximated. Most probably the ridges fuse regularly in the older adults of all species of *Synaptomys*; but fully mature skulls of Microtinæ are naturally comparatively rare.

portions of the temporal fossæ; supratympanic fenestræ relatively large; owing to the slighter lateral saliency of the lambdoid crest, the supratympanic portions of the temporal fossæ are less extensive transversely than in *Lemmus*. Interparietal rather longer in relation to its width, truncated laterally (although not crossed by the temporal ridges), and usually with a boldly convex posterior border. In the ventral view the great width and shortness of the rostrum are conspicuous. Antero-palatal foramina rather short but unusually broad. Cheek-teeth narrower in proportion to their length, the tooth rows, about equal to the diastema in length, diverging posteriorly, though not so rapidly as in *Lemmus*. Palate posteriorly nearly as in *Microtus*; the posterior median sloping septum longer and better developed than in *Lemmus*, the inner or mesial borders of the post-palatal pits not extending so far forwards but bending inwards to make a junction with the sides of the median septum whereby an appearance, closely similar to that seen in many species of *Microtus*, is imparted to the hinder edge of the palate. Pterygoid fossæ slightly longer but a little shallower than in *Lemmus*, their floors being scarcely dorsal to the ventral surface of the basisphenoid. Choanæ, presphenoid, basisphenoid, and fore-part of basioccipital all considerably narrower than in *Lemmus*. Auditory bullæ relatively large and globular, more closely approximated to the middle line below, their inner sides being conspicuously more inflated than in *Lemmus*; in each bulla the external meatus is very shortly tubular; the walls are densely spongy, the sponge being connected with the surface of the petrous portion by a wide meshwork of strong bony trabeculæ; canaliculus tympanicus ossified until it reaches the stapes; mastoid portion and tegmen tympani less inflated than in *Lemmus*.

Mandible essentially as in *Lemmus*, but condylar process in each ramus shorter and the groove between the cheek-teeth and the ascending ramus more evenly and smoothly continuous with the concave inner surface of the angular process behind.

*Dentition*.—Incisors like those of *Lemmus* as regards their courses and lengths. Upper incisors strongly curved, "opisthodont," each with a longitudinal groove near the outer edge of its anterior surface; cutting edges of upper incisors as in *Lemmus*, when uninjured, the soft dentine worn back and hollowed considerably, the hard and resistant anterior enamel plate becoming very salient and forming a tubular or gouge-like termination.

Cheek-teeth rootless; infolds filled with cement; enamel well differentiated into thick and thin portions forming respectively the concave and the convex sides of the salient angles. Enamel pattern essentially as in *Lemmus*; but in some species persistent though quite vestigial traces of the median row of tubercles occur frequently (Fig. 73). In  $m^3$  the second and third transverse



Fig. 1a.



Fig. 2a



Fig. 3a.



Fig. 1b.



Fig. 2b.



Fig 3b

FIG. 73.—Cheek-teeth of *Synaptomys*.

Crown views: *a.* upper molars; *b.* lower molars:—

1. *S.* (*Synaptomys*) *fatuus*, Ontario.
2. *S.* (*Mictomys*) sp. Metlakatla, British Columbia.
3. *S.* (*Mictomys*) *borealis*. Type.

loops are separated by the very deep second outer fold, the first inner infold being but slightly developed. In the lower molars the outer infolds may be deep enough to close triangles (subgenus *Synaptomys*, Fig. 73, 1b); or so weakly developed that the teeth consist of transverse loops and have crenulate instead of serrate outer borders (subgenus *Mictomys*, Fig. 73, 2b, 3b).

*Subgenera and species.*—Eleven species, comprising thirteen forms, are at present included in the genus; but future work will probably reduce the number of species and increase the number of geographical races. The known forms may be arranged in two subgenera, viz., *Synaptomys* Baird and *Mictomys* True, distinguished as follows:—

Mammæ, 1 — 2 = 6.

Lower cheek-teeth with closed triangles.

Rostral part of skull very stout; palate without long posterior spine.

Subgenus *Synaptomys* Baird.

Mammæ, 2 — 2 = 8.

Lower cheek-teeth without closed triangles.

Rostral part of skull slender; palate with long spinous process behind.

Subgenus *Mictomys* True.

Subgenus: **SYNAPTOMYS** Baird

1857. *Synaptomys* Baird, Mamm. N. America, p. 558 (genus).

1896. *Synaptomys* Miller, N. Amer. Fauna, No. 12, p. 34 (subgenus of *Synaptomys*); Merriam, Proc. Biol. Soc. Washington, 10, 1906, p. 57.

*Genotype.*—*Synaptomys cooperi* Baird.

*Range.*—Eastern North America, from Virginia and Kansas northwards through the eastern United States into eastern Canada and westwards to Minnesota.

*Characters.*—Externally as described under the genus. Mammæ, 1 — 2 = 6.

Skull with remarkably heavy rostrum; palate nearly as in *Microtus*, without long posterior spine. Incisors very large and broad; grooves of upper incisors usually well defined and externally placed. Mandibular cheek-teeth with deep outer infolds and closed triangles substantially as in *Lemmus*.

*Geographical differentiation.*—Four forms referred to three species are at present recognized; but according to Rhoads (Proc. Acad. Nat. Sci. Philadelphia, 1897, pp. 305–307) all should be regarded as subspecies of *S. cooperi*. Only one of these forms is well represented in the material before me, and I can therefore come to no decision; but after carefully studying the literature and my material I am inclined to think that Rhoads is right.

### 1. *Synaptomys (Synaptomys) cooperi* Baird.

1857. *Synaptomys cooperi* Baird, Mamm. N. America, p. 558.  
 1893. *Synaptomys stonoi* Rhoads, Amer. Nat., 27, p. 53; described from May's Landing, Atlantic County, New Jersey; type in collection of S. N. Rhoads.  
 1894. *Synaptomys cooperi* Bangs, Proc. Biol. Soc. Washington, 9, p. 99; Miller, "List," 1924, p. 394.

*Co-types*.—U.S. National Museum.

*Type locality*.—Unknown; probably northern New Jersey or southern New York.

*Range*.—Eastern United States from Minnesota eastwards to eastern Massachusetts; south to Iowa, Indiana, and Maryland, and in the mountains to North Carolina and Tennessee. In the Boreal and parts of the Transition Zones, finding a boreal atmosphere south of the Boreal Zone in cold sphagnum swamps.

*Characters*.—Distinguished from *S. healetes* by smaller feet and lighter skull. Hind-foot 18 mm.

Colour of upper parts grizzled grey and yellowish brown abundantly mixed with black-tipped hairs; under parts dirty white darkened by the hair-bases. Tail bicoloured, brownish above, whitish below.

Skull and teeth relatively small and weak compared with those of *S. healetes*; zygomata more widely spreading; brain-case shorter; rostrum, nasals, and upper incisors narrower. Mandible less robust.

For *external and cranial measurements*, see tables at end of volume.

### 2. *Synaptomys (Synaptomys) fatuus* Bangs.

1896. *Synaptomys fatuus* Bangs, Proc. Biol. Soc. Washington, 10, p. 47; Miller, "List," 1924, p. 394.  
 1897. *Synaptomys cooperi fatuus* Rhoads, Proc. Acad. Nat. Sci. Philadelphia, 1897, p. 306.

*Type*.—Collection of E. A. and O. Bangs.

*Type locality*.—Lake Edward, Quebec, Canada.

*Range*.—Quebec, Ontario, and New Brunswick; limits of range unknown.

*Characters*.—Very similar to *S. cooperi* but described as slightly smaller, with decidedly smaller skull and narrower upper incisors. Hind-foot 18–19 mm.

Colour of upper parts grizzled yellowish brown, abundantly mixed with black-tipped hairs; under parts varying from slate-grey to whitish washed with buff on belly. Tail only slightly paler below than above.

Skull similar to that of *S. cooperi* but described as smaller and weaker, with narrower rostrum; the basisphenoid broader posteriorly; upper incisors very much narrower.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—The material available comprises two or three topotypes from the Bangs Collection and a fine series from Ontario in the Miller Collection. Unfortunately our material representing *S. cooperi* is very meagre. So far as the skull and teeth are concerned, I can see no tangible difference between *S. fatuus* and a specimen of *S. cooperi* from Brookeville, Indiana, presented by Dr. Coues (No. 78.6.24.2); the skull of the latter, however, is imperfect.

### 3. **Synaptomys (Synaptomys) helaletes** Merriam.

(Synonymy under subspecies.)

*Range.*—Kansas and Virginia.

*Characters.*—Distinguished from *S. cooperi* externally by its larger head and feet and longer tail, and by its larger and more massive skull and teeth, much broader rostrum and more robust mandible. Hind-foot 19–20 mm.

Two subspecies are at present recognized:—

1. Colour as in *S. cooperi*; skull with shorter rostrum and larger auditory bullæ.

*S. h. helaletes* Merriam, Virginia.

2. Colour probably redder; skull with longer rostrum and smaller auditory bullæ.

*S. h. gossii* Coues, Kansas.

Dr. Merriam says (Proc. Biol. Soc. Washington, 10, p. 59) that the difference in breadth and massiveness of rostrum, mandible and upper incisors between *helaletes* and *gossii* "is so great that skulls of the two require no comparison. Still, specimens recently collected by V. Bailey in a sphagnum swamp near Washington, D.C., are somewhat intermediate and indicate that intergradation may exist."

#### 3a. **Synaptomys (Synaptomys) helaletes helaletes** Merriam.

1896. *Synaptomys helaletes* Merriam, Proc. Biol. Soc. Washington, 10, p. 59.

1897. *Synaptomys cooperi stonei* Rhoads, Proc. Acad. Nat. Sci. Philadelphia, 1897, p. 305.

1912. *Synaptomys helaletes helaletes* Miller, U.S. Nat. Mus., Bull. No. 79, p. 204, and "List," 1924, p. 394.

*Type.*—U.S. National Museum.

*Type locality.*—Dismal Swamp, Norfolk County, Virginia.

*Characters.*—Colour as in *S. cooperi*; toes usually partly white.

Skull and teeth larger, heavier and more massive; zygomata less strongly bowed outwards; nasals broader posteriorly; brain-



case longer; rostrum, upper incisors and mandible remarkable for breadth and massiveness.

For *external and cranial measurements*, see table at end of volume.

### 3b. *Synaptomys (Synaptomys) helaletes gossii* Coues.

1877. *Arvicola (Synaptomys) gossii* Coues, Monogr. N. Amer. Rodentia, Muridæ, p. 235 (published as a synonym of *Synaptomys cooperi* but name stated to apply to specimens from Kansas, and of these descriptions and measurements are printed on p. 236).  
 1896. *Synaptomys helaletes gossii* Merriam, Proc. Biol. Soc. Washington, 10, p. 60; Miller, "List," 1924, p. 394.  
 1897. *Synaptomys cooperi gossii* Rhoads, Proc. Acad. Nat. Sci. Philadelphia, 1897, p. 307.

*Co-types*.—U.S. Nat. Mus., Nos. 8464, 8508–8517; eleven collected 1865–1866, by B. F. Goss.

*Type locality*.—Neosho Falls, Woodson County, Kansas.

*Characters*.—Similar to *S. h. helaletes*, but skull with longer rostrum and smaller auditory bullæ.

Colour not satisfactorily known, but probably more reddish-brown above than *S. h. helaletes* or *S. cooperi*.

Skull similar to that of *S. h. helaletes* but even larger, with longer rostrum and nasals; zygomata more bowed outwards in the middle; orbital fossæ larger. In ventral view rostrum and incisive foramina conspicuously longer; post-palatal pits deeper, defining a distinct median ridge which projects slightly into the mesopterygoid fossa; auditory bullæ smaller, the sides of the basioccipital less deeply excavated and the vacuity on each side of the basisphenoid much larger. Incisors very broad and heavy as in the typical subspecies; molars nearly as large.

For *external and cranial measurements*, see tables at end of volume.

### Subgenus: **MICTOMYS** True.

1828. *Arvicola* Richardson, Zool. Journ., 3, p. 517 (in part). Not of Laccpède, 1801.  
 1830. *Lenmus*, Fischer, Syn. Mamm., p. 585 (in part). Not of Link, 1795.  
 1894. *Mictomys* True, Proc. U.S. Nat. Mus., 17, No. 999, p. 242. Advance sheet, April 26, 1894 (genus).  
 1896. *Mictomys* Merriam, Proc. Biol. Soc. Washington, 10, p. 57 (subgenus); Miller, N. Amer. Fauna, No. 12, 1896, p. 35.

*Genotype*.—*Mictomys inuitus* True.

*Range*.—North America; in the Hudsonian Zone, from Labrador to Alaska, and southwards to New Hampshire and northern California.

*Characters*.—Externally as in the typical subgenus, but mammary formula  $2 - 2 = 8$ .

Skull with relatively slender rostrum; post-palatal septum

produced into a spinous process which juts into the mesopterygoid fossa. Pterygoid bones usually longer and more slender, the hamular processes less strongly bent outwards than in *Synaptomys*.

Incisors much weaker relatively; upper incisors with their grooves less well defined and more centrally situated than in *Synaptomys*. Mandibular cheek-teeth with crenulate outer borders, lacking closed triangles in consequence of the feeble development of the outer infolds.

*Species and remarks.*—The characters separating this subgenus from true *Synaptomys* although slight are apparently quite definite and constant. Eight species and nine forms of *Mictomys* are at present recognized, but some of them are of very doubtful validity. Several of the described forms are undoubtedly entitled to systematic recognition; but it is not improbable that all eventually will have to be regarded as more or less well-marked subspecies of *S. borealis* Richardson, the earliest and unfortunately one of the least known of the described forms. Richardson's type is in the British Museum, but the skull is in fragments, and until further material is obtained from the neighbourhood of the type locality it will be impossible properly to appreciate the characters of *S. borealis*.

Four specimens from Metlakatla, British Columbia, collected and presented by the Rev. J. H. Keen, indicate that the characters of  $m^3$  and  $m_3$ , upon which many authors have laid stress when describing species of *Mictomys*, are subject to considerable variation in different individuals and in the same individuals at different stages of growth.

#### 4. *Synaptomys (Mictomys) borealis* Richardson.

1828. *Arvicola borealis* Richardson, Zool. Journ., 3, p. 517; 1829, Fauna Boreali-Americana, p. 127.  
 1830. *Lemmus borealis* Fischer, Syn. Mamm., p. 585.  
 1902. *Synaptomys (Mictomys) bullatus* Preble, Proc. Biol. Soc. Washington, 15, p. 181; described from Trout Rock, near Fort Rae, Great Slave Lake, Mackenzie, Canada; type in U.S. Nat. Museum.  
 1902. *Synaptomys bullata* Preble, *op. cit.*, p. 182; misprint for *bullatus*.  
 1907. *Synaptomys borealis* Osgood, Proc. Biol. Soc. Washington, 20, p. 49.

*Type.*—B.M., No. 42.10.7.10; adult in full pelage, taken "in spring after snow had melted" (skin good; skull in fragments); presented by Sir J. Richardson.

*Type locality.*—Fort Franklin, Great Bear Lake, Mackenzie, Canada.

*Range.*—N.W. Canada between Great Bear Lake and the Rocky Mountains; southwards as far as Fort Halkett at least.

*Characters.*—Size small, hind-foot 14–16 mm. Fur very long and dense, about 22 mm. in length upon the rump. Ears completely hidden by the fur. Colour of upper parts chestnut

mixed with blackish hair-tips; under parts leaden-grey. Rufous mark under each ear. A white patch over each hip. Tail round, well clothed with short stiff hairs which completely conceal the scales; clove-brown above, greyish-white beneath. Paws clove-brown above.

Skull known from fragments only. Each upper incisor with a broad, but quite shallow sulcus upon its outer face, and with a much narrower notch-like groove upon its hinder surface. Cheek-teeth:  $m^3$  with large posterior loop; outer fold of  $m_3$  moderately deep, leaving the outer and inner portions of the middle transverse loop about half confluent (Fig. 73, 3).

For *external and cranial measurements of type*, see tables at end of volume.

*Remarks.*—What is left of the skull of the type shows that it was a perfectly adult individual with the temporal ridges completely fused in the interorbital region.

Notwithstanding Richardson's remarkably full and good description and his statement that this animal might be regarded as intermediate between the lemmings and the voles, it was not until Osgood's paper of 1907 that "*Arvicola borealis*" was identified as a member of the present genus. A subadult male from Fort Halkett (B.M., No. 63.1.6.12 in al., presented by B. R. Ross) may be referred to *S. borealis*, agreeing with the type in general character, in the small size of the hind-foot (15.6), and in the pattern of the molars; the outer fold of  $m_3$ , however, is deeper, nearly closing off an outer triangle, but I am not inclined to attach much importance to this character.

*Synaptomys bullatus* described from Fort Rae, Great Slave Lake, a locality some considerable distance to the south-east of the type locality of *S. borealis*, is treated by Miller ("Lists," 1912 and 1924) as a synonym of the present species; but since the hind-foot is considerably larger (18 mm.) and the colour, judging from Preble's description, is somewhat different, it may be a distinct form.

It is quite likely that, as Hollister (Canadian Alpine Journal, Special Number, pp. 19-20, Feb. 17, 1913) has suggested, all the forms inhabiting north-western North America will eventually have to be regarded merely as more or less well-marked subspecies of *S. borealis*.

##### 5. *Synaptomys (Mictomys) dalli* Merriam.

1896. *Synaptomys (Mictomys) dalli* Merriam, Proc. Biol. Soc. Washington, 10, p. 62.

*Type.*—U.S. National Museum; skeleton.

*Type locality.*—Nulato, Alaska.

*Characters.*—Generally resembling *S. wrangeli*, but with larger auditory bullæ and less reduced cheek-teeth.

Colour (according to Osgood, N. Am. F., No. 19, p. 37, 1900) :

Upper parts chiefly raw umber mixed with black; lower parts uniformly bluish-white; feet and tail dusky. Ears medium, partly hidden by long hairs growing from the anterior base; a conspicuous bluish-white side-gland is present in males.

Skull differs from that of *S. wrangeli* chiefly in its larger bullæ; the other peculiarities mentioned by Merriam in his original description stated by Osgood to be inconstant and to vary with age. Cheek-teeth:  $m_2$  and  $m_3$  each with the outer re-entrant angle deeper than in *S. wrangeli* resembling the condition seen in *S. truci*;  $m^3$  with small posterior loop.

For *external and cranial measurements*, see tables at end of volume.

### 6. *Synaptomys (Mictomys) wrangeli* Merriam.

1896. *Synaptomys (Mictomys) wrangeli* Merriam, Proc. Biol. Soc. Washington, 10, p. 63.

*Type*.—U.S. National Museum.

*Type locality*.—Wrangel, Alaska.

*Characters*.—Similar to *S. innuitus innuitus*, but larger, with the tail and hind-foot longer, and the skull narrower.

Upper parts grizzled greyish-brown, with a yellowish cast; under parts plumbeous, tipped with whitish; tail bicoloured, brownish above, whitish below, darker at tip.

Skull narrower and less depressed than that of *S. innuitus*; zygomata narrower and less spreading anteriorly; braincase narrower and less depressed; auditory bullæ less inflated anteriorly. Cheek-teeth:  $m^3$  with very small posterior loop;  $m_3$  with outer fold shallower than in *S. innuitus* and enamel folds of all teeth more loosely spaced.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—No material in collection.

### 7. *Synaptomys (Mictomys) andersoni* Allen.

1903. *Synaptomys (Mictomys) andersoni* Allen, Bull. Amer. Mus. N.H., 19, p. 554.

*Type*.—American Museum N.H.; adult female.

*Type locality*.—Level Mountain, northern British Columbia.

*Characters*.—Hind-foot 18 mm.

Upper parts dark brown, faintly suffused with clay colour and strongly varied with blackish; under surface ashy grey, rather sharply defined against the yellowish-brown flanks. Tail black above, greyish on sides and lower surface. Upper surfaces of paws blackish-brown; hind-feet rather darker than fore-paws. Ears small; in autumn pelage wholly concealed in the fur.

Skull much as in *S. wrangeli*, but bullæ much more inflated, especially anteriorly;  $m_3$  with a deep re-entrant outer fold;

$m^3$  with a large posterior loop, about two-thirds the size of the middle loop.

For *external and cranial measurements*, see tables at end of volume.

### 8. *Synaptomys (Mictomys) chapmani* Allen.

1903. *Synaptomys (Mictomys) chapmani* Allen, Bull. Amer. Mus. N.H., 19, p. 555.

*Type*.—American Museum N.H.; adult male, collected July 1901.

*Type locality*.—Glacier, Selkirk Range, British Columbia.

*Characters*.—A short-tailed, large-eared species of greyish-brown general colour; hind-foot 20 mm.

Upper parts greyish-brown, with a slight suffusion of buff which is strongest on the front of the head, the whole region in front of the eyes being conspicuously washed with buff; under surface dark grey, the plumbeous underfur very slightly tipped with whitish, not sharply defined laterally. Ears large, prominent above fur, coloured like the surrounding pelage. Feet dusky greyish-brown. Tail very short, darker above than below, well pencilled. Flank-glands in front of hips, covered by conspicuously lighter, almost whitish fur.

Skull much larger than that of *S. andersoni*, narrower, with relatively narrower braincase and more elongated rostrum; anterior palatal foramina longer and narrower; auditory bullæ much smaller and less inflated. Cheek-teeth as in *S. andersoni*;  $m_3$  with deep re-entrant outer fold;  $m^3$  with large posterior loop.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—No material examined.

### 9. *Synaptomys (Mictomys) truei* Merriam.

1896. *Synaptomys (Mictomys) truei* Merriam, Proc. Biol. Soc. Washington, 10, p. 62.

*Type*.—U.S. National Museum; subadult.

*Type locality*.—Skagit Valley, north-western Washington.

*Range*.—Known only from the type locality.

*Characters*.—Generally resembling *S. wrangeli* in outward appearance and size; distinguished by its slightly longer ears, more reddish-brown colour and the form of  $m_3$ .

Upper parts dull umber brown, fading gradually to plumbeous of under parts; belly hairs tipped with whitish. Tail bicoloured, dark above, whitish below. Type and only known specimen in moult and in very poor condition, hence the colours may not be as in the normal animal.

Skull characters unknown. Cheek-teeth with enamel loops both above and below much fuller and more bluntly rounded

than in *S. innuitus* and *S. wrangeli*; outer infold of  $m_3$  very deep, almost closing off an outer triangle; posterior loop of  $m^3$  small. Upper incisors narrower and each with a shallower sulcus than in other species.

For *external and cranial measurements of type*, see table at end of volume.

*Remarks.*—No material in collection; the type is still the only specimen that has been recorded.

### 10. *Synaptomys (Mictomys) innuitus* True.

(Synonymy under subspecies.)

*Range.*—Labrador.

*Characters.*—In the absence of material it is not possible to decide what are the specific characters distinguishing this animal from *S. borealis*, and I suspect that when all the known forms of *Mictomys* are revised they will have to be treated as subspecies of *S. borealis*.

There are two well-marked forms of *S. innuitus* in Labrador judging from the descriptions cited below, and to one of them Preble's *S. sphagunicola* from New Hampshire is apparently very closely related.

#### 10a. *Synaptomys (Mictomys) innuitus innuitus* True.

1894. *Mictomys innuitus* True, Diagnoses of new N. Amer. Mamm., p. 3; Proc. U.S. Nat. Mus., **17**, p. 242.

1896. *Synaptomys (Mictomys) innuitus* Merriam, Proc. Biol. Soc. Washington, **10**, p. 61.

1912. *Synaptomys (Mictomys) innuitus innuitus* Miller, U.S. Nat. Mus., Bull. No. **79**, p. 205.

*Type.*—U.S. National Museum.

*Type locality.*—Fort Chino, Ungava, Labrador.

*Characters.*—Size small (hind-foot 17.5); tail short; general appearance much as in *S. cooperi*, but outwardly distinguishable by slightly longer ears.

Colour (of alcoholic specimen): Upper parts greyish-brown, under surface grey; face pale brown; lips, end of nose, and chin white; feet pale brown; tail bicoloured, pale brown above, white below.

Skull very broad and flat; braincase strongly depressed; zygomata broadly spreading and standing out squarely from rostrum; auditory bullæ strongly inflated anteriorly. Cheek-teeth:  $m^3$  with broad posterior loop;  $m_2$  and  $m_3$  with moderately deep outer infolds.

For *external and cranial measurements of type*, see tables at end of volume.

*Remarks.*—No material examined; the above account embodies the essential part of the description given by Dr. Merriam in his revision of 1896.

10b. **Synaptomys (Mictomys) innuitus medioximus** Bangs.

1900. *Synaptomys (Mictomys) innuitus medioximus* Bangs, Proc. N. Engl. Zool. Club, 2, p. 40.

*Type*.—Bangs Collection; adult male.

*Type locality*.—L'Anse au Loup, Strait of Belle Isle, Labrador.

*Characters*.—Distinguished from *S. i. innuitus* by its larger size and proportionally flatter skull.

Fur very long and soft, in full winter pelage (April) nearly concealing ears.

Colour of upper parts rich brown; back and head dull russet very thickly set with black-tipped hairs; rump and flanks shading decidedly towards hazel and with fewer black-tipped hairs; long hairs on ears, and in front of and behind ears, hazel; patches at base of whiskers meeting across nose, dull hazel. Under parts dull smoke grey; underfur slate-colour. Feet and hands dusky; tail dusky above, greyish below.

Skull much larger than that of *S. i. innuitus* but proportionally flatter; rostrum less deflected; visible portion of posterior ends of frontal much larger, much less encroached upon by the overlapping edges of the squamosals.

For *external and cranial measurements*, see tables at end of volume.

11. **Synaptomys (Mictomys) sphagnicola** Preble.

1899. *Synaptomys (Mictomys) sphagnicola* Preble, Proc. Biol. Soc. Washington, 13, p. 43.

*Type*.—U.S. National Museum; adult male.

*Type locality*.—Fabyans, Coos County, New Hampshire.

*Characters*.—Larger than *S. innuitus innuitus*, with larger skull, longer hind-foot (20 mm.) and tail. Apparently more like *S. i. medioximus*.

Colour of upper parts sepia-brown, "quite thickly interspersed with black-tipped hairs"; side glands marked by white patches. Under parts greyish-white. Ears internally slightly darker than general colour of upper parts; a few hairs at bases of ears and on sides of cheeks light chestnut. Tail sharply bicoloured, dorsally and ventrally concolorous with the body.

Skull larger and longer than that of *S. i. innuitus* with longer and narrower interorbital region; rostrum longer and stouter; braincase lengthened posteriorly; larger incisive foramina; deeper post-palatal pits and more conspicuous median sloping septum; and longer and more rounded auditory bullæ. Cheek-teeth as in *S. innuitus*.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—No material.

Genus : **3. MYOPUS** Miller.

1844. *Myodes* Lilljeborg, Ofversigt af Kongl. Vetenskaps-Akad. Förhändl. Stockholm, 1, p. 33 (in part).  
 1910. *Lemmus* Trouessart, Faune Mamm. d'Europe, p. 199 (in part).  
 1910. *Myopus* Miller, Smithsonian Miscell. Coll., 52, p. 497.

*Genotype*.—*Myodes schisticolor* Lilljeborg.

*Range*.—Southern Norway and Sweden eastwards across Russia and Siberia to the Sea of Okhotsk. Apparently strictly confined to the fir forests of northern Europe and Asia.

*Characters*.—External form vole-like, but a little more thick-set than in *Synaptomys*. Fur soft and dense; colour slaty black with a more or less intense, extensive, and well-defined rufous mantle. Ears small but well developed, rounded, provided with a meatal valve ("antitragus"), and well haired within and without; projecting very little beyond the fur. Hands and feet slender, nearly as in normal voles; the fore-claws not enlarged but shorter and more slender than those of the hind-foot; the palms and soles with well-developed pads and not exceptionally hairy. In the hand the thumb is small and is furnished with a large flattened nail, resembling though smaller than the thumb-nail of *Lemmus*; the two longest digits (III and IV) are subequal and have long metacarpals which slightly exceed the phalanges taken together in length; digits II and V are considerably shorter and subequal; the ungual phalanges of all the fingers are small and normal, much shorter than the combined lengths of the first and second phalanges. Palms naked, save for a few scattered and minute hairs, granulo-tuberculate, with four well-developed pads (that normally present at the base of the thumb being absent), of which the postero-external is larger and more elongate than usual. Hind-foot with normal claws and digits; soles densely haired behind the pads, naked and like the palms in front; plantar pads six, the four anterior at the bases of the digits large and somewhat crowded, the two posterior small and rounded. Tail short, slightly longer than the hind-foot, rather densely clothed but the annulations not quite concealed; terminal pencil slender and about half the length of the vertebral portion or tail proper. Mammæ, 2 — 2 = 8.

Skull in all essential respects similar to or approaching that of *Lemmus*. It is distinguished by its smaller size and lighter build; the zygomatic arches are a little less widely expanded, but the jugals are somewhat more reduced; the braincase is a little narrower, the squamosals more widely separated anteriorly, and the posterior or intertemporal breadth of the frontals is much greater; the supratympanic fenestra of each squamosal is very small, smaller than in *Lemmus*. The rostrum is shorter than in *Lemmus*, but more slender than in *Synaptomys*, the anterior palatal foramina being large as in the latter genus. The cheek-teeth are relatively heavy, the length of a tooth-row



equalling or exceeding that of the diastema. In the rapid posterior divergence of the tooth-rows, the structure of the hinder part of the palate, the choanæ, pterygoid fossæ, and basis cranii, as well as in the shortening of the post-glenoid region, *Myopus* closely resembles *Lemmus*. The auditory bullæ are, however, more globular, like those of *Synaptomys* in shape, but smaller and less closely approximated below; their internal structure is essentially as in *Synaptomys*, but the walls of the bullæ are more densely spongy and the trabeculæ passing between them and the petrous portion are finer and more numerous; the canaliculus tympanicus is very slender where it passes through the stapes, but it appears to be ossified at this point as elsewhere.

Mandible and dentition essentially as in *Lemmus*; incisors relatively slender, their enamel pale yellow; upper incisors "orthodont," their anterior faces nearly flush with the tips of the nasals. Cheek-teeth exactly like those of *Lemmus* in pattern; but  $m^3$  usually shorter and broader in relation to  $m^1$  and  $m^2$ , its elements more crowded antero-posteriorly; in  $m_3$  the outer infold occasionally fails to close off an external triangle, a variation recalling the subgenus *Mictomys* but never seen in *Lemmus*.

*Geographical differentiation.*—Our knowledge of this interesting and well-marked genus has increased greatly in recent years. Originally described from Scandinavia it was next detected by Middendorff on the coast of the Sea of Okhotsk, a circumstance which led both Middendorff and Lilljeborg to conjecture that the range of these peculiarly rare lemmings extended right across northern Europe and Asia. Middendorff's record was, however, generally doubted or ignored until 1912, when Hollister described a species *M. morulus* from the Altai. A little later I described another (*M. saianicus*) from the Syansk Mountains 600 miles further east, and in the same year, 1914, G. M. Allen gave an account of yet another species (*M. thayeri*) inhabiting North-east Siberia. Quite recently Vinogradov has re-examined Middendorff's original material from the Sea of Okhotsk together with other specimens since obtained in N. Amur Land and on the eastern shore of Lake Baikal; and upon the basis of this material he has established his *M. middendorffi*. The same observer has also found that a fossil lemming, of which skeletons and soft parts frozen in the ice-bound soil of a cave in Northern Siberia were found by Tscherski, who originally described them as *Myodes brandti*, is a member of the present genus.

The characters separating the six forms now recognized are comparatively slight, relating chiefly to the greater or less development of the mantle, the size of the skull, the size and degree of inflation of the auditory bullæ and the strength of the incisors and cheek-teeth. On the whole *M. saianicus* appears to be the most specialized form. Allen remarks that "it seems likely that the Altai and the Syansk forms must be very closely related, and both perhaps hardly more than subspecies of *M. schisticolor*

of Europe." I am now inclined to go further and think it probable that all the known forms of *Myopus*, recent and fossil, will

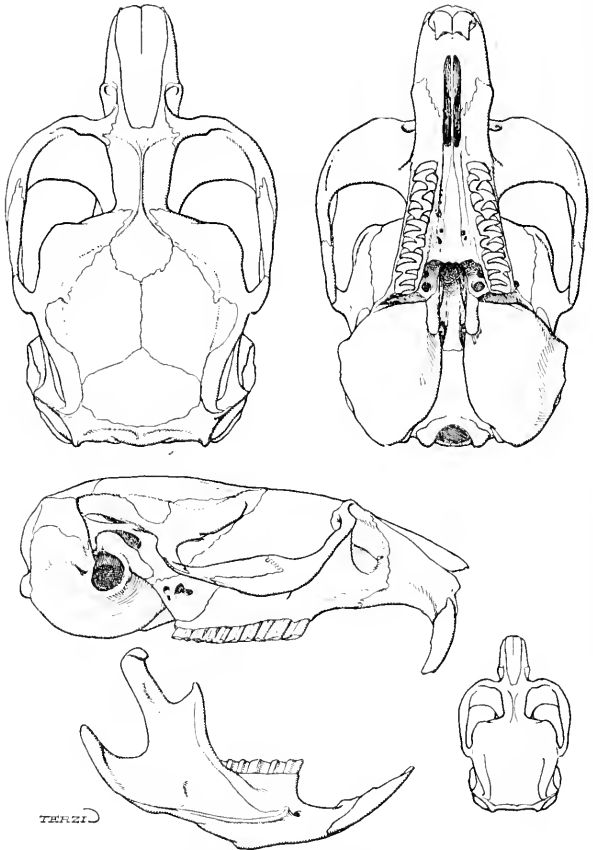


FIG. 74.—*Myopus saianicus* Hinton.

Dorsal, ventral, and lateral views (enlarged) of the skull of the type; the small outline is a natural-sized representation of the skull in dorsal view.

eventually have to be treated as subspecies of *M. schisticolor*; but as four of the six are unknown to me personally I refrain from making such a drastic reduction on the present occasion.

1. *Myopus schisticolor* Lilljeborg.

1844. *Myodes schisticolor* Lilljeborg, Ofversigt Kongl. Vetenskaps-Akad. Förhändl. Stockholm, 1. p. 33.  
 1910. *Lemmus schisticolor* Trouessart, Faune Mamm. d'Europe, p. 199.  
 1911. *Myopus schisticolor* Collett, Norges Pattedyr, p. 130; Miller, Catal. Mamm. W. Europe, p. 611.

*Type*.—Stockholm Museum.

*Type locality*.—Near Lillehammer at north end of Mjosen, Gudbrandsdal, Norway.

*Range*.—Southern Norway and central Sweden eastwards into Finland and Russia. Apparently confined to the fir forests.

*Characters*.—Size rather small, head and body about 100 mm.,

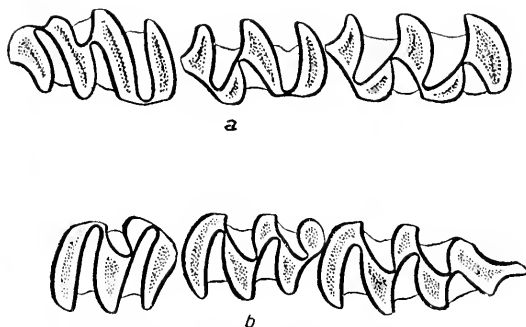


FIG. 75.—*Myopus schisticolor* Lilljeborg.

Crown views of molars: *a*. right upper, *b*. left lower teeth.

hind-foot 15–16 mm., condylo-basal length about 24. External characters as described above under the genus. Mantle represented by a broad, rather ill-defined, reddish-brown area on the centre of the back extending from the shoulders backwards to within about 15 mm. of the base of the tail. Remainder of the coat a uniform dark slaty-grey, slightly paler on ventral surface; upper surface with a peculiar metallic lustre produced by the silvery tips of the shorter hairs and less obviously lined by the longer black hairs. Feet and tail black, but hairs on under surface with a silvery lustre.

Skull and teeth as described above under the genus; distinguished by slightly smaller size, smaller auditory bullæ, and weaker upper incisors from the forms inhabiting eastern Asia.

For *cranial and external measurements*, see tables at end of volume.

*Remarks*.—Collett (Norges Pattedyr, 1911, p. 133) notes that

the colour is nearly uniform in both sexes at all seasons; but both the fur and the silvery hair-tips are a little longer in winter than in summer. It seems to be a rare animal leading a retired life in the dark recesses of the fir forests, and is usually taken only by accident, except in years of mouse-plague, when it becomes somewhat more numerous. Its runs are found in moss under the roots of trees or beneath fallen trunks. The food consists of mosses (*Dicranum*), stems of red wortleberry, and the bark of juniper.

## 2. *Myopus morulus* Hollister.

1912. *Myopus morulus* Hollister, Smithsonian Miscell. Coll., 60, No. 14, p. 1.

*Type*.—U.S. Nat. Mus., No. 175,197; adult male, skin and skull, collected August 16, 1912, by N. Hollister.

*Type locality*.—Tapucha, 125 miles S.E. of Bijsk, Altai Mountains, Siberia. Altitude, 6875 feet.

*Range*.—Known only from the type locality.

*Characters*.—Size as in *M. schisticolor*; hind-foot 16 mm.; condylo-basal length 22.7. Colour darker and blacker; rusty mantle duller but more extensive, extending forwards between ears to crown of head, becoming more intense in colour posteriorly, and broadening to cover lower back between hips. Face between eyes, cheeks, sides, and under parts dark slate grey; the nose slightly lighter. Hands like sides. Feet and tail black.

Skull like that of *M. schisticolor*, but distinguished by its smaller and much flatter bullæ.

Incisors weaker. Cheek-teeth compressed laterally, with rounded enamel loops, and slightly smaller though of about the same length as in *M. schisticolor*.

For *cranial and external measurements*, see tables at end of volume.

## 3. *Myopus saianicus* Hinton.

1912. *Lemmus obensis* Thomas, Ann. Mag. N.H., [8], 9, p. 401. Not of Brants, 1827.

1914. *Myopus saianicus* Hinton, Ann. Mag. N.H., [8], 13, p. 343.

*Type*.—B.M., No. 12.4.1.126; adult male, skin and skull, collected June 12, 1910, by Douglas Carruthers.

*Type locality*.—Syansk Mountains, 100 miles west of Lake Baikal, Central Asia. Altitude, 2200 feet; trapped "in wet moss."

*Range*.—Known from the Syansk Mountains and from the forest area bordering the northern Gobi desert in Northern Mongolia, whence it is recorded by G. M. Allen (Amer. Mus. Nov., No. 133, 1924, p. 2).

*Characters*.—Size as in *M. schisticolor*, hind-foot 16 mm., condylo-basal length 25.8 ±.

General colour considerably lighter and brighter than in *M. schisticolor*, the rusty mantle more extensive, as in *M. morulus*.

Ground-colour of the rest of the body dark grey or slate, lightened by silver hairs, which are abundant everywhere, and particularly so on the ventral surface; a few silver hairs also appear through the rusty mantle in the neighbourhood of the rump. Hands concolorous with sides. Feet dark brown (near "sepia") above, buffy brown below. Tail black above, buffy brown below.

Skull, compared with that of *M. schisticolor*, with the rostrum shallower and longer, the diastema a little longer, and the nasals less steeply inclined. Squamosals more closely approximated anteriorly, indicating an increased development of the anterior portions of the temporal muscles apparently in correlation with larger molars; the distance between the squamosals in front 1.1 mm. instead of 2.3 as in an equal-aged skull of *M. schisticolor*; the bistephanic width 3.9 instead of 4.7. Posterior edge of palate gently convex centrally, instead of being furnished with a small median spinous process. Pterygoid fossæ shorter. Auditory bullæ greatly enlarged and globosely inflated.

Upper incisors slightly stronger and a little more recurved than in *M. schisticolor*, in section more closely resembling those of *Lemmus*. Cheek-teeth noticeably larger and broader but exactly like those of *M. schisticolor* in form.

For *cranial and external dimensions*, see tables at end of volume.

*Remarks.*—The type is the only specimen known to me, but G. M. Allen has lately referred to this species a fine series of fourteen from the neighbourhood of Urga and four from Sain Noin Khan, Northern Mongolia, obtained by the Second and Third Asiatic Expeditions of the American Museum.

#### 4. *Myopus middendorffi* Vinogradov.

1853. *Myodes schisticolor* Middendorff, Sibirische Reise, 2, Th. 2, p. 108.

1922. *Myopus middendorffi* Vinogradov, Ann. Mus. Zool. Acad. Sc. Russ., 23, pp. 374 (name only), 512.

*Type.*—Zool. Mus. Acad. Sc. Russia (Leningrad), No. 72; collected August 19, 1845, by Wosnessensky. (Skin and imperfect skull.)

*Type locality.*—Aldoma River, near Ayan, west coast of the Sea of Okhotsk.

*Range.*—From the Okhotsk coast and northern Amur Land westwards to the eastern shore of Lake Baikal. Vinogradov records the "type locality" as "upper course of the river Maly (Small) Okonon, Yablanovy Ranges, Northern part of Amour-Land," but gives the locality of the type specimen as "Aldoma River, etc.," as quoted above. He states also that the species occurs on the Bargusinsky Range, east coast of Lake Baikal.

*Characters.*—Hind-foot 15-16.3 mm.; condylo-basal length 25-26.2 mm. Like *M. thayeri*, but with the rufous mantle more

developed, extending over the upper surface from the forehead to the base of the tail and to the flanks; the precise hue of the mantle varies from a shade between "sayal-brown" and "russet" to one between "vernon-brown" and "mars-brown." Forehead (and sometimes the whole upper surface of the head), cheeks, shoulders, flanks, thighs and lower rump grey, intermediate between "neutral grey" and "drab." Ventral surface between "pale smoke grey" and "pale neutral grey." Hindfeet a little narrower and with less developed nails than in *M. thayeri*; more robust and with more prominent plantar tubercles than in *M. schisticolor*; "cinnamon drab" or else "light neutral grey" to "drab-grey" above. Tail less hairy than in either *M. schisticolor* or *M. thayeri*; above coloured like the feet but darker, below very light grey.

Skull slightly larger than that of *M. schisticolor* and *M. morulus*; most closely resembling that of *M. saianicus*. It agrees with the latter in the large size and convexity of the auditory bullæ; but differs in having the squamosals more widely separated anteriorly (by 2-3 mm., instead of 1.1; bistephanic breadth 4.3-5 instead of 3.9); and in the palate being furnished with a posterior median spinous process.

Upper incisors robust as in *M. thayeri* and *M. saianicus*; cheek-teeth not peculiar.

For cranial and external measurements, see tables at end of volume.

*Remarks.*—This form, as was to be expected, has now been shown by Vinogradov to be more nearly related to the neighbouring species *M. saianicus* and *M. thayeri* than to the more western members of the genus (*M. morulus* and *M. schisticolor*). Vinogradov calls attention to the well-developed interorbital crest and to the divergent lachrymal crests which extend from the anterior end of the interorbital crest to the anterior angles of the orbits in *M. middendorffi*; those crests are, of course, developed in fully mature specimens of all the species, and they merely indicate that Vinogradov has been fortunate enough to work with really mature material.

##### 5. *Myopus thayeri* G. M. Allen.

1914. *Myopus thayeri* G. M. Allen, Proc. New Engl. Zool. Club, 5, p. 58.

*Type.*—Mus. Comp. Zool. Harvard Univ., No. 15, 264; adult male, skin and skull, collected March 28, 1912, by J. Koren.

*Type locality.*—Nijni Kolymsk, near the mouth of the Kolyma River, N.E. Siberia.

*Range.*—Known only from the type locality.

*Characters.*—Size as in *M. schisticolor* or slightly larger, hind-foot 18 mm., condylo-basal length 25.8, dorsal rufous mantle practically absent. Fur (in winter pelage) remarkably thick

and long, attaining a length of 23 mm. on back, slightly shorter on head; ears quite hidden. Entire pelage "deep neutral grey," lined with white hairs, which predominate ventrally; hairs of the mid-dorsum with a faint subterminal band of "russet" giving a faint tinge to that region, but imperceptible except on close inspection. Feet thinly haired, "drab" with a silvery tinge. Tail like the body above, whitish below. At the wrist, ventrally, is a cluster of stiff whitish hairs, which, however, do not cover the palm; tarsus well clothed with pale brownish hair.

Skull slightly larger than in *M. schisticolor* and *M. morulus*;  $m_3$  with outer triangle closed.

For *external and cranial measurements*, see tables at end of volume.

### 6. † *Myopus brandti* Tscherski.

1879. *Myodes brandti* Tscherski, *Извѣстія*—Bull. E. Siber. Sect. Russ. Geogr. Soc., 10, Nos. 1-2, p. 22.

1892. *Lemmus obensis* Tscherski, *Mém. Acad. Imp. Sci. St. Petersb.*, [7], 40, p. 12.

1922. *Myopus brandtii* Vinogradov, *Ann. Mus. Zool. Acad. Sc. Russia*, 23, p. 373.

*Type*.—Zool. Mus. Russ. Acad. Sc. Leningrad, No. 1731; rostral and palatal part of a skull with the molar series of the left side, a piece of skin with the left fore-foot, and the right fore-foot covered with skin.

*Type locality and horizon*.—Cavern of Nishne-Udinsk, East Sayan, 90 kilometres N.W. of Irkutsk, Siberia. Pleistocene (soft parts preserved in the frozen soil of the cave).

*Range*.—Known only from the type locality and horizon.

*Characters*.—Fore-claws and skeleton of manus as in the genus; thumb-nail truncated distally without any incisure. Salient angles of inner sides of upper molars sharp and not truncated as in other species of *Myopus* or *Lemmus*; crown of  $m^1$  narrower than that of  $m^2$ . Incisors more robust than in *M. schisticolor*; rostrum of the same length and palate furnished with a small median spinous process behind as in the latter species.

For *cranial measurements*, see table at end of volume.

*Remarks*.—Although Tscherski came to the conclusion that his *Myodes brandti* was indistinguishable from *Lemmus obensis* the details recently published by Vinogradov prove conclusively that this interesting fossil is a member of the genus *Myopus*. Its specific characters, however, are not very clear, and it is to be hoped that further material will be acquired in order that the precise relations of the fossil with the living forms may be determined.

Genus: 4. **LEMMUS** Link.

1758. *Mus* Linnæus, Syst. Nat., ed. 10, 1, p. 59 (in part).  
 1777. *Glis* Erxleben, Syst. Reg. Anim., 1, p. 371 (in part). Not of Brisson, 1762.  
 1795. *Lemmus* Link, Zool. Beytr., 1, pt. 2, p. 75.  
 1811. *Hypudæus* Illiger, Prod. Syst. Mamm., p. 87 (in part).  
 1811. *Myodes* Pallas, Zoogr. Rosso-Asiatica, 1, p. 172 (in part).  
 1821. *Marmotta* Blumenbach, Handbuch d. Naturgesch., 10th Aufl., p. 86. Not of Frisch, 1775.  
 1827. *Hypudæus* Lesson, Man. Mamm., p. 276 (in part).  
 1896. *Lemmus* Miller, N. Amer. Fauna, No. 12, p. 36.

*Genotype*.—*Mus lemmus* Linnæus.

*Range*.—Circumpolar. Northern Europe and Asia, from Scandinavia to Kamtschatka, northwards to Novaya Zemlya and the New Siberian Islands. In the late Pleistocene period southwards and westwards in Europe to Ireland, Great Britain, and to the Pyrenees and Alps. In North America from the Pribilof Islands and Alaska eastwards to Baffin Land.

*Characters*.—External form, skull, and dentition highly modified for fossorial habits and for subsistence upon a coarse and but slightly nutritious vegetable diet. Fur dense and long; coloration usually much more brilliant than in *Synaptomys* and *Myopus*.

General form much heavier and stouter than usual in voles, the head relatively large very broad and somewhat flattened, the neck, limbs and tail very short and muscular, the hands and feet very broad. Eyes small. Ears small, though larger than in *Dicrostonyx*, completely hidden in the fur and destitute of meatal valves. Hands large and broad with short stout fingers; thumb very short, provided with a large flattened strap-shaped and distally truncate nail; other digits armed with large simple claws, sharper or blunter according to the degree of use, but considerably longer than those of the hind-foot; in the two longest fingers (III and IV, of which III is slightly the longer) the metacarpals are much shorter than the phalanges measured together, and in all the fingers the unguis phalanges are somewhat longer than the combined length of the first and second phalanges. Palms, to the bases of the digits, densely clad with stiff hairs, about 3 mm. in length. Palmar tubercles reduced usually to a single functionless vestige placed at the bases of digits III and IV.<sup>1</sup> Feet short and broad with five digits, of which II, III, and IV are longer and subequal (III being the longest), and I and V considerably shorter, provided with

<sup>1</sup> Occasionally the reduction of the palmar pads does not proceed so far. In one specimen of *L. lemmus* before me there are four vestigial pads on each palm arranged as in *Synaptomys* and *Myopus*, three alternating with the bases of digits II to V, the fourth being a minute postero-external or carpal pad.



strong, simple claws of large size, though distinctly smaller than those of the fingers. Soles densely clothed with stiffened hairs like the palms. Plantar tubercles reduced usually to four vestigial pads occupying their normal positions at the bases of contiguous digits.<sup>1</sup> Tail slightly shorter than the hind-foot, robust and clavate, its diameter greater in the terminal third than at the base, clothed with long stiff hairs which do not completely conceal the rather narrow and ill-defined annulations; terminal pencil about half the length of the caudal vertebrae. Mammae,  $2 - 2 = 8$ .

Skull (Fig. 76) massively built, somewhat depressed, and very broad; with long, stout and sharply deflected rostrum; widely and abruptly spreading zygomata; short, broad and depressed braincase which appears to be pressed forwards, encroaching upon the orbito-temporal vacuities to a greater extent than in other members of the subfamily (*Myopus* alone excepted); the post-glenoid region strikingly shortened. Nasals more or less broadly expanded anteriorly, where they end slightly behind the front faces of the incisors; behind they terminate in line with the premaxillaries, slightly in front of the anterior margins of the orbits. Zygomata very strong and heavy, given off from the base of the rostrum at right angles, widely expanded, the greatest zygomatic breadth occurring in front on the maxillary portions of the arches and equal to about 68% of the condylo-basal length; each zygoma formed for more than half its length by the maxillary zygomatic process which expands distally into a broad fork clasping the broad but short jugal; upper border of jugal boldly convex, the jugal and maxillary process together forming a broad, central, fusiform expansion of the zygoma; the outer surfaces of these central expansions are obliquely inclined and sharply convergent dorsally, so that they partly roof the orbito-temporal vacuities and appear broadly in the dorsal view of the skull; the squamosal root of each zygoma is much lighter, its lower border being, however, widened and flattened as a facet for the origin of the posterior portion of the masseter medialis muscle, and it is given off from the side of the braincase at a right angle. Infraorbital canal nearly normal; its inferior slit-like portion somewhat reduced by the alveolar capsules of the upper incisor and  $m^1$ ; its wider upper portion transmits a small slip of the masseter medialis as usual, the origin of the muscle just impinging upon the hinder and lower edge of the ascending branch of the premaxilla; the outer wall of the canal, giving origin to the masseter lateralis, is very broad and in consequence of the abrupt anterior expansion of

<sup>1</sup> Usually there is no trace of the tarsal pads, but in the Lemming mentioned in the preceding footnote there are five vestigial plantar tubercles, the fifth being postero-internal and representing the inner of the two tarsal pads normally present in Muridae. In this specimen both the palmar and plantar tubercles, although very small, are not concealed by the dense hair, and therefore they cannot be said to be altogether functionless.

the zygoma looks more directly forwards than in other members of the group. Interorbital region in fully adult skulls rather long and narrow; shorter and broader in young adults. Tem-

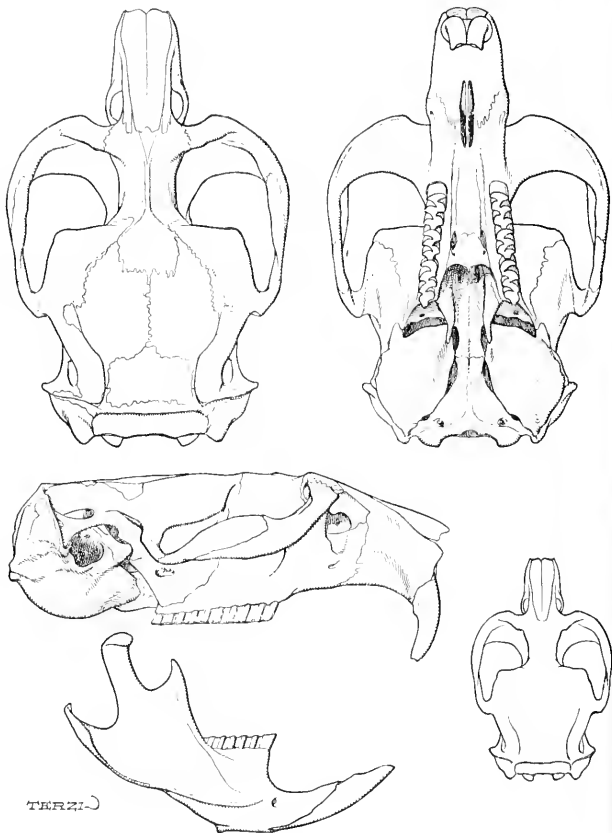


FIG. 76.—*Lemmus lemmus* Linnæus.

Dorsal, ventral, and lateral views of skull; the small figure shows the skull in dorsal view, natural size.

poral ridges in adults fusing into a sharp and salient median interorbital crest; in their backward course over the braincase the ridges, sharply salient throughout, diverge to points in line with the front edges of the glenoid articulations; thence they are convergent to the hinder part of the parietal region, where

they become rather closely approximated, and then more slowly diverge again to their junctions with the occipital crest. The ridges are situated throughout the greater part of their course upon the upper edges of the squamosals; as the ridges become more and more approximated throughout their course with advancing age the squamosals encroach progressively and at a corresponding rate upon the frontals, parietals, and interparietal; in old age the squamosals are separated in front by only a very small interval, and the posterior or intertemporal breadth of the frontals and the area of the dorsal surface occupied by the parietals and interparietal are very greatly reduced. Squamosals

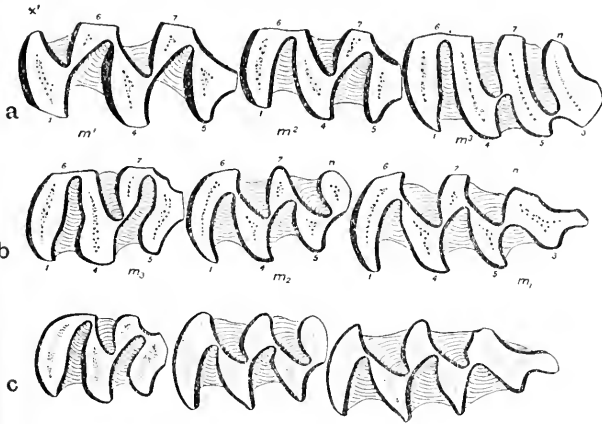


FIG. 77.—*Lemmus lemmus* Linnaeus.

Cheek-teeth (crown views): *a.* right upper, *b.* left lower molars arranged and lettered to show the homologies of the cusps. Recent.  
*c.* Left lower molars of a fossil jaw from the Doneraile Cave, Co. Cork, Ireland. Pleistocene.

anteriorly forming large post-orbital crests which form the somewhat squared shoulders of the braincase; posteriorly their supratympanic portions are very short and broad; supratympanic fenestra on each side very small and more forwardly placed than in voles. Lambdoid crest very salient laterally and formed chiefly by the hinder edge of the supratympanic portions of the squamosals, the lateral processes of the supraoccipital being very short. Occiput rather low and depressed, somewhat oblique in old age, with strongly developed median and lateral crests.

In ventral view the rostrum is conspicuously longer than in *Synaptomys* and *Myopus*, its greater length being due to the relatively larger incisors; in the two genera just named the diastema is barely equal to or even less than the length of the

molar series; but in *Lemmus*, with still heavier teeth, the diastema is considerably longer than the tooth-row. Anterior palatal foramina rather small; somewhat shorter and much narrower than in *Synaptomys* and *Myopus*. Cheek-tooth rows rapidly divergent posteriorly. Palate posteriorly essentially as in *Microtus*, but the posterior median sloping septum is represented merely by a short, broad and free spinous process, the inner margins of the post-palatal pits effecting a junction with the base, instead of with the tip of the median process, relatively far forwards and under the cover of the lateral bridges. Mesopterygoid fossa very short and broad. Hamular processes of pterygoids short, thickened, and closely applied to the eustachian portions of the auditory bullæ. Pterygoid fossæ unusually short and deep; their floors conspicuously dorsal to the ventral surface of the basisphenoid. Basisphenoid and fore-part of basioccipital relatively broad. Auditory bullæ ovate or pyriform, their inner borders very slightly convex; mastoid portion and tegmen tympani noticeably though slightly inflated; external meatus produced as a very short but rather well-marked tube; internal structure of bulla essentially as in *Synaptomys* and *Myopus*, but the spongy tissue of its walls denser than in either.

Mandible with very stout horizontal rami, in correlation with the heavy cheek-teeth and wholly lingual courses of the lower incisors, and light and delicate ascending rami; condylar processes relatively long and slender; coronoid processes short and delicate; angular processes robust, the lower border of each thickened, splayed out distally as a conspicuous facet for the insertion of the anterior portion of the masseter lateralis muscle. Alveolus of lower incisor terminates on the inner surface of the jaw near the front edge of  $m_3$ ; alveolar capsules of  $m_1$ ,  $m_2$  and  $m_3$  make slight but usually noticeable protuberances just below or on the sharply salient crista masseterica.

*Dentition.*—Incisors rather deeper than broad, their enamel pale yellow in colour. Upper incisor with anterior face sharply bent into a wider outer and a narrower inner reflected portion; outer part of anterior face often with a vestigial trace of the anterior longitudinal groove; worn surface of the tooth peculiar, tubular or gouge-like, the soft dentine wearing away for a considerable distance above the cutting edge of the enamel; alveolar capsule terminating just above the palatal surface of the maxilla slightly in front of  $m^1$ . Lower incisor slender, extending backwards as far as  $m_3$ .

Cheek-teeth rootless, very broad and heavy; enamel about equally thick on convex and concave sides of salient angles, becoming thin at points of re-entrant angles, and very thin or altogether lacking at tips of salient angles; re-entrant folds partly filled with cement. Enamel pattern (Fig. 77) characterized by the inequality of the outer and inner salient angles and infolds; in upper teeth (except in the hinder part of  $m^3$ )

the outer infolds are much deeper and the outer salient angles much larger than those of the inner side; in lower teeth (except in the fore-part of  $m_1$ ) the converse is the case. In upper teeth certain of the inner salient angles are remarkably and broadly truncated; and a similar though less conspicuous truncation is shown by certain of the outer salient angles in the lower molars. The upper tooth-row is further remarkable for the great size and especially the great breadth of  $m^3$ , which is often decidedly larger than  $m^1$ . The pattern of the upper teeth is as follows:— $m^1$ , with three salient angles on each side, consists of an anterior transverse loop and four alternating closed triangles, the first and third being internal and small with truncated tips, the second and fourth being external and normally angular;  $m^2$ , with three outer and two inner salient angles, consists of an anterior loop and three closed triangles, of which the first and third are external, large, and normally angular, the second internal, small, and squarely truncated; the first outer fold in this tooth is deep and transverse, so that the junction of the first outer triangle with the anterior loop is effected on the inner border of the tooth instead of in the centre of the crown as in normal Microtines, and the first inner salient angle, made up as it is of the inner extremity of the anterior loop and the base of the first outer triangle, has accordingly a remarkable appearance of abrupt truncation; this last character is reflected in the alveolus, for the alveoli are closely moulded to the teeth, and is often of great practical importance to the palæontologist when dealing with fragmentary palates from which the teeth have fallen out;  $m^3$ , with three or four outer and three inner salient angles, consists of an anterior transverse loop followed by four triangles and a small posterior loop; of the four triangles, the first is external and exactly like that of  $m^2$ , the first outer infold being transverse so that the junction of this first triangle with the anterior loop takes place on the inner border of the tooth near the centre of the abruptly truncated first inner salient angle; the second and third triangles are opposed and confluent with each other, and shut off from the first triangle behind by a deep inner fold and a much shallower outer one; the fourth triangle is internal and confluent with the small posterior loop, which may be regarded as consisting chiefly of a fifth outer triangle; this terminal part of the tooth is separated from the parts in front by a deep inner infold and a shallow or quite vestigial outer fold. In the lower jaw  $m_1$ , with three outer and four inner salient angles, consists of a posterior transverse loop, three alternating closed triangles (of which the first is internal), and an anterior loop formed of a broadly confluent pair of triangles and a small anterior loop proper;  $m_2$ , with three salient angles on each side, consists of a transverse posterior loop and four alternating closed triangles of which the first and third are internal;  $m_3$ , with two outer and three inner salient angles,

consists of a posterior loop and three alternating triangles of which the first and third are internal; this tooth is essentially similar to  $m_2$ , but the fourth triangle or third outer salient angle is reduced and obsolete, and the first inner infold is transverse and nearly as deep as the first outer infold in  $m^2$  and  $m^3$  above, producing similar though less marked effects upon the form of the first outer salient angle and upon the relation of the posterior loop with the triangle in front.

*Geographical differentiation.*—At the present time twelve forms, referred to ten distinct species of *Lemmus* are recognized by systematists; but the characters distinguishing them are far from being satisfactorily known. The genus indeed is a very difficult one to deal with. All the forms are very closely related and vicarious. For the most part they have been imperfectly described from scanty and often unsuitable material. No single form, not even the Common Norwegian Lemming is properly represented in our collections. In view of the abundance of specimens of *L. lemmus* this last statement may seem surprising, but it can be justified in a few words.

Like so many other Microtines the members of this genus grow almost indefinitely; and they acquire sexual maturity and adult-looking coats at a very early age. In ordinary years they are not easily caught; but in "Lemming years" it is only too easy to collect long series of specimens—of a sort. In such long series the individuals are hardly ever more than adolescent. Owing to the circumstance that in this genus the temporal ridges are at the moment of their inception rather closely approximated in the interorbital region, the unsatisfactory nature of our abundant material is not at first sight apparent; because the ridges meet and fuse to form a weak interorbital crest much sooner than they do, for example, in *Arvicola*, and the skull therefore acquires an adult appearance long before the Lemming is really grown up. In all the long series of skulls of *L. lemmus* that I have examined there is but one (B.M. 7.7.7.3260 Kola Peninsula; ex Miller Collection) that can be regarded as tolerably adult; and that a skull even in that stage of growth may be greatly modified with advancing age will be readily apparent from an inspection of Pl. VI, where it is compared with a fragmentary but mature skull of *L. obensis* from the island of Waigatsch. The latter specimen, which I owe to the generosity of the late Dr. Forsyth Major, transformed as it is by long-continued growth has not yet reached the limit of possible development; its sutures are still open, although they have now acquired the tortuous courses characteristic of late stages of growth, and the dentinal pulps and enamel organs of the cheek-teeth were still vigorously active at the moment of the animal's death. Comparing such a skull with those "fine series" upon which the numerous species described in recent years have been based, we find it not difficult to appreciate why in this genus the skull

has given so little help to the systematist and why the species of *Lemmus* are still so imperfectly understood.

The described forms fall into two well-marked groups distinguished by the colour-pattern of the dorsal surface. In the first group, characterized by its striking chequered dorsal pattern of intense black and brilliant yellow, there is only a single form, the Norwegian Lemming inhabiting Scandinavia and ranging eastwards to the western shore of the White Sea. The second group, characterized by its more sober, essentially uniform dorsal pattern, variegated at the most by a more or less distinct black dorsal stripe on the head and neck, by an indistinct lateral streak on each side of the head, and by anterior dullness and posterior brightness or intensity of colour, comprises all the remaining eleven forms. Of these, five range vicariously through northern Europe and Asia, from the eastern shore of the White Sea to Kamtschatka, one inhabits the Pribilof Islands, and five the North American continent, ranging from Alaska eastwards to the Cumberland Peninsula, Baffin Land, and southwards to Alberta and the southern shore of Hudson's Bay. Some of these members of the second group, e.g., *L. yukonensis* with its greatly enlarged auditory bullæ, *L. nigripes* with its black feet, and *L. o. novosibiricus* subject to remarkable seasonal changes (paralleling those normal in *Dicrostonyx*) in its high northern station, are quite strikingly different from normal *L. obensis* in certain respects. But in all essential structural characters and in the general colour scheme they are not more widely different, so far as the available material and descriptive literature permit one to form a judgment, from each other and from typical *L. obensis* than are the subspecies of *Microtus agrestis* or those of *Evotomys rufocanus* from each other.

The latter species affords indeed (as explained below) a very close analogy to the present case. It is possible that really adult material will reveal more important differences between the members of the present group than those now apparent; and in the absence of such material I propose to leave things as I find them. But in my opinion it is most probable that all the forms in question will have to be treated as subspecies of *L. obensis* hereafter, and that we shall revert, with fuller knowledge and no doubt for better reasons, to the views of an earlier generation.

Fossil remains of *Lemmus* occur abundantly in the later Pleistocene deposits of the British Isles and Western Europe; but the material is fragmentary and after a close study of it extending over many years I am not prepared to determine any of these fossils specifically.

### 1. *Lemmus lemmus* Linnæus.

1758. *Mus lemmus* Linnæus, Syst. Nat., 10th ed., 1, p. 59.  
 1777. *Glis lemmus* Erxleben, Syst. Reg. Anim., 1, p. 371.

1795. *Lemmus lemmus* Link, Zool. Beytr., 1, pt. 2, p. 75.  
 1811. *Myodes lemmus* Pallas, Zoogr. Rosso-Asiat., 1, p. 172.  
 1820. *Lemmus borealis* Nilsson, Skand. Faun., 1, p. 185 (substitute for *lemmus*).  
 1821. *Marmotta lemmus* Blumenbach, Handb. Naturgesch., 10<sup>te</sup> Aufl., p. 86.  
 1822. *Lemmus norvegicus* Desmarest, Mamm., 2, p. 287.  
 1827. *Hypudæus norvegicus* Lesson, Man. Mamm., p. 277.  
 1829. *Hypudæus norvegicus* Fischer, Syn. Mamm., p. 297 (misquoting Lesson).  
 1848. *Myodes lemurus* Gray, P.Z.S., 1848, p. 43, Sweden [misprint for *lemmus*].

*Type*.—Unknown.

*Type locality*.—Mountains of Lappmark, Sweden.

*Range*.—From sea-level upwards in northern Scandinavia and Finland, eastwards to the western coast of the White Sea. In normal years extending southwards upon the mountains, in the Birch Zone and at higher levels, to the neighbourhood of Christiansand in Norway, and to northern Wermland in Sweden. In "Lemming years" the species descends to sea-level, overrunning the coastal districts even in the extreme south of Norway.

*Characters*.—Essential external, cranial and dental characters as described under the genus; hind-foot 17 to 20 mm., condylo-basal length 27.6 to 33.

Colour brilliant; pied black and yellow above, yellow below. Hairs everywhere with dark bases, except on lips and chin where they are light throughout. Fore-part of upper surface, including the top of head and withers, black; the black area sharply defined laterally, its boundary running backwards from the tip of the muzzle along the lower borders of the eyes to the ears; thence curving upwards to the spine behind the shoulders, whence it is continued along the spine to the middle of the back or to the rump as a more or less well-defined narrow dorsal stripe. This black area is interrupted on each side by a conspicuous buffy patch which lies above the ear and is connected with the posterior canthus of the eye by a narrow buffy streak, and sometimes with the ochraceous colour of the ventral surface by a post-auricular ventral extension; sometimes these patches are continuous with each other across the nape, but usually they are separated by a black stripe which connects the solid black areas on the top of the head and over the shoulders. On the posterior half of the back a more or less sharply defined blackish streak runs backwards along the upper flank on each side and inwards over the hip to meet its fellow in a rather sharp V on the rump. Remainder of the body ochraceous or tawny; darker, mixed with dusky hair-tips, over the loins; clearer and paler on the ventral surface, lightening to pale buff or whitish on throat, chin, and upper lips. Hands and feet light buff with a more or less evident silvery gloss. Tail pale buff, with a more or



less evident sprinkling of blackish hairs above, its terminal pencil whitish.

Seasonal changes of colour inconspicuous. The winter coat is acquired gradually in September or October, and owing to the greater length of the ochraceous hair-tips the black markings, particularly on the hinder part of the upper surface, are more or less concealed. The young are born naked, pink, and blind, the eyes remaining closed until the eleventh day; a full coat resembling that of the adults in summer pelage, with the black markings sharply defined owing to the shortness of the fur, is acquired by the tenth day. In September and October the young, like the adults, gradually assume the winter dress; but occasionally all the cover-hairs are shed simultaneously, the young then appearing for a time in a uniformly dusky garb without any marked trace of the yellow parts.

For *external and cranial measurements*, see tables at end of volume.

*Range in time.*—Fossil remains of a form or forms not certainly distinguishable with available material from *L. lemmus* occur abundantly in the late Pleistocene deposits of Western and Central Europe.

The following is a list of the materials which have passed through my hands.

## A. GREAT BRITAIN.

### SOMERSETSHIRE. *Hutton Cave.*

One right and five left mandibular rami described by Sanford (Q.J.G.S., 26, 1870, p. 125, pl. viii, figs. 3a, b), who referred them to "*L. norvegicus*" var., saying, "they are, however, slightly smaller [than those of the Norwegian Lemming], and the condyle, with its neck, is slightly more slender in proportion to the size of the jaw; we cannot, with our present means of information, ascribe to these differences a greater than varietal value."

*Taunton Museum.*

### SOMERSETSHIRE. *Avclinc's Hole, Burrington Coombe.*

A large number of fragmentary skulls and mandibular rami representing at least 125 individuals collected by the Bristol University Spelæological Society (Hinton, Proc. Spel. Soc. Bristol Univ., 1, p. 75, 1921; 2, p. 35, 1923; many other specimens since obtained).

### SOMERSETSHIRE. *Cave at Uphill, near Weston-super-Mare.*

Three fragmentary mandibular rami and a detached  $m^1$ ; lent by Dr. H. C. Male.

### HEREFORDSHIRE. *Valley of the Wye; Merlin's Cave near Symond's Yat.*

Fragmentary skulls and mandibular rami representing at least 110 individuals, collected by the Bristol University Spelæological Society (Hinton, Proc. Spel. Soc. Bristol Univ., 2, 1924-1925, p. 157; many other specimens since obtained).

HEREFORDSHIRE. *Wye Valley; cave near Symond's Yat—possibly Merlin's Hole.*

Parts of three skulls, together with two right and two left mandibular rami, collected by Miss D. M. A. Bate;  $m^1$  and  $m^2$  of one of the skulls (M. 7782) and  $m_1$  and  $m_2$  of a left ramus (M. 7781) figured by Miss Bate, *Geol. Mag.*, [iv], 8, p. 104, 1901.  
*British Museum, Geol. Dept. M. 7781-7783.*

LANCASHIRE. *Dog Holes, Warton Crag, near Carnforth.*

Two palates and five mandibular rami presented by Mr. J. Wilfrid Jackson; and other material at Manchester not seen by me (Jackson, "*Lancashire Nat.*," 1909, p. 227).  
*British Museum.*

DERBYSHIRE. *Langwith Cave, near Mansfield.*

Several fragmentary skulls and mandibular rami (Rev. E. H. Mullins, *Derbyshire Archæol. and N.H. Soc. Journ.*, 1913, p. 15 of separate).

DEVONSHIRE. *Chudleigh Fissure.*

Several mandibular rami; lent by Mr. A. S. Kennard.

KENT. *Middle Terrace brickearth of Thames at Crayford and Erith.*

Some fragmentary jaws in the Spurrell Collection from Erith; and several detached teeth in various private collections from Crayford (Newton, *Geol. Mag.* [3], 7, p. 455, 1890).  
*Museum of Practical Geology.*

KENT. *Fissure deposit at Ightham, near Sevenoaks.*

Anterior part of a skull (Lewis Abbott Collection B.M.) and several mandibular rami (Newton, *Q.J.G.S.*, 50, p. 196, 1894).  
*British Museum; Museum of Practical Geology; and Collection of Dr. Frank Corner.*

## B. IRELAND.

Fragmentary jaws and teeth occur abundantly in the caves of Cos. Clare, Cork, and Sligo, associated with the remains of *Dicrostonyx*. It is a remarkable fact that, although remains of Lemmings are common in the Irish Pleistocene, no trace of a Vole living or fossil has been found in Ireland. A very large collection of fragments and detached teeth was lent to me some years ago by the Irish National Museum, in order that I might search for a Vole; on going through the lot with the utmost care I found nothing but *Dicrostonyx* and *Lemmus*.

## C. CONTINENTAL EUROPE.

Fossil remains of *Lemmus* have been found at many localities in Germany, Austria, Hungary, Russia, France and Belgium, and have been recorded by Hensel, Nehring, Woldrich and others. Nehring, who refers these remains to *L. obensis*, has given a list of such occurrences ("*Ueber Tundren und Steppen*," 1890, p. 147). I have seen lower jaws from Thiede, Brunswick (British Museum), and Kleine Schener, Wurttemberg (lent by Dr. Frank Corner), but have no other personal knowledge of the Continental fossil form.

Recently *Lemmus lemmus* has been recorded from the Pleistocene of

Cambrai, Northern France, by Dubois (Ann. Soc. Géolog. du Nord, 44, p. 93, 1919).

[Note on "*Lemmus lemmus crassidens*" Nehring.

1896. *Myodes lemmus* Barrett-Hamilton, P.Z.S., London, 1896, p. 304.  
 1899. *Myodes lemmus crassidens* Nehring, Sitzungsber. Berlin Gesellsch. naturf. Freunde, 1899, March 21, p. 55, and Wiegmann's Archiv f. Naturgesch., 56, 1, p. 175; translated Ann. Mag. N.H., [7], 4, p. 292.  
 1912. *Lemmus lemmus crassidens* Miller, Catal. Mamm. W. Europe, p. 621.

*Type*.—Cambridge University Museum, No. 866e (No. 2, Nehring); skull and part of a skeleton. *Paratypes*, No. 866e, four skulls and portions of skeletons. Presented by Dr. H. Gadow.

*Type locality*.—Caves near Athouguia, Estremadura, Portugal.

*Characters*.—Distinguished from *L. lemmus* by broader molars and alleged greater breadth of coronoid process of mandible.

*Remarks*.—This nominal subspecies is based upon some remarkable specimens believed by Dr. H. Gadow to be mummies found by him in the dusty soil of some caves near Athouguia, Portugal. Dr. Gadow collected his specimens in 1886, but seems to have paid little attention to them until the early part of 1895, when he handed them (or what he took to be them) over to Major Barrett-Hamilton for determination. On March 3, 1896, Barrett-Hamilton exhibited what was left of the mummies before the Zoological Society of London and made the following remarks:—"Thinking the remains were those of Voles I put them aside for a time; but later on, when I had an opportunity of examining them more carefully, I found, to my surprise, that they consisted of some skeletons and detached bones of the Norway Lemming, *Myodes lemmus*. When first received by me the remains consisted of a good many fragments and single bones, and of two almost complete skeletons. These latter were completely enveloped in the original skin, which had become so dried and hardened that in order to enable myself to examine the skeletons I had to get it removed. The whole appearance of the specimens was so fresh that, unaware as I was of their true character, I had the dried skin, which enveloped them like mummies, removed, so that, I regret to say, not one of these most interesting specimens has been preserved in the condition in which I received it. Some of the vertebræ, however, are still connected together by the dried remains of the ligaments. This, and the whiteness and excellent preservation of the bones, will show how easy it was to be deceived as to their nature, and to come to the belief that they were of recent origin and perhaps unimportant. . . . The present skulls resemble those of recent Lemmings very closely indeed. . . . I cannot find any characters

sufficiently important to enable me to separate the two specifically."

In 1899 Nehring published a detailed account (Wiegmann's Archiv f. Naturgesch., 56, p. 175) of these Lemming remains together with some further particulars concerning the caves at Athouguia furnished by Dr. Gadow. Finding that the cheek-teeth were relatively larger and especially broader than usual in *L. lemmus*, and fancying that he could see some differences in the form of the coronoid processes of the mandible, Nehring referred the remains to a new subspecies his *Myodes lemmus crassidens*.

The "Portuguese" Lemmings met with a mixed reception, some like Dr. Scharff (Hist. European Fauna, 1899, p. 139; European Animals, 1907, p. 97) welcoming them as corroboration of certain theories of geographical distribution, others like Dr. Forsyth Major thinking that some mistake must have been made, the occurrence of any species of *Lemmus* in Portugal being "a faunistic impossibility."

In 1912 (Catal. Mamm. W. Europe, p. 623) Miller said:—"Through the courtesy of the authorities of the Cambridge Museum I have been able to compare the original *crassidens* material with a series of seventeen skulls of true *lemmus* in the British Museum. As submitted to me this material consisted of three perfect skulls (including the type), one skull without lower jaw, one rostral portion of skull together with palate and maxillary teeth, two complete lower jaws, and one single mandible, the whole representing not less than six nor more than eight individuals. The specimens are well preserved, with most of the teeth in place, and have all the appearance of fresh material. In size and form the skulls show no peculiarities. No old individuals are represented; the measurements therefore do not attain the maximum. . . . The coronoid processes are broken at the tip, giving them the short, blunt appearance noted by Nehring. In one complete skull and the old mandible the teeth are of the same size as in ordinary average specimens of true *lemmus*; in the type they equal those of the largest-toothed Norwegian specimen in the series (from Mølmen, northern Gudbrandsdal); in one complete skull, one skull without lower jaw, and one odd lower jaw they are slightly above the maximum for *lemmus*; while in the fragmentary skull and two odd jaws they are decidedly above the maximum. That is, assuming that eight individuals are represented, three are perfectly matched among the seventeen Scandinavian specimens, while five are not. This makes it impossible at present to synonymize *crassidens* with *lemmus*. On the other hand, it seems almost equally impossible to believe that the specimens came from Portugal, and that some confusion of material did not take place during the period when Dr. Gadow's Athouguia mummies, regarded as 'unimportant,' were 'put aside.'"

In turn I am indebted to the authorities at Cambridge for two opportunities of studying this material, which tallies exactly with the description given by Miller; and as regards a comparison with Norwegian material I can only confirm Miller's observations. Some years ago I was asked by Dr. Gadow to compare "*crassidens*" with the skull of an old Lemming from the Kola Peninsula<sup>1</sup> sent over by Mr. Miller for this special purpose; but although the Kola skull is from a much older individual than any of those represented in the "*crassidens*" series its teeth are not quite so broad absolutely, while relatively they are considerably narrower since the antero-posterior dimension of each tooth, and particularly of  $m_2^3$ , is increased; other slight differences in the proportions of the skull led me, after making allowance for the difference of age, to conclude that the Kola skull could not be regarded as specifically identical with "*crassidens*." Recently, however, I have made another series of comparisons and as a result find that "*crassidens*" is probably identical with one of the subspecies of *L. obensis*; it would not be safe to attempt upon the basis of such material to identify it with any particular subspecies; but the great breadth of the molars, the relative shortness of  $m_2^3$ , and the cranial proportions seem to me to be exactly in agreement with *L. obensis* from the Taimyrland. How close the dental agreement is can be seen from the micrometer readings<sup>2</sup> recorded in the table on p. 200.

One word about the condition of the remains may be permitted. It has been suggested to me that these Lemmings are old dried-up spirit specimens which by some mischance were substituted for the mummies collected by Dr. Gadow; but I do not think that can be the explanation, because the skulls have not the appearance so characteristic of specimens that have been immersed in alcohol. In condition they are exactly like the skulls of naturally mummified Lemmings that I have from time to time received from friends visiting Norway. At the same time I think that some such substitution must have been made, either between 1886 and 1895, when the material was in Dr. Gadow's possession, or between 1895 and 1896, when Major Barrett-Hamilton put the mummies aside.

Since the above note was written Miss Bate has kindly supplied me with references to two papers by Harlé which confirm the opinion expressed above.

One of the collectors of the Geological Survey of Portugal, Ramão de Souza, was sent to Athougua with instructions to search the caves thoroughly for Lemming remains. He found nine caves mostly of small size, and by means of careful digging and sifting made a collection of bones, all of recent species. These remains were determined by Harlé as belonging to Badger,

<sup>1</sup> Now B.M., No. 7.7.7.3620. Miller Collection (Plate VI, fig. a).

<sup>2</sup> I have not thought it worth while to reduce these readings to millimetres; 5 mm. = 44 on the micrometer scale.

MICROMETER MEASUREMENTS OF CHEEK-TEETH OF *Lemmus*.

Mm. Condylo-basal length. Dental length	<i>L. lemmus</i> .																				<i>L. obensis</i> .			<i>L. nigripes</i> .	<i>L. trimicro- natus</i> .	<i>L. helveticus</i> .	<i>L. yukonensis</i> .			
	Norway.										"Portugal."										Waigatsch.									
	78	8	8	8	8	8	8	8	8	7	3	2	1	4	5	26	26	28	27	28	28	31	19							
<i>m</i> <sup>1</sup>	24	27	26	27	23	26	24	24	28	26	26	28	27	28	26	26	28	27	28	28	31	19	27	26	24	30	24	30	17	7
<i>m</i> <sup>2</sup>	14	15	13	15	12.5	13	14	14	14	20	20	20.5	20.5	21	20	20	20.5	20.5	21	21	22.5	7.7	21	23	18	22	21	23	10	6
<i>m</i> <sup>3</sup>	9	25	10	5	10	5	10	19	23	12.5	13	13	14	=	24	26	26	25	27	13	15	3252	23	25	20	27	11	13	10	14
<i>m</i> <sub>1</sub>	12	12	11	12.5	11	12	11	12	12	13	12	13.5	13	13	27	24	26	25	27	13	16	13	12	14	11	14	12	14	11	14
<i>m</i> <sub>2</sub>	30	30	30	30	27	30	30	32	32	30	31	31	33	31	32	30	31	33	31	35	=	=	31	30	26	33	31	30	14.5	14.5
<i>m</i> <sub>3</sub>	15	13	12.5	14.5	12.5	13	13	14	14	14	14	15	15	15	24	20	20	21	21	22	=	=	21	21.5	18	23	21	21.5	11	14
	20	20	19	21	17	19	19	24	24	13	13	13	14	13	13	13	13	13	14	14	=	=	12	14	11	14	12	14	11	14
	12	12	11	13	11	12	11	12	12	18	20	20	19	19	18	18	20	19	19	22	=	=	20	22	18	23	20	22	18	23
	12	11	11	13	10	12.5		12	12	13	12	13	14	13	12	12	13	14	13	15	=	=	12	13	11.5	15	12	13	11.5	15
	28.3	27.9	=	=	=	=	=	30.5	33	29.1	29.2	29.9	30.1	=	29.1	29.2	29.9	30.1	=	30	=	=	30	=	=	31.1	30	=	=	31.1
	18.7	19	=	=	=	=	=	19.6	22.3	19.4	19.9	20	19.9	21.3	19.4	19.9	20	19.9	21.3	20.1	23	19.6	19.6	=	=	17.6	19.6	=	=	20.5

44 = 5 mm.  
Micrometer Readings.

Goat, Rabbit, Shrews, Mice and Voles. No trace of a Lemming was found, and Harlé concludes that the "mummies" described by Barrett-Hamilton certainly did not come from Portugal. (HARLÉ, Bull. Soc. géol. France, 1909, p. 85, and Commun. Comm. Serv. Geol. Portugal, 8, 1910-11, pp. 52, 81.)

## 2. *Lemmus obensis* Brants.

(Synonymy under subspecies.)

*Range*.—Northern Europe and Asia, from the eastern shore of the White Sea eastwards to Kamtschatka and the shores of the Sea of Okhotsk; northwards to the islands of Waigatsch, Novaya Zemlya, and the New Siberian Archipelago; southern limits of range unknown.

*Characters*.—Essential external, cranial, and dental characters as in *L. lemmus*. Colour pattern normal or subdued; upper surface nearly uniform dark reddish or yellowish-brown, often with a rather well-defined black median stripe extending backwards from the top of the head for a variable distance along the spine, and with a less obvious blackish streak, on each side, extending from the tip of the muzzle backwards over the eye to the ear. Flanks more or less tawny or ochraceous. Under surface whitish or yellowish darkened by the slaty bases of the hairs. Hands, feet and tail usually pallid; tail indistinctly bicoloured, brownish above, buffy below.

### 2a. *Lemmus obensis obensis* Brants.

1779. *Mus lemmus* Pallas, Nov. Sp. Quadr. Glir. Ord., p. 186.  
 1811. *Myodes lemmus* var. *minor* Pallas, Zoogr. Rosso-Asiatica, 1, p. 173.  
 1827. *Myodes obensis* Brants, Ges. d. Muizen, p. 55; Middendorff, Sibirische Reise, 2, Th. 2, p. 99, 1853.  
 1822. *Lemmus norvegicus* var. *A*, Desmarest, Mammal., pt. 2, p. 287.  
 1825. *Hypudæus migratorius* Lichtenstein, Eversmann's Reise, p. 123.  
 1924. *Lemmus obensis bungei*, Vinogradov, Ann. Mag. N.H., [9], 14, p. 186 (Nomen nudum; mouth of the Lena River).

*Type*.—Unknown.

*Type locality*.—Mouth of the Obi River, Siberia.

*Range*.—Northern Europe and Asia from the eastern shores of the White Sea, eastwards to N.E. Siberia.

*Characters*.—Summer pelage (June to September):—Fur dense, rather harsh, attaining a length of about 20 mm. on back. General colour of back dark reddish-brown, produced by the reddish and yellowish tips of the longer hairs mixed with comparatively scanty dark brown and black hair-tips and much darkened by the slaty hair bases. Upper surface of head duller and greyer, clothed by shorter white-tipped and blackish hairs. Mid-dorsal stripe present and more or less well defined, extending from the muzzle over the forehead to the region immediately

behind the shoulders, produced by a concentration of the black hairs along the spine; in some individuals more or less definite traces of this stripe can be seen between the withers and the rump. On each side of the head a faint blackish streak extends backwards from the muzzle, through the eye to the ear, where it often broadens out to form a rather conspicuous pre-auricular blackish patch. Flanks, including the upper lips and sides of face and neck, and under surface yellow or whitish; yellow and clearer laterally at the junction with the dark dorsal colour. Belly darkened irregularly by the slaty bases of the hairs. Hands, feet, and tail light brown above, paler, buffy white, below and at the sides.

Winter pelage:—According to Middendorff (Sibir. Reise, 2, Th. 2, p. 101) the winter coat, in Taimyrland in lat. 71° N., begins to appear about the middle of September and is completed by the end of October. Fur thicker and more silky than in summer. Colour paler reddish-yellow, less intensely orange, above and without trace of a median black stripe either on the head or on the back. Palms and soles more densely haired than in summer.

Young have much shorter, darker and duller coats than adults; dull blackish-brown, very lightly tinged with reddish-yellow above, the black dorsal stripe more or less evident; mouse-grey below. The young assume the adult summer pelage very early in life; and Middendorff observed it in one with a total length of only 82 mm.

Skull and teeth essentially as in *L. lemmus*; the cheek-teeth, however, in individuals of equal age, rather larger and heavier than in the latter species.

For *external and cranial dimensions*, see tables at end of volume.

*Remarks.*—Middendorff (*op. cit.*, p. 104), observed a great disproportion in the numerical representation of the sexes in Taimyrland, adult males apparently outnumbering the females by twenty-five to one, and among the nestlings males were far more numerous than the females. A good account of this Lemming and its habits in Waigatsch and Novaya Zemlya is given by Henglin (Reisen n. d. Nordpolarmeer, 3, p. 16, 1874).

### 2b. *Lemmus obensis novosibiricus* Vinogradov.

1924. *Lemmus obensis novosibiricus* Vinogradov, Ann. Mag. N.H., [9], 14, p. 187.

*Co-types.*—Zool. Mus. Russ. Acad. Sci. (Leningrad); ten specimens (skins and skulls, and a skeleton) collected by the Russian Arctic Expedition 1901–1902, the Yana Expedition of Toll and Bunge, and the Hydrographic Expedition to the Northern Ocean 1912.

*Type locality.*—“Kotelmy and Liakhov Islands, New Siberian Archipelago, N.E. Siberia.”



*Range*.—New Siberian Archipelago.

*Characters*.—Summer pelage like that of the typical subspecies, but ears more rusty yellow and sharply contrasted with the colour of the head; brownish colour of top of head extending to the lips. In winter with a superficial resemblance to winter specimens of *Dicrostonyx*, the fur almost white, the claws greatly enlarged (but not bifurcate), blunt, with enlarged horny ungual pads. Fur in winter very long and silky, light "pinkish buff," greyer on the back, paler ("cartridge buff") on the belly.

Skull compared with that of *L. o. obensis* with shorter nasals, which do not completely cover the nasal aperture in the dorsal view. Zygomatic arches less widely spreading. Interorbital crest in fully adult specimens very low or absent. Braincase large, nearly smooth and rounded even in quite adult specimens. Interparietal about half as long as wide. Auditory bullæ larger. Upper incisors more projecting; cheek-teeth heavier.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Vinogradov says that the peculiar characters of this interesting form almost entitle it to specific rank; but some of the specimens have the characters less sharply developed, and his *L. o. bungei* inhabiting the region around the mouth of the Lena is in some respects intermediate between *L. o. obensis* and *L. o. novosibiricus*. The superficial resemblance of the latter in winter to *Dicrostonyx* is no doubt, as Vinogradov suggests, a case of convergent or rather parallel evolution between two forms living under the same severe climatic conditions on the far northern border of Siberia.

## 2c. *Lemmus obensis chrysogaster* Allen.

1903. *Lemmus obensis chrysogaster* Allen, Bull. Amer. Mus. N.H., 19, p. 153.

*Type*.—American Museum N.H., No. 18762; young specimen, skin and skull, collected July 1901 by N. G. Buxton of the Jessup North Pacific Expedition.

*Type locality*.—Gichiga, west coast of Okhotsk Sea.

*Characters*.—Colour (in dried out spirit specimen) yellowish-brown above varied with black, more greyish-brown and less yellowish on the head and neck, the fulvous tint gradually increasing in brightness and amount from the shoulders posteriorly, becoming strong yellowish-rufous on the lower back and rump; sides and ventral surface orange ochraceous, paler on the throat and at base of tail; chin and sides of mouth soiled buffy white; top of nose pale dusky brown, passing posteriorly into the dull yellowish grey-brown of the upper surface of head. Feet dusky greyish-brown; claws dusky horn-colour. Ears very small, orbicular, wholly concealed. Tail very short, dusky

above; its lower surface and long pencil greyish-white. Incisors pale yellow.

In a second specimen (skin of a young adult) the colour is much darker and less ochraceous; dorsal surface dusky brown, almost blackish over the middle region of the back, with a very short tipping of pale rusty on some of the hairs, imparting a faint rusty general tint; sides ochraceous; ventral surface rusty buff, palest on throat.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—In describing this animal, Allen thought that he was dealing with the species referred long ago by Middendorff to "*Myodes schisticolor*"; but subsequent discoveries, and the re-examination of Middendorff's material by Vinogradov, show that Middendorff's animal really was a *Myopus* and Allen's conjecture wrong.

Judging from the description, *L. o. chrysogaster* is possibly most nearly related to the more recently described *L. amurensis*; it is to be hoped that a direct comparison of these two forms will be made possible in the near future.

[MYODES KITTLITZII Brandt. Middendorff (Sibir. Reise, 2, Th. 2, p. 107) says:—"Unser Akademisches Museum besitzt durch Kittlitz noch einen Lemming aus Kamtschatka, welcher von Brandt (in Tschichatscheff, Voyage Sci. dans l'Altai, p. 14) *Myodes kittlitzii* benannt, aber nicht beschrieben worden ist. Dieses Thier steht dem *Myodes obensis* höchst nahe, und wir bedürfen fernerer Materiales um zu entscheiden, ob es nicht eine seltene albinotische Varietät der obengenannten Art sein möchte. Der Balg (Wintertracht) dieses Exemplares ist durchgängig und einfartig rostgelt; er ercheint auffallend heller als selbst die Wintertracht de *Myodes obensis*, bei genauerer Betrachtung finden wir jedoch, dass diese hellere Färbung nicht die Folge einer helleren Färbung der Haarspitzen ist, sondern dadurch bedingt wird, dass die Wurzelhälfte der Haare nicht dunkelbraunschwarz ist, wie stets beim *Myod. obensis*, sondern weissgrau."]

### 3. *Lemmus amurensis* Vinogradov.

1924. *Lemmus amurensis* Vinogradov, Ann. Mag. N.H., [9], 14, p. 186.

*Type.*—Zool. Mus. Russ. Acad. Sci., No. 13722; adult female, collected April 20, 1914, by C. Dorogostaisky.

*Type locality.*—Pikan, on the Zeya River, a tributary of the Amur River, East Siberia.

*Range.*—Known only from the type locality.

*Characters.*—Size very small, head and body 96 mm., hind-foot 14, condylo-basal length 26.2.

Fur long and soft. Colour of upper surface uniform brown (near "verona brown") faintly tinged with rusty on head and

rump; intermixed white-tipped hairs impart a peculiar ash-grey shade to the dorsum; a faint, broad, dark stripe marked on the neck but less evident on the back. Sides somewhat lighter than cinnamon-rufous. Belly uniformly cinnamon, paler than the sides. Fore-claws somewhat weaker than in other species, but more robust than in *Myopus*; palms and soles densely haired, the vestigial plantar tubercles completely hidden.

Skull with zygomata less widely spreading than in other species. Interorbital crest rather well developed. Braincase relatively larger and smoother than in other Palearctic forms, *L. obensis novosibiricus* excepted. Length of interparietal about one and a half times its width. Auditory bullæ relatively large and inflated.

For *external and cranial dimensions*, see tables at end of volume.

*Remarks*.—Vinogradov says that *L. amurensis* is sharply distinguishable from all other Siberian species, and he calls attention to the interest of the occurrence of a living member of the genus in such a low latitude (about 52° N.). It is to be hoped that a direct comparison will be made of this species with Allen's *L. o. chrysogaster*, a form apparently of similar small size inhabiting the west coast of the Sea of Okhotsk near its northern extremity.

#### 4. *Lemmus paulus* G. M. Allen.

1914. *Lemmus paulus* G. M. Allen, Proc. New England Zool. Club, 5, p. 60.

*Type*.—Harvard University, Mus. Comp. Zool., No. 15,268; adult male, skin and skull, collected June 22, 1912, by J. Koren.

*Type locality*.—Kalaschowo, near the mouth of the Kolyma River, north-eastern Siberia.

*Range*.—Known from the type locality and from Nijni Kolymsk.

*Characters*.—Size small, hind-foot 17.5 mm.; condylo-basal length 29.5; colour uniform.

In *summer pelage* (represented by the type which still retains a portion of the long winter coat on the lower part of the back) the general colour above is buffy, largely mixed with blackish on the head, becoming clearer posteriorly and at the sides. Individual hairs slaty for their basal three-fourths, with "pale buff" tips; mixed with these are wholly blackish hairs in the dorsal area, but these disappear at the sides where the buffy tips become more ochraceous; sides of the neck and body and the ventral surface ochraceous, the hairs with slaty bases except on the chin, throat, anal region and forearms where they are white to their bases. Tail "pale buff" above, slightly paler below. Ears small, round, quite concealed. Feet silvery with a dusky tinge.

*Winter pelage* (represented by a specimen without skull

taken at Nijni Kolymask, October 31, 1911) about 24 mm. long on the rump. Colour nearly uniform ochraceous buff above and below, slightly deeper on the rump paler on the belly. Dorsal region from muzzle to middle of back darkened by a considerable mixture of black hairs which disappear posteriorly. Throat nearly white; fore-arms and legs below pale buffy.

Skull nearly a fifth smaller than in *L. obensis*, slightly smaller than in *L. lemmus*. Anterior palatal foramina strongly and abruptly contracted behind. Palate produced medially to form a well-marked sharp process, instead of being blunt as in *L. lemmus*.

Incisors nearly milk-white with a faintly buffy tinge, instead of being clear yellow as in *L. lemmus*;  $m^3$  differs from that of the latter species in having the enamel walls of the prisms nearly straight instead of curved, and the prisms themselves slope antero-internally instead of being nearly transverse.

For *cranial and external measurements*, see tables at end of volume.

*Remarks*.—No material seen. Mr. Allen says the species is remarkable for the uniform coloration of both summer and winter pelages, the white incisors, and the compressed enamel walls of  $m^3$ . "It does not closely resemble *L. lemmus* nor the large *L. obensis*. To judge from descriptions alone, it is similar in many of its characters to *L. minusculus*, described by Osgood from the base of the Alaska Peninsula, but seems less brightly coloured, though of about the same size." It is probably the Siberian representative of *L. minusculus*.

### 5. *Lemmus nigripes* True.

1894. *Myodes nigripes* True, Diagnoses of new North American Mammals, p. 2; reprinted Proc. U.S. Nat. Mus., 17, 1894, p. 242.

1896. *Lemmus nigripes* Miller, N. Amer. Fauna, No. 12, p. 37; "List," 1912, p. 206; "List" 1924, p. 396.

*Type*.—U.S. National Museum.

*Type locality*.—St. George Island, Pribilof Islands, Alaska.

*Range*.—Known only from the type locality.

*Characters*.—Essential characters and size nearly as in *L. lemmus*; colour subdued. Upper surface dark brown, clothed with a mixture of dark brown, dusky, and bright ochraceous hair-tips darkest on top of head palest below and behind ears and on the rump. Tip of muzzle black. Sides of muzzle, upper lips and flanks bright ochraceous. Under parts duller and paler irregularly darkened by the slaty bases of the hairs. Chin whitish. Hands and feet dark brown to blackish; palms and soles hairy, the pads at bases of toes not completely concealed. Tail dark brown above, paler below.

For *external and cranial measurements*, see tables at end of volume.

6. *Lemmus alascensis* Merriam.

1843. ? *Myodes albigularis* Wagner, Schreber's Säugethiere Suppl., p. 602.  
 1885. *Myodes obensis* True, Proc. U.S. Nat. Mus., 7, (1884), p. 596 (in part).  
 1900. *Lemmus alascensis* Merriam, Proc. Washington Acad. Sci., 2, p. 26; Miller, "List," 1912, p. 206; "List" 1924, p. 396.

*Type*.—U.S. Nat. Mus., No.  $\frac{5491}{6186}$  (Merriam Collection); "adult" female.

*Type locality*.—Point Barrow, Alaska.

*Range*.—Point Barrow and St. Michaels, Alaska.

*Characters*.—Size medium (slightly smaller than either *L. lemmus* or *L. nigripes*); ears smaller than in *L. nigripes*; feet and nose pale. Colour golden fulvous, darkest on head, where it is mixed with black hairs; brightest on sides, where it is almost orange fulvous; palest on feet and around mouth.

Skull like that of *L. lemmus*, but slightly smaller, with smaller and less flattened braincase and less widely spreading zygomata; angle of mandible much less everted. Upper incisors broader. Compared with the skull of *L. nigripes* that of the present animal is said to be "decidedly smaller and less massive; nasals much shorter and smaller; rostrum more slender; frontals not elevated into tubercles anteriorly; angle of jaw much smaller and less everted. Molar series shorter."

For *external measurements*, see table at end of volume.

(*Skull measurements* not recorded.)

*Remarks*.—Probably based upon young material.

*Myodes albigularis* Wagner, was based, according to Middendorff (Sibir. Reise, 2, Th. 2, p. 107), probably upon a specimen from the N.W. coast of America.

7. *Lemmus yukonensis* Merriam.

1900. *Lemmus yukonensis* Merriam, Proc. Washington Acad. Sci., 2, p. 27; Miller, "List," 1912, p. 207; "List" 1924, p. 396.

*Type*.—U.S. Nat. Mus., No. 98849; adult female, collected August 9, 1899, by W. H. Osgood.

*Type locality*.—Charlie Creek, Yukon River, Alaska.

*Characters*.—Size small, ears relatively large. General colour dark anteriorly, with bright fulvous or rufous rump and flanks. Head, shoulders, and anterior half of back greyish-brown, grizzled with black and yellowish-fulvous, darkest on top of nose; rump and hinder part of back rich rusty fulvous or orange fulvous; lower sides and belly golden fulvous, deepest and brightest on flanks; sides of nose greyish or greyish-brown; a band of golden fulvous on lower part of face from nose to below ear. Hands and feet dusky. Tail bicoloured, dusky above, buffy below.

Skull with braincase large and broad, produced posteriorly to cover the enlarged bullæ; frontal narrow interorbitally, with

a narrow median sulcus, but not "pinched in" as in *L. alascensis*; rostrum small; zygomata squarely set but not widely spreading, the sides parallel; interparietal large, usually pentagonal; anterior palatal foramina rather short; auditory bullæ remarkably large and strongly inflated.

For *external and cranial measurements*, see tables at end of volume.

### 8. *Lemmus minusculus* Osgood.

1904. *Lemmus minusculus* Osgood, N. Amer. Fauna, No. 24, p. 36; Miller, "List," 1912, p. 206; "List," 1924, p. 396.

*Type*.—U.S. Nat. Mus., No. 119612 (Biol. Surv. Coll.); adult male, collected, September 1, 1902, by W. H. Osgood and A. G. Maddren.

*Type locality*.—Kakhtul River, near its junction with the Malchatna River, Alaska.

*Characters*.—Size much smaller than in *L. alascensis*. General colour ochraceous, mixed with black or blackish on upper surface, where the black is usually concentrated to form an indistinct median line from nose to shoulders, nearly clear or tawny on flanks and below. Rump patch hazel or light chestnut, less extensive and less contracted than in *L. alascensis* or *L. trimucronatus*. Ears dusky, or occasionally with a few ochraceous hairs. Feet seal brown. Tail variable, sometimes dusky or blackish above and light buff below, and sometimes nearly uniform pale buff above and below.

Skull similar to that of *L. alascensis* but very much smaller; zygomata less angular and bowed out; naso-frontal region decidedly elevated and rostrum depressed. Auditory bullæ more nearly parallel, usually more inflated and less inclined to be compressed anteriorly, the basioccipital and basisphenoid correspondingly slender.

For *external and cranial measurements*, see tables at end of volume.

### 9. *Lemmus trimucronatus* Richardson.

1825. *Arvicola trimucronata* Richardson, Journ. Parry's Second Voyage, App., p. 309.

1829. *Arvicola (Georychus) trimucronatus* Richardson, Fauna Boreali-Americana, p. 130.

1848. *Myodes trimucronatus* Gray, P.Z.S., 1848, p. 44.

1853. *Myodes obensis* Middendorff, Sibirische Reise, 2. Th. 2, p. 107 (in part); Baird, Mamm. N. Amer., 1857, p. 559; Coues, Mon. N. Amer. Rodentia, Muridæ, 1879, p. 241.

1900. *Lemmus trimucronatus* Stone, Proc. Acad. Nat. Sci. Philadelphia, p. 35; Preble, N. Amer. Fauna, No. 27, 1908, p. 181; Miller, "List," 1912, p. 207, and "List," 1924, p. 396.

*Type*.—B.M., No. 42.10.7.13; adult female, collected by Captain Back, and presented by Sir J. Richardson.

*Type locality*.—Shores of Point Lake, Mackenzie, Canada.

*Range*.—Eastern Boreal North America, ranging northwards to Fort Anderson and the Arctic Coast, eastwards to the southern and western shores of Hudson's Bay; and north-east to the neighbourhood of Repulse Bay and in Baffin Land to the Cumberland Peninsula.

*Characters*.—Essential cranial, dental, and external characters as in *L. obensis*. Fur soft and fine, from 13 to 19 mm. long on back. Colour of head and anterior portion of back mixed reddish-grey, produced by the mingling of clove-brown, yellowish-brown, and black hair-tips in nearly equal proportions; posterior part of back chestnut brown, many of the longer hairs being tipped with black; sides reddish orange; under parts grey, intermixed with many yellowish orange hairs. Nose deep black. Ears somewhat shorter than fur, thinly clothed. Tail clothed with stiff hairs, bicoloured, dark brown above, greyish-white or yellowish below, its terminal pencil about 9 mm. long. Feet dusky brown above, lighter below.

Preble notes, from specimens collected near the mouth of the Thiewiaza River, Hudson's Bay, that the "rusty ochraceous" of the lower parts and sides extends forwards on the "cheeks and lips, sometimes tinging slightly the head and shoulders" and he adds: "In some of the half-grown specimens in fresh pelage the head and shoulders are considerably flecked with the colour of the sides and there is an indistinct dusky stripe extending from between the ears to the middle of the back. Younger specimens are nearly unicolor throughout, the plumbeous fur tipped with yellowish-brown."

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Richardson states that the type collected June 26, 1821, was a female containing six fully formed but hairless embryos. Preble found that a few females, taken August 4-8 (the breeding season being then nearly over) at Thiewiaza River, contained from four to six embryos; and that the mammary formula is  $2 - 2 = 8$  as in other members of the genus.

#### 10. *Lemmus helvolus* Richardson.

1828. *Arvicola (Lemmus) helvolus* Richardson, Zool. Journ., 3, p. 517.

1829. *Arvicola (Georychus) helvolus* Richardson, Fauna Boreali-Amer., p. 128.

1848. *Myodes helvolus* Gray, P.Z.S., 1848, p. 43.

1853. *Myodes obensis* Middendorff, Sibirische Reise, 2, Th. 2, p. 107; Baird, Mammals N. Amer., p. 559, 1857; Coues, Mon. N. Amer. Rodentia, Muridae, p. 241, 1879 (in part).

1908. *Lemmus helvolus* Preble, N. Amer. Fauna, No. 27, p. 182; Miller, "List," 1912, p. 206, and "List," 1924, p. 396.

*Type*.—B.M., No. 42.10.7.11; subadult, collected by Thomas Drummond 1826, presented by Sir J. Richardson.

*Type locality*.—"Rocky Mountains, inhabiting Alpine swamps in latitude 56°" (Richardson). "Near the headwaters of one of the southern tributaries of Peace River, or between there and the Jasper House region," Alberta, Canada (Preble).

*Range*.—Unknown.

*Characters*.—Essential characters as in other members of the genus. General colour, in the type a young adult changing into winter pelage, reddish-orange, palest on the ventral aspect; interspersed with a number of longer black-tipped hairs on back and sides. Black hairs more numerous on upper part of head, around the eyes, and on the nape, the fur in these places having a mixed black and orange colour. Nose greyish-brown; sides of face pale orange; upper lips white. Feet brownish. Tail coloured like the body. Fur on body about 19 mm. long, very short on nose and extremities.

Skull broken; but its characters apparently and those of the teeth essentially as in other species of *Lemmus*.

For *external and cranial dimensions*, see tables at end of volume.

*Remarks*.—This species is still apparently only represented by the type, but it is not improbable that when further material comes to hand from Alberta *L. helvolus* will be found to be identical with one or other of the forms described from western North America in recent years. Preble (*loc. cit.*) says:—"Though specimens referred to *Lemmus helvolus* have recently been recorded from Cassiar Mountains, Telegraph Creek, and other points in northern British Columbia, this region is so far from the actual type locality of *helvolus* that the specific identity of the specimens must at present be considered merely as assumptive."

## GROUP: MICROTI.

Lower incisor long, its alveolus extending backwards at least to the base of the condylar process, lingual to  $m_1$  and  $m_2$ , labial to  $m_3$ .

### Genus: 5. EVOTOMYS Coues.

1811. *Myodes* Pallas, Zoograph. Rosso-Asiat., 1, p. 173 (in part; genus based upon *Mus lemmus* Liun., and therefore antedated by *Lemmus* Link, 1795).
1814. *Brachyurus* Fischer, Zoognosia, ed. 111, 3, p. 55 (in part).
1831. *Hypudæus* (with misprints *Hypudacus*, and *Hypudæus*, Mehlis, Oken's Isis, 24, p. 874 (genus based on *H. hercynicus* Mehlis = *Mus glareolus* Schreber); Keyserling and Blasius, Die Wirbelthiere Europas 1840, pp. viii and 34 (subgenus). Not of Illiger, 1811.
1839. *Myodes* de Selys-Longchamps, Études de Micromamm., p. 87 (group).



1874. *Evotomys* Coues, Proc. Acad. Nat. Sci. Philadelphia, p. 186 (genus); Miller, N. Amer. Fauna, No. 12, p. 42, 1896.
1883. *Myodes* Lataste, Le Naturaliste, p. 349 and Ann. Mus. Civ. Stor. Nat. Genova, [2], 4, 1887, p. 271 (subgenus of *Microtus*).
1900. *Evotomys* Schultze, Zs. f. Naturwiss., 1900, p. 203; Collett, Norges Pattedyr, 1911, p. 78.
1900. *Crascomys* Miller, Proc. Wash. Acad. Sci., 2, p. 87 (subgenus based on *Hypudæus rufocanus* Sundevall); Thomas, P.Z.S., 1906, p. 863 (genus).
1902. *Evotomys* Forsyth Major, P.Z.S., 1902, 1, p. 107 (misprint for *Evotomys*).
1903. *Phaulomys* Thomas, Ann. Mag. N.H., [7], 15, p. 493 (subgenus based on *Evotomys smithii* Thomas).
1908. *Eothenomys* Thomas, Abstr. P.Z.S., 1908, p. 45, and P.Z.S., 1908, p. 976 (subgenus of *Microtus*). Not of Miller.
1911. *Caryomys* Thomas, Abstr. P.Z.S., 1911, p. 4, and P.Z.S., 1911, p. 175 (subgenus of *Microtus*); genotype *Microtus* (*Eothenomys*) *inez* Thomas; Hinton, Ann. Mag. N.H., [9], 11, p. 146, 1923 (genus); G. M. Allen, Amer. Mus. Nov., No. 133, 1924, p. 6 (subgenus of *Microtus*).

*Genotype*.—*Mus rutilus* Pallas.

*Range*.—Circumpolar in the northern hemisphere, from the Arctic southwards to the Pyrenees, the mountains of Southern Italy, Rumania and Trebizond in Europe; to the Thian-Shan and Kinghan Mountains of Mongolia, Pekin, the Shansi Mountains of North China, the mountains of Hupeh, South China, Korea, Saghalien, and Japan (from Hokkaido to Kiushiu) in Asia; to the mountains of Colorado and North Carolina, and to the coast of North Carolina, in North America. Not known in Greenland, the islands of the Polar Sea, Newfoundland, Spitzbergen, Novaya Zemlya, Iceland or Ireland.

*Range in time*.—The earliest remains of the genus yet discovered are those from the late Pliocene or earliest Pleistocene of Britain (Cromer Forest Bed Series and High Terrace of the Thames). Fossil remains occur abundantly in the late Pleistocene and Holocene deposits of Western Europe.

*Characters*.—External form without special peculiarities. Skull with the bony palate terminating posteriorly as a simple transverse shelf; and with the temporal ridges not fused in the interorbital region. Lower incisor relatively short ending in the base of the condylar process below the level of the dental foramen. Cheek-teeth provided with two distinct fangs each in adults.

The members of this genus are small or medium-sized species. Outwardly they differ from typical voles (genus *Microtus*) by their rather lighter and more elegant form, larger eyes, more conspicuous ears, and longer tail. The tail is always well clothed with hair and is often provided with a distinct terminal pencil. Hands and feet small and normal, each with five digits; the thumb very short, provided with a flat nail; the other digits long, armed with small but sharp claws; palms and soles naked; palmar pads 5, plantar pads 6. Mammæ, 2 — 2 = 8.

Fur dense, long and soft in winter, shorter and harsher in summer. Colour of back usually rufous, darker and richer in humid and wooded regions, lighter and yellower in open country and in the north, where there is some tendency to winter whitening. The reddish tint usually forms a more or less well-defined mantle extending from the crown of the head to the rump and laterally, to a greater or less degree, encroaching upon the flanks. Hairs everywhere with slaty bases.

Skull agreeing in general form with that of other members of the subfamily, but more lightly built, rounder, less angular and ridged than in higher genera (e.g., *Microtus*). Interorbital region broad. Temporal ridges weakly indicated, always widely separated in the interorbital region. Squamosals light, showing little or no tendency to encroach upon the frontals or parietals anteriorly; post-orbital crests of squamosals usually weak or absent. Interparietal strap-shaped. Bony palate terminating posteriorly as a thin-edged, transverse shelf continuous between the alveoli of the posterior molars ( $m^2 - m^3$ ); the posterior median sloping septum of the palate of *Microtus* is absent, although the post-palatal lateral pits are present, deep, and extensive. Mesopterygoid fossa wide; presphenoid relatively broad. Ectopterygoid plates low. Pterygoid fossæ shallow, their floors not dorsal to the ventral surface of the basisphenoid. Auditory bullæ well inflated, simple, internally without spongy tissue.

Mandible nearly normal; groove between molars and ascending ramus open posteriorly, not "pocketed" by alveolus of lower incisor as in *Microtus*, etc.; coronoid process relatively slender and angular process relatively larger.

*Dentition.*—Incisors slender. Upper incisors without grooves, terminating posteriorly between the premaxillary suture and  $m^1$ . Lower incisors relatively shorter than in *Microtus*, passing from lingual to labial side of jaw between  $m_2$  and  $m_3$ , but not causing any marked lingual displacement of the latter tooth, and terminating in the base of the condylar process below the level of the dental foramen.

Cheek-teeth with tubercular caps when quite unworn, showing a prismatic pattern when worn. Enamel thin in superficial, thick in deeper portions of the crowns. Re-entrant folds partly filled with cement. Pulp cavities and cement spaces closing below in adults, each tooth then developing two roots, an anterior and a posterior, which grow in length as the crowns are worn away. In extreme old age the crowns of the teeth may be entirely worn away and the abraded summits of the fangs may then appear alone above the gums.

In average specimens, with well but not excessively worn teeth, the enamel pattern, in most species, is characterized by the rounded form of the salient angles and the confluency of the dentinal spaces, the last-named feature being particularly noticeable in lower molars. In pattern  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  are

essentially as in normal members of the subfamily—apart from the peculiarities just noticed;  $m_1$  has always a short anterior loop and in most species, even in very young stages of wear, no more than four outer and five inner salient angles can be recognized. On two occasions, however (Fig. 78, 1 and 5b), I have found in young teeth an ephemeral enamel islet representing the last trace of a fourth outer infold, and in another case (Fig. 78, 2) the fourth outer angle is complicated by a prism fold in front of which there is a distinct vestige of a fourth outer valley; so that we may conclude that *Evotomys* has descended from an ancestor with a more complex  $m_1$  than that now normal in the genus. Much more definite evidence pointing in the same direction is afforded by the  $m^3$ , which in practically all members of the genus is more complex in early stages of wear than it is in ordinary adult specimens. In this tooth, in some species, as many as five salient angles may be traced on each side in early stages of wear; but the posterior elements are more or less evanescent, and the tooth is commonly reduced to one with three outer and three or four inner salient angles. In very old specimens  $m^3$  acquires a pattern strongly resembling those found in such genera as *Alticola* and *Hyperacrius*, and as explained above in the general introduction this supports the belief that the genera in question are offshoots from ancient forms of *Evotomys*.

*Superspecific groups.*—The numerous species of *Evotomys* now recognized are all very closely related to each other. They may be arranged in four groups respectively typified by *E. glareolus*, *E. rutilus*, *E. nageri*, and *E. rufocanus* among Old World forms. The earliest remains of the genus yet discovered are those occurring in the Cromerian (Norfolk Forest Bed Series) deposits, in the High Terrace of the Thames, and in early Middle Terrace deposits. These fossils, judging from the teeth which alone are known, must be ranked as early members of the *glareolus* or *nageri* groups. They indicate clearly that the genus was fully developed in Cromerian or Upper Pliocene times and that we must look for the more primitive ancestral forms in considerably older horizons.

Of the four groups, that of *E. glareolus* is the most primitive in that it seems to contain forms primitive enough to be regarded as representing the central stock from which the other rather higher groups may have descended. The primitive characters, brachyodonty, greater complexity of cheek-teeth, weakness of jaw muscles, small size, delicacy, and roundness of the skull, moderate inflation of auditory bullæ, small bodily size, greater length of ears and tail, nakedness of feet and tail, dark coloration and diffuseness of mantle, are most clearly shown by the members of this group.

From such a generalized *glareolus* stock the *rutilus* and *nageri* groups seem to have directly arisen and diverged.

The *rutilus* group appears to be an offshoot from some of the lowest members of the *glareolus* group which has become adapted

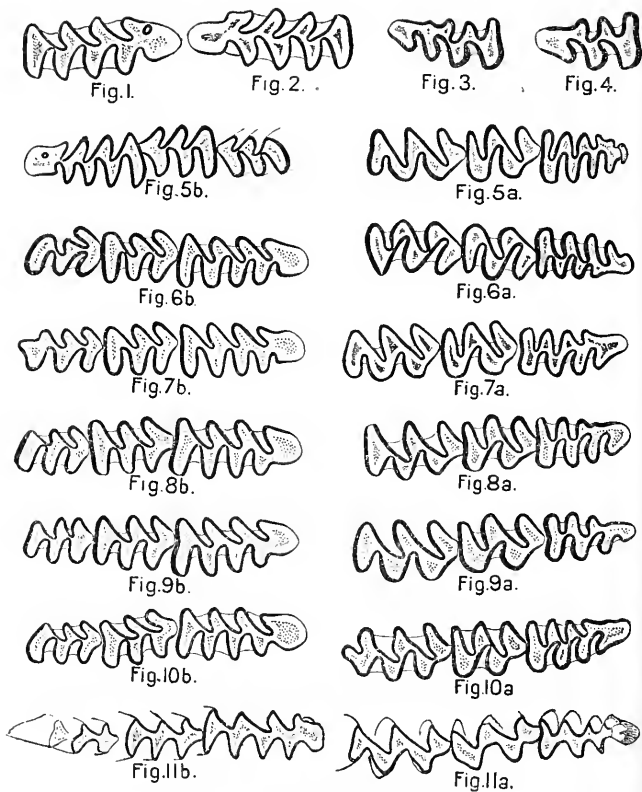


FIG. 78.—Cheek-teeth of *Erotomys*.

- 1 and 2. *E. rufocanus regulus*, left and right  $m_1$  of young individual (*B.M.*, No. 6.12.6.93).  
 3. *E. skomerensis*, right  $m^3$ .  
 4. *E. glareolus*, right  $m^3$ .  
 5a and b. *E. amurensis*, upper and lower molars of young individual (*B.M.*, No. 7.2.5.81).  
 6a and b. *E. mikado*, upper and lower molars (*B.M.*, No. 7.2.7.89).  
 7a and b. *E. mikado*, upper and lower molars (*B.M.*, No. 7.2.7.87).  
 8a and b. *E. wosnessenskii*, upper and lower molars (*B.M.*, No. 83.2.24.5).  
 9a and b. *E. ponticus*, upper and lower molars (*B.M.*, No. 6.3.6.174).  
 10a and b. *E. gapperi*, upper and lower molars (*B.M.*, No. 7.7.7.1339).  
 11a and b. *E. rufocanus smithii*, upper and lower molars very young (*B.M.*, No. 6.1.4.333).

for life within the Arctic Circle. In small size, delicacy of skull and lightness of the cheek-teeth it remains primitive, more primitive indeed than are most of the living members of the *glareolus* group. The internal changes are not great;  $m^3$  is a little simplified as a rule and the auditory bullæ have become somewhat enlarged, but neither character is carried beyond what is found in some members of the *glareolus* group. On the other hand the peripheral parts, external ears, limbs and tail, have all been shortened or withdrawn, and they have acquired an unusually dense covering of hair. In the highest members of the group the colour is greatly brightened, and while the rufous mantle becomes less and less diffuse, more restricted to the spinal region, it extends further backwards to end by spreading along the dorsal surface of the tail.

The *nageri* group seems also to have arisen from low members of the *glareolus* group;  $m^3$  for one thing has retained much of its primitive complexity. For some reason, possibly enforced subsistence upon rather tougher and less nutritious vegetable substances than those usually devoured by *E. glareolus*, the cheek-teeth have become larger and taller-crowned, the jaw muscles more powerful, the skull more robust and more strongly ridged, and the general size has increased. These changes have been brought about by a gradual and long-continued course of adaptive evolution; for the least modified members of the *nageri* group are scarcely to be distinguished from some of the larger members of the *glareolus* group, and from them many gentle gradations lead upwards to the highest forms, e.g., *E. cesarius* and *E. n. nageri*.

In the Far East and high North by a course of much more intense adaptive modification the *rufocanus* group has been evolved apparently from members of the *nageri* group. The modifications follow the same general course as in the latter, but they go much further. The animal has become unusually robust and has acquired unusually heavy cheek-teeth, powerful jaw muscles, and a skull which in strength and angularity rivals that of many species of *Microtus*. In young individuals the skull and cheek-teeth (with their confluent dentinal spaces) resemble those of ordinary *Evotomys*, and  $m^3$  is frequently complex with four or five salient angles on each side; but in adults the dentinal spaces become rather tightly closed and the teeth bear a strong resemblance to those of *Microtus*, particularly noticeable in  $m_1$ , while  $m^3$  is simplified. The animal looks mature long before it is full-grown and long before the molars show the slightest sign of rooting. So great is the difficulty of estimating the ages of individuals in this group, and so different are the young from the adults in skull, dentition, and to some extent in outward appearance, that competent observers have commonly referred young and adults of one and the same form to different genera, under the impression that all their specimens were really mature.

Among the American forms *E. gapperi* (and its numerous

subspecies), *E. brevicaudus*, *E. carolinensis*, and *E. idahoensis* appear to represent the Old World *glareolus* group; *E. caurinus*, *E. dawsoni*, *E. orca*, *E. ungava*, *E. mazama*, *E. obscurus*, *E. occidentalis* and *E. nivarius* are, judging from the descriptions, possibly more or less modified members of the *rutilus* group; while *E. phæus* and *E. wrangeli* appear to represent the *nageri* group. *E. rufocanus* does not seem to have any American equivalent unless indeed *E. mazama*, and *E. californicus* can be regarded as dwarfed representatives; possibly too *E. proteus* may belong to the same group.

A.—*glareolus* group.

†**Evotomys**, sp.

1882. *Arvicola (Evotomys) glareolus* Newton Vert. Forest Bed, p. 82, Pl. XIV, figs. 1-1c.  
 1900. *Microtus (Evotomys) glareolus* Hinton and Kennard, Essex Nat., 11, p. 348.  
 1910. *Evotomys* sp. Hinton, Proc. Geol. Assoc., 21, p. 497.

Remains of a small species of *Evotomys* occur in the Cromerian Upper Freshwater Bed at West Runton, Norfolk, in the High Terrace deposits of the Thames at Ingress Vale, near Greenhithe, Kent, and in the early Middle Terrace deposits of the Thames at Grays Thurrock, Essex.

Apart from one or two fragmentary mandibular rami from West Runton the material available from the deposits mentioned consists merely of a considerable number of isolated cheek-teeth. In enamel pattern and rooting these are exactly like those of *E. glareolus*; but they are perhaps a trifle smaller and the infolds contain rather less cement than in the recent species. Pending the discovery of more complete remains it is not possible to define this early member of the *E. glareolus* group with precision.

1. †**Evotomys harrisoni** sp. n.

1910. *Evotomys* sp. Hinton, Proc. Geol. Assoc., 21, p. 494 (second or smaller species of the Ightham Fissures).  
 1914. *Evotomys glareolus* Barrett-Hamilton, History of British Mammals, 2, p. 421.

*Type*.—An adult skull, lacking the interparietal, jugals and right auditory bulla, but otherwise perfect; collected by Dr. Frank Corner.

*Type locality and horizon*.—Fissure deposit of Ightham, near Sevenoaks, Kent, England. Late Pleistocene.

*Range in time and space*.—Probably widely distributed in the late Pleistocene deposits of Britain; but remains sufficiently perfect to admit of precise determination have hitherto been found only at Ightham.

*Characters*.—Skull somewhat smaller (condylo-basal length, in old age, 22.8 mm.) than in equal-aged *E. glareolus britannicus*,

shorter and broader generally. Braincase nearly square, instead of oblong, noticeably more depressed. Interorbital region broader and shorter, retaining in adult stages of growth something of the condition found in young *E. glareolus*. Nasals slightly more steeply inclined anteriorly, relatively longer, constricted posteriorly in much the same way as, but to a lesser degree than in *E. skomerensis* and *E. caesarius*. Palate relatively broader. Incisors straighter and with shorter exerted portions than in *E. g. britannicus*. Cheek-teeth very light. Enamel pattern of molars normal;  $m^3$  short with three salient angles only on each side.

Mandible distinguished by its small size, rather large angular processes, and very light cheek-teeth.

For skull measurements, see table at end of volume.

*Remarks.*—This fossil species is probably more closely related to *E. glareolus* than to any other recent species; but the broader interorbital region, square and depressed braincase, and lighter cheek-teeth are characters which seem to call for specific recognition. In the lightness of the cheek-teeth the fossil approaches *E. rutilus*, but the  $m^3$  is simpler than in the latter and the skull form is conspicuously different.

The species is named in honour of my old friend the late Benjamin Harrison, the veteran geologist of Ightham.

## 2. *Evotomys glareolus* Schreber.

(Synonymy under subspecies.)

*Range.*—Through the wooded lowlands and uplands of boreal and temperate Europe, exclusive of the Iberian Peninsula, from Scotland, Scandinavia, and corresponding latitudes in Russia, southwards to the Pyrenees, Alps, Rumania and probably to the shores of the Black Sea. Eastwards it ranges from Wales and Scotland at least to the Syansk Mountains, 100 miles west of Lake Baikal, where it ascends to 1600 feet; but the details of its distribution in European and Asiatic Russia are still unknown.

*Characters.*—Size small; hind-foot (15–19 mm.) usually less than 18 mm.; condylo-basal length of skull in adults, with well-developed molar roots, rarely exceeding 24 mm. Colour of upper parts, in most of the geographical races, brighter and redder as a rule than in subspecies of *E. nageri*. Skull small, lightly built, short and broad, with short and wide mesopterygoid fossa; post-orbital processes of squamosals usually distinct though small. Cheek-teeth normal.

*Geographical differentiation.*—Eight subspecies are at present recognized, and of these seven are European and one Asiatic. Probably other forms remain to be discovered in European and Asiatic Russia. The subspecies differ very slightly from one another, the plastic characters being those of size and proportion, general colour, the greater or less development of the rufous

mantle, the form of the auditory bullæ and the structure of  $m^3$ . The differences for the most part are only of an average kind and therefore are only appreciable upon inspection of long series of specimens.

Very closely related to *E. gapperi* of N. America; the latter indeed, and its numerous subspecies, might be treated as so many geographical races of *E. glareolus*.

**2a. *Evotomys glareolus glareolus* Schreber.**

1780. *Mus glareolus* Schreber, Säugthiere, iv, p. 680, pl. exc B.  
 1792. *Mus rutilus minor* Kerr, Anim. Kingd., p. 237; described from Casan and Gocctingen; based on Pallas, Glires, p. 247.  
 1792. *Mus rutilus B minor* Donndorff, Zool. Beyträge, 1, p. 452; based on Pallas, Glires, p. 247.  
 1803. *Lemmus arvalis* Geoffroy, Catal. Mammif. du Mus. Nat. d'Hist. Nat., p. 185; described from Meudon, Seine, France. (Not *Mus arvalis*, Pallas, 1778.)  
 1828. *Arvicola fulvus* Millet, Faune de Maine-et-Loire, 2, p. 40; described from Angers, Maine-et-Loire, France. (Not *Lemmus fulvus* Geoffroy, 1803.)  
 1831. *Hypudæus* (misprint for *Hypudæus*) *hercynicus* Mehlis, Oken's Isis, 24, p. 876; described from the Harz Mountains, Germany [*Hypudæus* and *Hypudæus* occur also in the same article].  
 1834. *Lemmus rubidus* Baillon, Mém. Soc. Royale d'Emulation d'Abbeville, 1833, p. 54; described from Abbeville, Somme, France.  
 1834. *Hypudæus glareolus* Melchior, Den Danske Stats og Norges Pattedyr, p. 116.  
 1836. *Arvicola rufescens* de Sélys-Longchamps, Essai Monogr. sur les Campagnols des Environs de Liège, p. 13; described from Longchamps-sur-Geer, Belgium.  
 1842. *Arvicola pratensis* F. Cuvier, Hist. Nat. des Mammif., 7, Tabl. Gen. et Méth. Described and figured in Livr. 68 of same work, 1834, from Abbeville, Somme, France.  
 1857. *Arvicola glareolus a.* Blasius, Säugethiere Deutschlands, p. 337 (in part.)  
 1896. *Evotomys glareolus* Miller, N. Amer. Fauna, No. 12, p. 44.  
 1900. *Evotomys hercynicus hercynicus* Miller, Proc. Washington Acad. Sci., 2, p. 100 (in part.)  
 1900. *Evotomys hercynicus rubidus* Miller, Proc. Washington Acad. Sci., 2, p. 102.  
 1909. *Evotomys glareolus* Miller, Ann. Mag. N.H., [8], 3, p. 419; Trouessart, Faune Mamm. d'Europe, p. 170.  
 1912. *Evotomys glareolus glareolus* Miller, Catal. Mamm. W. Europe, p. 632.

*Type*.—Unknown.

*Type locality*.—Island of Lolland, Denmark.

*Range*.—West-Central Europe north of the Alps and Pyrenees and south of the Baltic; from the Atlantic coast eastwards to Silesia; the north-eastern limit of range not known.

*Characters*.—Size small (hind-foot 16.6–18 mm.; condylo-basal length of skull 23–24.6 mm.). Colour of upper parts rather bright though dark-toned, the mantle broad and diffuse.



*Colour*.—In winter pelage : rufous mantle diffuse and ill-defined, extending from eyes nearly to base of tail and tending to spread slightly over sides. In general colour it is very nearly the "mars-brown" or "prouts-brown" of Ridgway, usually with a tinge of russet, the exact shade resulting from various combinations of cinnamon-rufous, vinaceous-rufous and black. Sides and cheeks dull brownish buff thickly sprinkled with black. Flank colour merging insensibly in that of back, sharply contrasted with that of belly. Under surface grey, with a variable but usually conspicuous wash of buff. Hairs everywhere with slaty bases, which irregularly darken the sides and under parts. Ears reddish like the back. Feet whitish, more or less distinctly tinged with brown. Tail sharply bicoloured, dark brown above, dirty white or buffy below.

In summer pelage paler above.

Skull small, the cheek-teeth light. Auditory bullæ not abruptly inflated on inner side, a character scarcely appreciable, however, except on comparison with *E. g. isticus*;  $m^3$  with third inner infold present in about one-half the specimens examined.

For *external and cranial measurements*, see tables at end of volume.

### 2b. *Evotomys glareolus britannicus* Miller.

1832. *Arvicola riparia* Yarrell, P.Z.S., 1832, p. 109, and Loudon's Mag. Nat. Hist., 5, 1832, p. 599; not *Arvicola riparius* Ord, 1825 (= *Microtus pennsylvanicus*).

1837. *Arvicola pratensis* Bell, Hist. Brit. Quadr., p. 330.

1874. *Arvicola glareolus* Alston in Bell, Hist. Brit. Quadr., ed. 2, p. 327.

1895. *Microtus glareolus* Lydekker, Brit. Mammals (*Allen's Nat. Libr.*), p. 213.

1898. *Evotomys glareolus* Thomas, Zoologist, p. 101.

1900. *Evotomys hercynicus britannicus* Miller, Proc. Wash. Acad. Sci., 2, p. 103.

1903. *Evotomys glareolus britannicus* Barrett-Hamilton, Proc. R. Irish Acad., p. 317; Trouessart, Faune Mamm. d'Europe, 1910, p. 170; Miller, Catal. Mamm. W. Europe, 1912, p. 634; Barrett-Hamilton, Hist. Brit. Mamm., 2, p. 405, 1913.

*Type*.—B.M., No. 7.7.7.2944 (Miller Coll.); adult female, skin and skull, collected by G. S. Miller.

*Type locality*.—Basingstoke, Hampshire. Yarrell described his "*Arvicola riparia*" from a specimen obtained at Birchanger, Essex, England.

*Range*.—Great Britain.

*Characters*.—Distinguished from *E. g. glareolus* by deeper general colour and slightly smaller average size (hind-foot 15–18 mm., condylo-basal length of skull 21.4–24.2 mm.).

The reddish mantle extends from the forehead in front of the eyes to the base of the tail, and in colour is usually near "vandyke brown," strongly washed with "cinnamon rufous," and

sprinkled with longer black hairs. Flanks, cheeks, and face before the eyes are lighter; the flanks greyer and less buffy than in the typical form. There is no distinct line of demarcation. Underside whitish, frequently washed to a variable extent with yellowish or buff. Feet greyish. Tail distinctly though often inconspicuously bicoloured. The colours are lighter red when faded, as in late winter.

*Moult*.—A coarser coat is assumed in October, after which in cold localities the flanks may be greyer. A moult has also been observed in early May.

Young specimens have less brightly coloured backs. In the woolly juvenal coat the underside is at first dusky; later, as longer hairs with light tips increase in number, the characteristic tints of the adult are gradually assumed, at first on the upper surface. A buff or yellowish belly, when present, is characteristic of the adult pelage, and is most conspicuous in winter specimens.

Skull like that of *E. g. glareolus*, but slightly smaller in average size;  $m^3$  usually with three salient angles and two infolds on each side; a third inner infold and a fourth inner salient angle are usually present, however, in the  $m^3$  of young and subadult individuals; according to Miller the third inner fold is present in about 25% of the individuals examined, but I find recognizable traces of this fold in at least 50% of the specimens before me.

For *external and cranial measurements*, see tables at end of volume.

### 2c. *Evotomys glareolus reinwaldti* Hinton.

1921. *Evotomys glareolus reinwaldti* Hinton, Ann. Mag. N.H., [9], 8, p. 128.

*Type*.—B.M., No. 20.11.6.4; adult female, original No. 306; collected August 11, 1920, and presented by Mr. E. Reinwaldt.

*Type locality*.—Hapsal, Esthonia "In Obst- und gemüsegarten."

*Range*.—Esthonia.

*Characters*.—Most like *E. g. succicus* in general character, but colour much darker.

Upper parts clothed with a fine mixture of dark reddish-brown and dusky hair-tips, the general effect produced, where brightest (as between ears and on nape), being no brighter than the "chestnut" of Ridgway; darkest on rump, where the elimination of rufous hair-tips leaves the colour dark slaty-grey. Rufous tinge traceable far back towards rump and far down flanks. Under parts silvery grey, much darkened by the slaty bases of the hairs. Ears dusky. Tail dusky above; its lower surface, together with the hands and feet, dirty white.

Skull similar to that of *E. g. succicus* in size and general appearance; zygomatic arches slightly less expanded; bullæ slightly

smaller and less inflated. Teeth normal;  $m^3$  often with a third re-entrant fold on inner side (in about 55% of specimens examined).

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—A good series representing this form has been collected and presented to the British Museum by Mr. Reinwaldt. Individuals taken in August are the darkest in colour, while July specimens are but slightly paler. In those captured in December the colour is much paler; the rufous mantle, extending from the forehead almost to the rump, is confined to the spinal region and is rather conspicuously contrasted with the grey flanks. In May specimens the mantle is broader and clearer, the grey of the flanks less evident. At its palest, in May, the general colour of the mantle is near the "Kaiser brown" of Ridgway; but in August, when darkest, the general effect, produced by a mixture of rufous and dusky hair-tips, is very near deep "chestnut brown."

### 2d. *Evotomys glareolus succicus* Miller.

1842. *Arvicola glareolus* Sundevall, K. Vetensk. Akad. Handl., 1840, p. 16.

1847. *Lemmus glareolus* Nilsson, Skand. Fauna, Däggdjuren, ed. 2, p. 362.

1865. *Hypudæus glareolus* Holmgren, Skand. Däggdjur, p. 258.

1874. *Arvicola glareolus* Lilljeborg, Sver.-och Norges Däggdjur, p. 284 (part).

1900. *Evotomys hercynicus succicus* Miller, Proc. Washington Acad. Sci., 2, p. 101.

1910. *Evotomys glareolus succicus* Trouessart, Faune Mamm. d'Europe, p. 171; Miller, Catal. Mamm. W. Europe, 1912, p. 636.

*Type.*—U.S. Nat. Mus., No. 85016; a young adult female.

*Type locality.*—Upsala, Sweden.

*Range.*—Lowlands of Sweden, Finland and South-eastern watershed of Norway.

*Characters.*—Like *E. g. glareolus*, but with a narrower and less diffused red mantle and greyer sides, face and rump. Skull and teeth as in typical form; but  $m^3$  with third inner infold less often present (in about one-third instead of about one-half of the individuals examined).

For *external and cranial measurements*, see tables at end of volume.

### 2e. *Evotomys glareolus isticus* Miller.

1900. *Evotomys hercynicus hercynicus* Miller, Proc. Washington Acad. Sci., 2, p. 100 (in part).

1909. *Evotomys glareolus isticus* Miller, Ann. Mag. N.H., [8], 3, p. 419; Trouessart, Faune Mamm. d'Europe, 1910, p. 172; Miller, Catal. Mamm. W. Europe, 1912, p. 637.

*Type*.—B.M., No. 4.4.6.72; adult male, skin and skull; collected by W. Dodson; presented by Lord Lilford.

*Type locality*.—Bustenari, Prahova, Rumania (in the Carpathians, north-west of Bucharest). Altitude 480 m.

*Range*.—Drainage basin of the Danube, from Bavaria through Hungary to Rumania and probably to Bulgaria and the coast of the Black Sea.

*Characters*.—Distinguished from other subspecies by its rather narrow, lighter, yellowish-rufous mantle; and by the form of its auditory bullæ which are more abruptly inflated on the inner side than in *E. g. glareolus*.

*Summer pelage*: dorsal stripe narrow and well defined, not tending to spread over sides. It is rufous slightly varied with yellowish wood-brown, and rather thickly sprinkled with black-tipped hairs. Face, cheeks, and sides pale yellowish wood-brown, tinged with grey: rump like sides, rather strongly contrasted with mantle. Under parts varying from creamy white to a yellowish cream-buff. Feet greyish white. Ears thinly haired, concolorous with mantle. Tail sharply bicoloured, brown above, soiled white below.

*Winter pelage*: mantle slightly less sharply defined than in summer, the rufous paler but warmer, considerably varied with wood-brown, but very inconspicuously sprinkled with black-tipped hairs. Face, cheek and sides more yellowish wood-brown than in summer, and scarcely tinged with grey. Rump slightly suffused with colour of dorsal area, and therefore less contrasted with back than in summer. Feet nearly pure white.

Skull like that of *E. g. glareolus*, but with larger auditory bullæ; inner margins of bullæ more nearly approaching each other, and rising more abruptly above level of basioccipital. Cheek-teeth normal;  $m^3$  with third inner infold present in about 64% of the skulls examined.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This is the brightest-coloured and best-marked subspecies of *E. glareolus* known.

### 2f. *Evotomys glareolus helveticus* Miller.

1900. *Evotomys hercynicus helveticus* Miller, Proc. Washington Acad. Sci., 2, p. 98.

1910. *Evotomys glareolus helveticus* Trouessart, Faune Mamm. d'Europe, p. 171; Miller, Catal. Mamm. W. Europe, 1912, p. 640; Barrett-Hamilton, History of British Mammals, 2, 1914, p. 409.

*Type*.—B.M., No. 2.6.7.1; adult male, skin and skull, collected by A. Robert, November 9, 1899; presented by Oldfield Thomas.

*Type locality*.—Montauban, Haute-Savoie, France (near Geneva, Switzerland). Altitude 900 m.

*Range*.—Jura Mountains; southwards through the non-Alpine parts of Switzerland and along the lower western portion of the French Alps.

*Characters*.—Size rather large (hind-foot 17–19 mm.; condylo-basal length of skull 23–24.5 or 25.4 mm.); colour somewhat paler and more buffy-greyish than in either *E. g. glareolus* or *E. nageri*. Skull rather strongly built;  $m^3$ , in about two-thirds of the specimens examined, with a third inner infold.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Of eleven adult skulls, ten, including the type and a good series from Cranves-Sales, Haute-Savoie, have the condylo-basal length ranging between 23.1 and 24.5, while in form they are strictly of the *E. glareolus* type. One skull from Cranves-Sales (B.M., No. 5.11.18.43♀) is much larger (its condylo-basal length 25.4 mm.) and in form it agrees very closely with *E. nageri*. I can detect no difference between the skin of this specimen and those of the others from the same locality; but it is possible that both *E. glareolus* and *E. nageri* are represented at Cranves-Sales. Apart from the specimen referred to, I can see no evidence of *E. g. helveticus* being in any way intermediate between the two species, and it seems to me to be a rather well-marked race of *E. glareolus*.

### 2g. *Evotomys glareolus sobrus* Montagu.

1923. *Evotomys glareolus sobrus* Montagu, P.Z.S., 1923, p. 867.

*Type*.—B.M., No. 21.12.1.16; adult female, collected September 13, 1921, by E. and V. Martino.

*Type locality*.—Rescetari, Nova Gradisca, Croatia.

*Range*.—Known only from the type locality.

*Characters*.—Size rather large (hind-foot 18 mm., condylo-basal length of skull 24.4 mm.). Tail relatively short, about 46% of head and body measurement.

Dorsal colour duller and more drab than in *E. g. helveticus*. Tail pale dust-colour above, instead of dark brown or dusky as in other forms, yellow-buff below.

Skull most like that of *E. g. helveticus*, but with slightly larger and more vaulted braincase. Check-teeth normal;  $m^3$  with three well-developed salient angles on each side and with weak vestiges of the fourth inner and outer angles in younger stages of wear.

For *external and skull dimensions*, see tables at end of volume.

*Remarks*.—The peculiarly short and pale tail satisfactorily distinguishes this form from other races of *E. glareolus*.

### 2h. *Evotomys glareolus saianicus* Thomas.

1911. *Evotomys glareolus saianicus* Thomas, Ann. Mag. N.H., [8], 8, p. 759.

*Type*.—B.M., No. 12.4.1.85; adult female, skin and skull, collected June 7, 1910, by Douglas Carruthers.

*Type locality*.—Syansk Mountains, 100 miles west of Lake Baikal. Altitude 1600 feet.

*Range*.—Known only from the type locality, where it is found together with *E. rutilus* and *E. rufocanus* (see Thomas, Ann. Mag. N.H., [8], 9, pp. 397, 398).

*Characters*.—Size small (hind-foot 16 mm.; condylo-basal length of skull 22.1—23 mm.).

Colour much as in dark European forms (e.g., *E. glareolus britannicus* and *E. g. succicus*). Rufous mantle narrower, so that grey flanks are more evident in dorsal view; head also greyer and less rufous. Sides and under surface dark grey in adults; light silvery grey in a young specimen. Belly with but little buffy suffusion.

Skull considerably smaller than in equal-aged *E. g. britannicus*, with slightly less expanded zygomata, shorter nasals, slightly longer diastema and with the braincase a little shorter and broader.

Cheek-teeth normal;  $m^3$  in adults without a fourth inner salient angle or third inner infold, but both structures feebly represented in the young specimen. Anterior root of  $m^1$  shows a distinct trace of the originally separate fang supporting the second inner prism.

For *external and cranial measurements*, see tables at end of volume.

### 3. *Evotomys centralis* Miller.

1906. *Evotomys centralis* Miller, Ann. Mag. N.H., [7], 17, p. 372; Thomas, *ibid.*, [8], 13, p. 568.

*Type*.—B.M., No. 5.12.4.14; adult male, collected by Mr. A. B. Bayley Worthington, Sept. 24, 1904.

*Type locality*.—Koksu Valley, Thian-Shan Mountains. Altitude 9000 feet.

*Range*.—Known only from the type locality.

*Characters*.—Size small (hind-foot 17 mm.; condylo-basal length of skull 23 mm.), tail short (about 41% of head and body length). Fur unusually long, dense and soft; hairs of back about 14 mm. in length. General colour pale and dull. Mantle rather narrow, yellowish-brown, conspicuously lined by dusky hair-tips. Face, flanks and rump ashy grey, slightly tinged with yellowish. Under parts whitish grey, rather heavily washed with buff, and not sharply contrasted with flanks. Tail very heavily haired, conspicuously pencilled, and sharply bicoloured; sooty black above and at tip, buffy-white below. Hands and feet soiled white above. Feet darkened on outer side of ankles.

Skull, compared with *E. g. britannicus* of equal age, slightly larger, with narrower braincase, shorter molars, longer nasals and diastema. Zygomata a little less expanded anteriorly.

Cheek-teeth of normal pattern, but with the salient angles a little less rounded than usual;  $m^3$  with third inner infold and fourth inner salient angle quite obsolete, its third outer fold and fourth outer angle vestigial; outer infolds of lower molars shallower than usual.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—In outward appearance this vole closely resembles *E. g. saianicus*, but is distinguished by its larger skull.

#### B.—*nageri* group.

##### 4. † **Evotomys kennardi** sp. n.

1910. *Evotomys* sp. (*nageri* group) Hinton, Proc. Geol. Assoc., 21, p. 494; Barrett-Hamilton, History of British Mammals, 2, 1914, p. 421.

*Type.*—Skull of a young adult (roots of  $m^2$  developed but very short), somewhat defective, the frontals damaged behind, the parietals, interparietal, right auditory bulla, jugals, and left  $m^3$  missing; collected by Dr. Frank Corner.

*Type locality and horizon.*—Fissure deposit at Ightham, near Sevenoaks, Kent, England.

*Range.*—Late Pleistocene of Britain. Known from the Ightham Fissures; Brixham Cave, Devonshire; St. Lawrence, I. of Wight.

*Characters.*—Size large (condylo-basal length about 25 mm.), as in *nageri* group, but a little smaller than in *E. caesarius*. Skull long and narrow. Zygomatic arches less widely spreading than in *E. g. britannicus*, the greatest zygomatic breadth falling in the jugal region or behind, the arches curving gently away from the rostrum in front. Nasals small, short, their lateral borders nearly straight. Interorbital region much constricted. Brain-case long and narrow, with very small post-orbital (squamosal) processes. Occiput high, its median height relatively greater than in *E. skomerensis*. Rostrum rather slender; diastema short; incisive foramina large. Palate rather narrow. Mesopterygoid fossa long and narrow. Auditory bullæ elongate, narrow transversely, with flattened outer faces and small external aperture; containing an appreciable quantity of spongy bone tissue within—a character unknown in other members of the genus. Tooth-rows short, but teeth rather heavy. Enamel pattern of cheek-teeth normal;  $m^3$  usually with a long posterior loop, a well-developed third inner fold and fourth inner salient angle; very rarely the fourth inner angle tends to become obsolete.

For *skull measurements*, see table at end of volume.

*Remarks.*—This species is named in honour of Mr. A. S. Kennard, who has done so much good work upon the British Pleistocene problem.

*E. kennardi* is a most interesting and well-marked species, belonging to the *nageri* group. It (or closely allied forms, with large skulls and heavy cheek-teeth) occurs abundantly in the later Pleistocene deposits of Britain and Western Europe in situations which show that the *nageri* group, although now restricted to the mountains and islands of Western and Central Europe, was formerly widely distributed in the plains. The group thus affords a parallel to the analogous cases of the Variable Hares and Snow Voles, and its present restricted and peculiar distribution is susceptible to a precisely similar explanation. The *nageri* group is most probably to be regarded as the older and once generally distributed representative of its genus in Western and Central Europe. In late Pleistocene times, however, species of the *glareolus* group invaded the region, arriving probably with *Microtus arvalis* (of modern type) and other voles, and successfully competing with the older group gradually dispossessed the latter of its foothold in the plains; so that to-day the older group survives only in the security of mountain fastnesses and insular seclusion.

#### 5. *Evotomys nageri* Schinz.

(Synonymy under subspecies.)

*Range*.—Mountainous regions of Western and Central Europe, including Western Norway, the French side of the Pyrenees, the Alps and the mountains of Italy southwards to Calabria. Allied species occur in the late Pleistocene of Britain and are found living in the Hebrides, on Skomer, and in the Channel Islands.

*Characters*.—Distinguished from *E. glareolus*, the lowland species of the region, by its larger size; hind-foot (17–21 mm.) usually 18 mm. or more; condylo-basal length of skull, in adults with well-developed molar roots, usually exceeding 24 mm. (23.6–26). General colour darker and greyer, less brightly rufous than usual in *E. glareolus*. Skull larger, more strongly built, longer and narrower throughout, with moderately well-developed post-orbital squamosal crests, and long and narrow mesopterygoid fossa.

*Geographical differentiation*.—Six subspecies are recognized, namely,

##### 5a. *Evotomys nageri nageri* Schinz.

1845. *Hypudæus nageri* Schinz, Synops. Mamm., 2, p. 237.  
 1852. *Myodes nageri* Gerbe, Rev. et Mag. Zool., p. 449.  
 1857. *Arvicola glareolus* b. Blasius, Säugethiere Deutschlands, p. 337.  
 1862. *Myodes bicolor* Fatio, Rev. et Mag. de Zool., [2], 14, p. 257; described from Genthal, Berne, Switzerland; type in Geneva Museum.  
 1869. *Hypudæus glareolus* Fatio, Faune Vert. de la Suisse., 1, p. 221.  
 1900. *Evotomys nageri* Miller, Proc. Washington Acad. Sci., 2, p. 94; Trouessart, Faune Mamm. d'Europe, 1910, p. 167.



1912. *Evotomys glareolus nageri* Miller, Catal. Mamm. W. Europe, p. 641.  
 1914. *Evotomys nageri nageri* Barrett-Hamilton, History British Mammals, 2, p. 421.

*Type*.—Unknown.

*Type locality*.—Oberalpsee, near Andermatt, Uri, Switzerland.

*Range*.—Alps (except westernmost portion) and mountains of Northern Italy.

*Characters*.—Size large (hind-foot 18.8–20 mm.; condylo-basal length of skull 25–26.2 mm.); red mantle narrow and dark, the flanks dull greyish in evident though not conspicuous contrast;  $m^3$  usually with third inner infold well developed.

Back with rather well-defined rufous mantle, extending from forehead to rump, but not showing much tendency to extend laterally; in colour the mantle is cinnamon rufous slightly varied with pale broccoli-brown and inconspicuously darkened by a sprinkling of black-tipped hairs, the general effect approaching chestnut, or something lighter and more yellowish. Face, cheeks, and sides light hair brown fading to smoky grey on lower part of sides. Rump, light broccoli-brown tinged with reddish-brown in median line, and forming usually a distinct though not very noticeable contrast with mantle. Under surface pale smoke-grey, washed to a varying degree with yellowish-brown, especially along median line, the slaty bases of hairs appearing irregularly at the surface. Feet dull white; darkened at outer side of ankle. Ears thinly haired, dull reddish-brown. Tail bicoloured, dark brown above, buffy whitish below.

The winter pelage tends to be darker than that of summer with less contrast between mantle and sides; but dull brownish individuals are not infrequent in summer.

Skull largest among continental European members of group, with the possible exception of *E. n. hallucalis*. Braincase relatively large. Zygomata not very abruptly expanded in front; their middle portions usually almost parallel. Anterior palatal foramina narrow (normal), their combined width about one quarter of their length.

Cheek-teeth large, but of normal pattern;  $m^3$  usually with a well-developed third inner infold.

For *external and cranial measurements*, see tables at end of volume.

#### 5b. *Evotomys nageri italicus* Dal Piaz.

1924. *Evotomys glareolus italicus* G. B. Dal Piaz, Studi Trentini, 5, No. 4, 1924, p. 3 (of reprint).

*Type*.—Adult male (Museo civico di Trento).

*Type locality*.—Brennero, Alto Adige, northern Italy; at an altitude of 1400 metres.

*Range*.—Known at present only from the Pass of Brennero.

*Characters*.—Like *E. g. nageri*, but with slightly smaller skull (condylo-basal length 24–25, instead of 25–26.2 mm.).

Colour of back cinnamon-rufous; face, cheeks, flanks and rump clear brown; under parts whitish or light greyish with a weak suffusion of yellowish-brown. Dorsal colour somewhat variable, ranging from the dark hues of the young and some adults through cinnamon-rufous, rust-red, to a pale yellowish red in some individuals. Line of demarcation usually distinct; much less evident in young and some adults. Feet whitish, sometimes clear and silvery, sometimes darkened. Tail above more or less deep brown, below white, whitish or light brown. Colour darker in summer than in winter; and in young than in adults.

Height apparently without influence on colour; an individual from 2545 m. like those from 1000 m.

Skull and teeth slightly but constantly smaller than in *E. g. nageri*;  $m^3$  usually with a well-developed third inner infold (87% of the individuals).

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—In size the skull is nearly as in *E. g. isticus*, the form inhabiting the Danube Basin; but in colour, size of hind-foot, and in the structure of the  $m^3$  the present form shows itself to be more nearly related to *E. g. nageri*, from which, judging by specimens sent by Signor Dal Piaz, it is scarcely distinguishable externally.

#### 5c. *Evotomys nageri vesanus* subsp. n.

*Type*.—B.M., No. 8.11.30.12; adult female, collected August 20, 1907, by Dr. C. I. Forsyth Major.

*Type locality*.—Mittelberg, near Kaufbeuern, Bavaria. Altitude 1200–1300 metres.

*Range*.—Known only from the mountains in the neighbourhood of Kaufbeuern, Bavaria at elevations between 4000 and 6000 feet.

*Characters*.—External appearance as in *E. n. nageri*, but possibly a trifle smaller (hind-foot in three specimens 18 mm.). Skull about as long as in *E. n. nageri*, but relatively narrower throughout. Check-teeth smaller and lighter;  $m^3$  without a third inner infold or fourth inner salient angle.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—The cranial peculiarities of this outlying representative of the Alpine *E. nageri* prevent me from referring it to either the typical form or to Dal Piaz's recently described *E. n. italicus*.

#### 5d. *Evotomys nageri hallucalis* Thomas.

1882. *Arvicola glareolus* Cavanna, Bull. Soc. Entomol. Ital., 14, p. 87; Serra Crispo, Monte Pollino, Basilicata, Italy.

1906. *Evotomys nageri hallucalis* Thomas, Ann. Mag. N.H., [7], 18, p. 221; Trouessart, Faune Mamm. d'Europe, 1910, p. 168; Barrett-Hamilton, History British Mammals, 2, p. 421, 1914.
1912. *Evotomys glareolus hallucalis*, Miller, Catal. Mamm. W. Europe, p. 643.

*Type*.—B.M., No. 6.8.4.9; young adult male, skin and skull, collected by A. Robert; presented by Oldfield Thomas.

*Type locality*.—Santa Eufemia d'Aspromonte, Calabria, Italy.

*Range*.—Mountains of Southern Italy.

*Characters*.—Externally like *E. n. nageri*, but with the under parts less washed with yellowish-brown. Skull with longer, narrower braincase, shorter rostrum, short wide incisive foramina and larger teeth.

Colour as in *E. n. nageri*, but under parts light grey washed with whitish cream-buff. Line of demarcation along sides ill defined. Feet dull whitish, somewhat lighter than is usual in *E. n. nageri*.

Skull (of only known specimen) somewhat defective, but differing from that of *E. n. nageri* and related forms in the decided elongation of the braincase and a slight shortening of the rostrum. Length of braincase, from back of interparietal to line joining tips of post-orbital processes, nearly equal to zygomatic breadth, instead of decidedly less than the zygomatic breadth as in the related large forms. Interorbital region rather wide and smooth. Rostrum relatively shorter than in *E. n. nageri*, and the incisive foramina much shorter and wider, their greatest combined breadth decidedly more than one-third instead of about one-fourth of their length as in the related forms. But all these cited distinctive characters are in part at all events attributable to the youth of the single known specimen, in which the molar roots are less than 1 mm. long.

Cheek-teeth heavier than in *E. n. nageri*, rather like those of *E. caesarius*. Pattern normal;  $m^3$  with well-developed third inner infold.

For *external and cranial measurements*, see tables at end of volume.

##### 5c. *Evotomys nageri vasconiae* Miller.

1900. *Evotomys vasconiae* Miller, Proc. Washington Acad. Sci., 2, p. 96; Trouessart, Faune Mamm. d'Europe, 1910, p. 168.
1912. *Evotomys glareolus vasconiae* Miller, Catal. Mamm. W. Europe, p. 639.
1914. *Evotomys nageri vasconiae* Barrett-Hamilton, History of British Mammals, 2, p. 421.

*Type*.—U.S. Nat. Mus., No. 86994; adult male.

*Type locality*.—Montréjeau, Haute-Garonne, France.

*Range*.—Pyrenees and region at their immediate base (at present known from the French side only).

*Characters*.—Most closely resembling *E. n. norvegicus*, but perhaps slightly larger (hind-foot 18.6–19.6 mm.; condylo-basal length of skull 25–26 mm.);  $m^3$  with usually only two inner infolds. With a duller narrower mantle and less buffy sides.

For *external and cranial measurements*, see tables at end of volume.

5f. ***Evotomys nageri norvegicus*** Miller.

1877. *Arvicola glareolus* Collett, N. Mag. f. Naturvsk., 22, p. 65.  
 1898. *Microtus glareolus* Collett, N. Mag. f. Naturvsk., 36, p. 278.  
 1900. *Evotomys norvegicus* Miller, Proc. Washington Acad. Sci., 2, p. 93; Trouessart, Faune Mamm. d'Europe, 1910, p. 166; Barrett-Hamilton and Hinton, P.Z.S., 1913, p. 829; Ann. Mag. N.H., [8], 12, p. 364, 1913.  
 1911. *Euotomys glareolus* Collett, Norges Pattedyr, p. 79.  
 1912. *Evotomys glareolus norvegicus* Miller, Catal. Mamm. W. Europe, p. 638.  
 1914. *Evotomys nageri norvegicus* Barrett-Hamilton, History of British Mammals, 2, p. 421.

*Type*.—U.S. Nat. Mus. No. 84674; adult female.

*Type locality*.—Bergen, Norway.

*Range*.—Western Norway, north at least to Nordland; apparently confined to the western watershed.

*Characters*.—Slightly smaller than *E. n. nageri* (hind-foot 18.4–19 mm.; condylo-basal length of skull 24.2–26.2 mm.); general colour nearly as in *E. n. nageri*; mantle broad, not sharply marked off from buffy-grey flanks; skull heavily built;  $m^3$  usually with only two inner infolds.

*Summer pelage*: mantle broad and rather ill defined, in colour dull ferruginous slightly varied with light wood-brown and much darkened by a uniform sprinkling of black-tipped hairs, fading rather abruptly into the light wood-brown of face, cheeks and sides. Rump wood-brown, tinged with red in median line and forming no noticeable contrast with mantle. Under surface pale drab-grey washed to a varying degree with yellowish-brown and irregularly darkened by slaty bases of hairs. Feet dull white, a dark shade at outer side of ankle. Tail sharply bicoloured, dark brown above, whitish below.

Skull averaging rather smaller than in *E. n. nageri*, but decidedly larger and more heavily built than in *E. glareolus*. Zygomatic heavy, abruptly expanded anteriorly, the greatest zygomatic breadth opposite anterior ends of molar series. Post-orbital processes distinct but very small. Braincase moderately high and rounded, distinctly rectangular in outline when viewed from above. Nasals squarely truncate posteriorly, ending a little in front of nasal branches of premaxillæ; they expand quite suddenly in front and have concave lateral borders.

Cheek-teeth normal;  $m^3$  usually with only two inner infolds.

For *external and skull measurements*, see tables at end of volume.

### 6. *Evotomys gorka* Montagu.

1923. *Evotomys gorka* Montagu, P.Z.S., 1923, p. 867.

*Type*.—B.M., No. 26.3.7.1; adult female, collected June 28, 1923, and presented by the Hon. Ivor Montagu.

*Type locality*.—Zalesina, the Gorski Kotar, Croatia.

*Range*.—Known only from the type locality.

*Characters*.—Size large (hind-foot 19 mm.; condylo-basal length of skull 26.6 mm.). Tail relatively short, about 43% of the head and body length.

Fur of back long and shaggy. Colour above bright rufous, the sides bright orange-brown so that the mantle is wide spreading and ill defined laterally. Under surface grey, somewhat darker than in the neighbouring races of *E. glareolus*.

Skull peculiarly long, narrow and smooth, the frontals in the interorbital region flattened, with scarcely a trace of the superciliary ridges. Zygomatic arches very little expanded, the zygomatic breadth scarcely greater than the mastoid width, curving away very gently from the rostrum in front. Rostrum and nasals very long and narrow, the nasals rather like those of *E. caesarius*. Interorbital region broad; the orbito-temporal vacuities strikingly small. Braincase smooth, subovate, and well arched; post-orbital processes of squamosals small and weak, about as in *E. nageri*. Diastema and anterior-palatal foramina very long. Tooth-rows long, the teeth narrow. Palate normal. Pterygoid fossæ short. Auditory bullæ very large, the tegmen tympani and mastoid portion a little more inflated and swollen than usual; basioccipital between bullæ narrower than in *E. nageri* and *E. caesarius*. Mandible normal.

Check-teeth of normal pattern;  $m^3$  with three outer and four inner salient angles, the third inner fold well developed.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This is a sharply distinguished member of the *nageri* group. In skull form it approaches Asiatic representatives of the group like *E. ponticus*, but differs from all in various important ways. Among European forms its skull is readily distinguishable by its large size, smoothness, gently rounded outline, slender rostrum and large auditory bullæ.

### 7. *Evotomys skomerensis* Barrett-Hamilton.

1903. *Evotomys skomerensis* Barrett-Hamilton, Proc. R. Irish Acad., p. 316; Trouessart, Faune Mamm. d'Europe, 1910, p. 167; Miller, Catal. Mamm. W. Europe, 1912, p. 644; Barrett-Hamilton, Hist. Brit. Mamm., 1914, 2, p. 419.

1903. *Evotomys scomerensis* Lydekker, Zool. Rec. Mamm., 1903, p. 34.

1905. *Evotomys hercynicus skomerensis* Millais, Mamm. Great Brit. and Ireland, 2, p. 250.

*Type*.—B.M., No. 3.7.4.3; adult male, skin and skull, collected April 7, 1908, and presented by G. H. Mills.

*Type locality*.—Skomer Island, off the coast of Pembrokeshire, Wales.

*Range*.—Skomer Island.

*Characters*.—Distinguished from *E. glareolus* by its larger size (hind-foot 17–19 mm.; condylo-basal length of skull 24.8–25.8 mm.); exceptionally light and bright dorsal colour, sharply contrasted buffy-white under surface, and by its large massive skull and complex  $m^3$ .

In late winter or spring pelage the mantle is broad, encroaching considerably on the paler sides; its general colour is between “orange rufous,” bright “cinnamon rufous,” and “madder brown.” On the face, sides of head, and flanks the bright rufous tints are less conspicuous, running through light “hazel” or “vinaceous cinnamon” to a dull “greyish-buff.” Rump and upper surface of the sharply bicoloured tail are “mummy brown.”

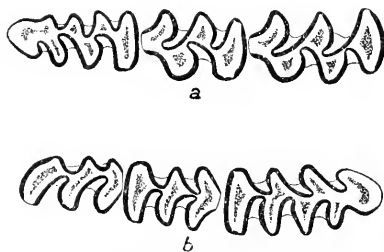


FIG. 79.—*Evolomys skomerensis* Barrett-Hamilton.  
a. Right upper, b. left lower molars (crown views).

Under surface of body and tail, with the legs and feet, are whitish, with a very perceptible wash of yellowish on the belly. Summer pelage unknown.

Skull large, as in *E. nageri* and related forms; differing in its great relative depth, short, broad, rather strongly ridged and angular braincase, conspicuous mastoid region, and unusually elongate, centrally contracted almost spatulate nasals, which are decidedly longer than the diastema. Post-orbital processes of squamosals small, but unusually well defined, sending well-developed ridges backwards and upwards nearly to the anterior edges of the parietals. Rostrum and incisive foramina normal. Zygomata rather abruptly expanded anteriorly as in *E. n. norvegicus*. Auditory bullæ relatively large.

Cheek-teeth like those of *E. nageri*;  $m^3$  normally with a third inner infold.

For *external and cranial measurements*, see tables at end of volume.

8. *Evotomys cæsarius* Miller.

1896. *Evotomys glareolus* Barrett-Hamilton, The Zoologist, [3], 20, p. 98 (Jersey).  
 1908. *Evotomys cæsarius* Miller, Ann. Mag. N.H., [8], 1, p. 195; Trouessart, Faune Mamm. d'Europe, 1910, p. 169; Miller, Catal. Mamm. W. Europe., 1912, p. 645.

*Type*.—B.M., No. 3.2.11.2; adult male, skin and skull, collected and presented by G. E. H. Barrett-Hamilton.

*Type locality*.—St. Helier, Jersey, Channel Islands.

*Range*.—Known only from the island of Jersey, Channel Islands.

*Characters*.—General size as in the other large European forms (hind-foot 18–20 mm.; condylo-basal length of skull 25–27.4 mm.), but tail distinctly less than half the length of head and body, and ear unusually short. Colour dark and rather dull, with no noticeable line of demarcation upon flanks. Skull very large and massive.

In winter pelage upper parts a rich, dark, reddish-brown, approaching the "cinnamon rufous" of Ridgway, but not so vivid. Flanks and outer surfaces of fore-legs paler, suffused with dull buff, though not sufficiently to produce any marked contrast with back. Under parts a clear rich buff (between the "buff" and "cream-buff" of Ridgway). Flank line of demarcation ill defined. Tail sharply bicoloured, blackish above, clear buff below. Feet dusky grey above, rather dark brown on furred portion of soles.

In summer pelage: red area restricted to back, and noticeably browner and duller than in winter, the exact shade nearly "hazel." Flanks broccoli-brown, in rather strong contrast with back, but fading insensibly into the dull buff of under surface. Tail and feet as in winter.

Skull larger than that of any other member of the *nageri* group (with the possible exception of *E. n. hallucalis*). It differs from that of other species in its greater depth, more convex dorsal profile, and especially in the greater angle at which the nasals are bent downwards. In the last character it is approached by *E. skomerensis*, but the dorsal surface of the braincase is not flattened as in the Skomer Vole. Interorbital region wide, not tending to assume a cylindrical form as in *E. rufocanus*, the lateral ridges noticeable in old age, but remaining widely separated by a broad median groove. Braincase relatively short and broad, but less ridged and angular than in *E. skomerensis*. Post-orbital processes of squamosals rather large, but less *Microtus*-like than in *E. rufocanus* and with no trace of a ridge extending obliquely backwards towards the parietal such as occurs in *E. skomerensis*. Nasals about as long as the diastema, moderately spatulate in outline. Rostrum more robust than in other European species; incisive foramina normal. Zygomatic arches not very abruptly

expanded in front, their median portions parallel. Auditory bullæ large, but of normal form.

Cheek-teeth unusually large; pattern normal;  $m^3$  usually with third inner infold;  $m_1$  with very short anterior loop.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—This interesting insular representative of the *nageri* group presents a very strong superficial resemblance to the typical alpine form, but is readily distinguished by its darker feet, shorter tail, and much larger and stronger skull and teeth.

### 9. *Evotomys alstoni* Barrett-Hamilton and Hinton.

1913. *Evotomys alstoni* Barrett-Hamilton and Hinton, Abstr. Proc. Zool. Soc., No. 119, p. 18, and P.Z.S., 1913, p. 827; Barrett-Hamilton, Hist. Brit. Mamm., 1914, 2, p. 422.

*Type.*—B.M., No. 14.1.30.4; old male, skin and skull, collected by R. W. Sheppard, June 18, 1921.

*Type locality.*—Island of Mull, Inner Hebrides, Scotland.

*Range.*—Known only from the type locality.

*Characters.*—Size rather large (hind-foot 18–19.5 mm.; condylo-basal length of skull 24.1–25.3 mm.); with relatively short ears and tail, long hind-feet, and peculiar skull.

Colour similar to that of adults of the deeply tinted forms of *E. glareolus*; deep russet above; under surface richly washed with yellowish or buffy tints.

Skull larger than in *E. g. glareolus*, agreeing in size with that of *E. n. norvegicus*. As in the latter form, the jugals are heavy; but the curvature of the zygomatic arches is as in *E. g. glareolus*. Braincase very broad and smoothly convex, the temporal ridges but faintly indicated even in aged skulls; parietal region convex instead of being flattened in dorsal profile, the highest point a little behind the middle of the parietals; these features impart an appearance of relatively greater cranial capacity than is seen in any of the other European species of the genus. Post-orbital (squamosal) processes not conspicuous. Interorbital region broad, with a wide shallow median sulcus. Nasals rounded or slightly and narrowly emarginate behind, ending flush with or slightly behind the ends of the premaxillæ, slightly longer than the diastema, expanded in front, their lateral borders slightly but distinctly concave. Rostrum shallow, as in *E. n. norvegicus*, its least depth behind the incisors not exceeding the anterior width. Auditory bullæ nearly as in *E. n. norvegicus*;  $m^3$  with a third inner fold and fourth inner salient angle, the latter usually well developed.

For *external and cranial measurements*, see tables at end of volume.



10. *Evotomys erica* Barrett-Hamilton and Hinton.

1913. *Evotomys erica* Barrett-Hamilton and Hinton, Ann. Mag. N. H., [8], 12, p. 361; Barrett-Hamilton, Hist. Brit. Mamm., 1914, 2, p. 424.

*Type*.—B.M., No. 14.1.30.5; adult male, collected April 15, 1913, by P. D. Montague.

*Type locality*.—Raasay, near Skye, Scotland.

*Range*.—Known only from the island of Raasay: "Trapped in big heather, rather scarce."

*Characters*.—Resembling *E. alstoni* in general appearance and colour, but slightly larger, with longer ears, more robust tail, stronger skull and larger cheek-teeth.

Size large (hind-foot 18–20 mm.; condylo-basal length of skull 25.2–25.4 mm.). General colour of upper parts deep russet; under surface much more heavily washed with buff than in *E. alstoni*, and sharply contrasted with the dark brown flanks. Under surface of tail clear buff, sharply contrasted with dark brown upper surface.

Skull most readily distinguished from that of *E. alstoni* by the larger cheek-teeth, broader zygomatic arches, heavier jugals (their upper borders boldly convex), more prominent and extensive post-orbital crests, less convex parietal region, wider pterygoid fossæ, correspondingly narrower choanæ, and vertical instead of ventrally divergent pterygoids. Antero-internal part of each auditory bulla bluntly pointed instead of being rounded. Outer wall of infraorbital canal slightly wider, the rostrum rather deeper and narrower, with smaller and narrower palatal foramina. Interorbital region slightly more constricted. Palate relatively wider. Mandible larger than in *E. alstoni*, with more robust coronoid, condylar and angular processes; its interior border much thicker, the lower margin of the angular process broadened throughout into a wide surface for the insertion of the superficial part of the masseter muscle; the width of this surface is 1.4 mm., but in *E. alstoni* the corresponding facet measures only 0.4 mm. in width.

Cheek-teeth of normal form, differing from those of *E. alstoni* merely by their larger size;  $m^3$  with a deep third inner fold, and usually with a large fourth inner salient angle.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—An adult female taken in October is thinner furred, darker above, and with a less heavy wash of buff below; possibly this specimen is in a rather worn breeding pelage.

11. *Evotomys ponticus* Thomas.

1906. *Evotomys ponticus* Thomas, Ann. Mag. N.H., [7], 17, p. 417.

*Type*.—B.M., No. 6.3.6.173; male, collected by A. Robert, October 29, 1905.

*Type locality*.—Sumela, about 30 miles south of Trebizond, Asia Minor.

*Range*.—Forest region south of Trebizond.

*Characters*.—Size large (hind-foot 19 mm.; condylo-basal length of skull 24.6 mm.) as in *E. nageri*, which it resembles in general colour. Distinguished from *E. nageri* by its greyer rump and sides, buffy-washed belly, and darker hands and feet. Tail heavily haired, black above and at the end, dull creamy below.

Skull large, remarkably smooth and rounded; the braincase long and narrow, less ridged and angular than in allied forms. Temporal ridges in the interorbital region weak and marginal; surface of frontals nearly plane, instead of bearing a shallow median sulcus as in most other species; dorsal profile evenly and smoothly convex. Zygomatic arches less expanded than in *E. nageri*; jugals very light. Anterior palatal foramina well open behind.

Check-teeth normal in pattern, but very light;  $m^3$  with a well-developed third inner infold and a rather small fourth inner salient angle; third outer infold of this tooth usually shallow and sometimes obsolete, there being no trace of a fourth outer salient angle.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Apparently more closely related to *E. nageri* than to other species.

## 12. *Evotomys frater* Thomas.

1908. *Evotomys frater* Thomas, Ann. Mag. N.H., [8], 1, p. 448.

*Type*.—B.M., No. 8.3.2.18; subadult female, skin and skull, collected by A. A. Kutsenko.

*Type locality*.—Thian-Shan; probably near Przewalsk.

*Range*.—Thian-Shan. Limits of range unknown.

*Characters*.—Size medium (hind-foot 19 mm.; condylo-basal length of skull about 24.5 mm.); colour dark and unusually brown.

Fur soft, loose, not so long as in *E. centralis*, the hairs of the back about 13 mm. in length. General colour above approaching "mummy brown," with a very slight rufous suffusion. Head and sides rather clearer brown. Rump smoky grey, almost blackish near the root of the tail. Under surface unusually dark, little paler than "hair brown," not defined on sides, the hairs slaty for four-fifths of their length, with dull "pinkish-buffy" tips. Hands and feet brownish-white. Tail of medium length, longer than in *E. centralis* and not so heavily haired as in that species; black above, dull whitish below.

Skull, in the only two specimens at present known, imperfect; jugal bones rather heavy; post-orbital crests of squamosals moderately developed; nasals lightly pinched in behind. Check-

teeth normal;  $m^3$  with fourth inner salient angle obsolete, or represented only in young stages of wear.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—Probably most nearly related to *E. ponticus* and the *nageri* group.

C.—*rutilus* group.

13. **Evotomys baikalensis** Ognev.

1924. *Evotomys baikalensis* Ognev, Bull. Soc. Nat. Moscow, N.S., 31, p. 73.

*Type.*—Zoological Museum of Moscow University, No. 3938; female, collected July 19, 1917.

*Type locality.*—БОЛЬШОЙ УШКАНИЙ, east of Lake Baikal.

*Range.*—Known only from type locality.

*Characters.*—Size medium (hind-foot 17-18 mm.; greatest length of skull 25.7 mm.). Mantle bright rusty-reddish brown, comparatively narrow, the "slight greyish-yellowish-buff" of the flanks extending far upwards. Ventral surface silvery white.

Tooth-rows relatively very short; the short, rounded salient angles of the molars are separated from one another by wide spaces;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—Apparently, judging from Ognev's figures, a species with an unusually long and slender rostrum, very long diastema, and small cheek-teeth. Probably closely related to *E. rutilus*.

14. **Evotomys laticeps** Ognev.

1924. *Evotomys laticeps* Ognev, Bull. Soc. Nat. Moscow, N.S., 31, p. 75.

*Type.*—Zool. Museum University of Moscow, No. 3911; female, collected July 6, 1912.

*Type locality.*—Хамар-Дабан, province of Irkutsk.

*Range.*—Known only from the type locality.

*Characters.*—Size medium (hind-foot 17.7 mm.; greatest length of skull 24.8 mm.). Mantle bright rusty-reddish brown, wide; flanks yellowish-buffy-grey with a slight rusty admixture, not sharply distinguished from the rufous mantle.

Skull rather large with broad rostrum and interorbital region; tooth-rows "exceedingly widely disposed." Cheek-teeth with roundish enamel angles;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—Probably related to *E. rutilus*.

15. **Evotomys parvidens** Ognev.

1924. *Evotomys parvidens* Ognev, Bull. Soc. Nat. Moscow, N.S., 31, p. 77.

*Type*.—Zool. Museum University of Moscow, No. 3907; female, collected July 2, 1912.

*Type locality*.—Хамар-Дабан, province of Irkutsk.

*Range*.—Known only from the type locality.

*Characters*.—Size medium (hind-foot 16.2 mm.; greatest length of skull 24.7 mm.). Mantle bright red-rusty brown, covering a large part of the back; flanks rusty-buffish with a visible reddish tinge.

Skull large, much elongated in the rostral region, smooth in the frontal region; coronal suture pressed far backwards. Though the tooth-rows are much shortened, the enamel loops are much extended laterally; the salient angles of the teeth are long and roundish;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Probably identical with *E. laticeps*.

16. **Evotomys otus** Turov.

1924. *Evotomys otus* Turov, Comptes Rendus de l'Acad. Sci. Russie, 1924, p. 110.

*Type*.—Zool. Mus. Russ. Acad. Sci. (Leningrad); in alcohol.

*Type locality*.—N.E. shore of Lake Baikal.

*Characters*.—The following diagnosis has been kindly furnished by Dr. Turov.—“Statura corporis haud magna; caput relative majus; auribus immensibus (16.9 mm.), capillis pareis obtectis; pars nasalis cranii solida; spatium interorbitale latum (4.5 mm.); ossa nasalia elongata (7.5 mm.); dentes minimi; series molarium (4.6 mm.).”

*Remarks*.—Doubtfully distinct from *E. rutilus*.

17. **Evotomys rutilus** Pallas.

(Synonymy under subspecies.)

*Range*.—Arctic Europe and Asia; southwards in Scandinavia to Tromsø, Norway, and Norbotten, Sweden; in Asia to the Altai, Syansk Mountains, Kinghan Mountains, and Ajan on the shore of the Sea of Okhotsk. Details of distribution in eastern Europe and Asia not well known.

*Characters*.—Size medium (hind-foot about 18 mm.; condylo-basal length of skull 25 mm.), tail short, less than half the length of the head and body, densely haired, with a long terminal pencil, its upper surface more or less concolorous with back.

Colour bright; mantle well defined, though not strikingly contrasted with the flanks, extending backwards from crown to root of tail, bright rufous chestnut scarcely darkened by the dusky tips of the longer hairs. Sides and cheeks pale, grey tinged with ochraceous buff merging below in the creamy or dull whitish under surface, which is irregularly darkened by the slaty bases of the hairs. Ears concolorous with the mantle. Feet whitish, with the soles hairier than usual, the posterior pads sometimes hidden. Tail sharply bicoloured, reddish-brown above, dirty white or cream below.

Skull distinguished from that of *E. glareolus* by its shorter and more nearly square braincase, its upper surface and that of the rather broad interorbital region somewhat flattened. Post-orbital (squamosal) processes very weak or not developed. Palate and choanæ narrower than in *E. glareolus*; the postero-lateral bridges of palate often incomplete. Auditory bullæ large.

Cheek-teeth smaller and lighter than in *E. glareolus*; enamel pattern normal, but re-entrant folds deeper and salient angles more acute, with the dentinal spaces rather tightly closed;  $m^3$  with deep first outer infold, so that its anterior loop does not present the *Alticola*-like appearance often seen in *E. glareolus*, etc., and with its inner infolds always well developed; outer infolds of  $m_2$  and  $m_3$  relatively deep;  $m_2$  with four substantially closed triangles in front of the posterior loop;  $m_3$  tending to assume a similar form.

*Geographical differentiation.*—Owing to the scantiness of material and to the very poor character of the descriptive literature, it is impossible to say how many geographical races of *E. rutilus* should be recognized or what status should be accorded to the many nominal species of *Evotomys* which in recent years have been described from Northern and Central Asia. *E. baikalensis*, *E. laticeps*, *E. parvidens* and *E. otus*, dealt with above, if distinct, are probably no more than subspecies of *E. rutilus*.

#### 17a. *Evotomys rutilus rutilus* Pallas.

1779. *Mus rutilus* Pallas, Nov. Spec. Quadr. Glir. Ord., p. 246.  
 1811. *Myodes rutilus* Pallas, Zoogr. Rosso-Asiatica, 1, p. 177.  
 1819. *Lemmus rutilus* Desmarest, Nouv. Dict. d'Hist. Nat., ed. 2, 5, p. 84; Fisher, Synops. Mamm., 1829, p. 295.  
 1822. *Arvicola rutilus* Desmarest, Mammalogie, p. 284; Poljakow, Mém. Imp. Acad. Sci. St. Petersburg, 39, 1881, Supplement, p. 51.  
 1827. *Hypudæus rutilus* Brants, Muizen, p. 70.  
 1874. *Evotomys rutilus* Coes, Proc. Acad. Nat. Sci. Philadelphia, p. 187 (in part); Miller, Proc. Washington Acad. Sci., 2, 1900, p. 91; Trouessart, Faune Mamm. d'Europe, 1910, p. 169; Miller, Catal. Mamm. W. Europe, 1912, p. 646.  
 1840. *Arvicola rutila* Eversmann, Hist. Nat. gouv. Orenbourg, 2, 167.  
 1887. *Microtus (Myodes) rutilus* Lataste, Ann. Mus. Civ. Storia Nat. Genova, (2), 4, p. 261.  
 1898. *Microtus rutilus* Collett, Nyt. Mag. f. Naturw., 36, p. 282.

1899. *Anaplogonia rutila* Cope, Journ. Acad. Nat. Sci. Philadelphia, (2), 11, p. 201.  
 1911. *Evotomys rutilus* Collett, Norges Pattedyr, p. 89.

*Type*.—Unknown.

*Type locality*.—Siberia, immediately east of the Obi.

*Range*.—Arctic Europe and Asia; exact limits unknown.

*Characters*.—As described above under the species.

For external and cranial dimensions, see tables at end of volume.

### 17b. *Evotomys rutilus russatus* Radde.

1862. *Arvicola (Hypudæus) russatus* Radde, Reisen im Süden von Ost-Sibirien, 1, p. 186.  
 1924. *Evotomys rutilus russatus*, G. M. Allen, Amer. Mus. Nov., No. 133, p. 2.

*Type*.—Perhaps in Leningrad (not seen by Mr. Montagu); a specimen in alcohol collected in the summer of 1857.

*Type locality*.—Eastern Syansk Mountains.

*Characters*.—Radde's careful description of the external characters of his specimen leaves no room for doubting that his *Arvicola (Hypudæus) russatus* is based upon *E. rutilus*; and the measurements (total length 86 mm.; head and body 63 mm.; tail 24 mm.; hind-foot with claws 17) indicate that the specimen was immature. The description does not, however, reveal any character by which this form can be satisfactorily distinguished from *E. r. rutilus*. The supposed differences in the  $m^3$  described by Radde are, in my opinion, imaginary; the last molars have apparently fallen out of their alveoli and have been replaced in a reversed position.

Mr. G. M. Allen has lately referred to this form a large series of specimens collected by the American Museum Asiatic Expeditions "in the wooded country five miles northeast of Urga, Mongolia. . . . These differ from a series from the Altai referred to *rutilus* in their slightly brighter colours and in having the tails usually more or less reddish like the back instead of blackish as in these latter. Although no specimens of *rutilus* from the Obi region are available as topotypes, it is assumed that the Altai specimens are the same, and I have therefore applied Radde's name to the Mongolian series."

### 18. *Evotomys wosnessenskii* Poljakov.

1881. *Arvicola wosnessenskii* Poljakov, Mém. Imp. Acad. Sci. St. Petersburg, 39, Appendix, p. 56; Lataste, Ann. Mus. Civ. Storia Nat. Genova, 20, 1884, p. 280.  
 1898. *Evotomys wosnessenskii* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1898, p. 361; Allen, Bull. Amer. Mus. N.H., 19, 1903, p. 146.

*Co-types*.—St. Petersburg (Leningrad) Museum; two collected

by Wosnessensky, in 1815; Nos. 443 and 7583; both young (examined by the Hon. Ivor Montagu).

*Type locality*.—"Kamtschatka."

*Range*.—Kamtschatka. Common on the mainland and upon Behring Island.

*Characters*.—Size small (hind-foot 16–18 mm.; condylo-basal length of skull 22–23 mm.); tail short, averaging about 30% of the head and body length. Fur short, hairs on back in December specimen about 8 mm. in length; tail well clothed with stiff bristly hairs forming a terminal pencil about 6 mm. long; soles thinly haired from heel to middle row of pads.

Colour bright; mantle well defined laterally, extending from crown of head to root of tail, brightest in winter when the tint is near cinnamon-rufous, whereas in autumn and summer it is a clear deep tawny. Cheeks and flanks much greyer and paler, but distinctly tinged with ochraceous buff. Under surface grey, irregularly darkened by slaty bases of hairs, with or without a more or less well-marked buff suffusion. Tail slender, less densely haired than in *E. rutilus*, bicoloured, reddish or tawny like the back above, clear cream-buff below. Feet and hands whitish. Immature specimens much darker and duller.

Skull slightly narrower and more depressed than in *E. rutilus*, with the rostral protuberances large and placed relatively far forwards. Auditory bullæ very small, not large as in *E. rutilus*. Cheek-teeth of normal pattern;  $m^3$  with the third inner fold and fourth inner angle usually more or less well developed.

For *external and cranial dimensions*, see tables at end of volume.

*Remarks*.—This well-marked member of the *rutilus* group is perhaps best characterized by its small auditory bullæ, very bright, narrow and sharply contrasted rufous mantle, short and rather thin fur. The colour and pelage, particularly the extent to which the tail and feet are clothed, are subject apparently to a good deal of seasonal change, which is but imperfectly understood, and perhaps is complicated by the house-haunting habits of the species. Some interesting notes by Mr. N. G. Buxton upon the food-stores and general habits of this vole have been published by Allen in the paper cited above.

### 19. *Evotomys jochelsoni* Allen.

1903. *Evotomys jochelsoni* Allen, Bull. Amer. Mus. N.H., 19, p. 148.

*Type*.—American Museum N.H., No. 19538; adult female, collected, February 1902, by W. Jochelson, of the Jessup North Pacific Expedition.

*Type locality*.—Verkhne Kolimsk, middle Kolyma River, N.E. Siberia.

*Characters*.—Size small (hind-foot 17 mm.; total length of skull 22 mm.). Back from front of crown to tail, bright rufous,

with a slight intermixture of black-tipped hairs; sides ochraceous, including the front and sides of the head; ventral surface bright buff. Tail dusky above, bright buff on sides and below, heavily clothed. Ears tipped with rusty internally.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This species is said by Dr. Allen to differ from *E. vosnessenskii* and *E. rutilus* in the much lighter red of the dorsal area, the strongly ochraceous sides, buffy under parts, and smaller size.

## 20. *Evotomys amurensis* Schrenck.

1859. *Arvicola amurensis* Schrenck, Reise Amur-lande, 1, p. 129; Poljakov, 1881, p. 55.

1907. *Evotomys amurensis* Thomas, P.Z.S., 1907, p. 413.

*Type*.—St. Petersburg [Leningrad] Museum, No. 1854-331; adult.

*Type locality*.—Mouth of the Amur River, near Nicolaïeff.

*Range*.—Amur; Saghalien (Thomas, P.Z.S., 1907, p. 413).

*Characters*.—Closely resembling *E. mikado* of Japan in general appearance, skull, and teeth. Size medium (hind-foot 18 mm.; condylo-basal length of skull about 24 mm.), tail rather long, about half length of head and body, and slender. Fur short and thin; hairs of the back attaining a length of about 10 mm. Colour dark and rich; mantle rather better defined laterally than in *E. mikado*, dark reddish brown; flanks and cheeks greyish tinged with ochraceous; under parts whitish-grey much darkened by hair bases. Tail very thinly haired, dusky above, yellowish-white below, with a thin pencil of dark and whitish hairs. Feet white, the soles very thinly haired, almost naked between heel and pads.

Skull smaller than in *E. mikado*, but very similar in all other respects. Cheek-teeth (Fig. 78, 5), showing a similar longitudinal crowding of parts;  $m^3$  with well-developed third inner fold and fourth inner angle, and with a fifth inner angle in youngish stages of wear.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—I am indebted to Mr. Montagu for notes upon the skull of the type in Leningrad Museum.

## 21. *Evotomys mikado* Thomas.

1905. *Evotomys mikado* Thomas, Abstr. P.Z.S., No. 23, p. 19, Dec. 5, 1905, P.Z.S., 1905 (1906), p. 352; *ibid.*, 1907, p. 413.

*Type*.—B.M., No. 6.1.4.296; adult female, skin and skull, collected Nov. 13, 1904, by M. P. Anderson; presented by the Duke of Bedford.



*Type locality*.—Aoyama, Hokkaido, Japan. Altitude 400 feet.

*Range*.—Hokkaido, Japan.

*Characters*.—Resembling *E. glareolus* in general appearance. Size medium (hind-foot 17 mm.; condylo-basal length of skull 24.7 mm.).

Rufous mantle covering the whole top of head and breadth of back, fairly well defined laterally, especially on the fore-quarters; rather redder than in *E. glareolus*, approaching "hazel" of Ridgway. Sides greyer. Belly washed with pale buff, not sharply defined laterally. Ears bright rufous. Hands and feet pale brownish-white above. Tail of medium length, well-haired and tufted, dark brown above, dull white below, the terminal tuft black above, whitish below.

Skull rather flatter than in *E. glareolus*, with a low weak muzzle and less convex frontal contour. Palatal foramina longer. Choanæ broad and low, their structure as usual. Compared with the skull of *E. amurensis* that of *E. mikado* is considerably larger, with slightly less expanded zygomata, narrower interorbital region and braincase, shorter molars, diastema, and nasals; nasals expanded anteriorly, but with straight lateral borders; rostral protuberances very salient; auditory bullæ rather large.

Cheek-teeth (Fig. 78, 6, 7) with the same essential pattern as in *E. glareolus* but, like those of *E. amurensis*, showing a remarkable antero-posterior compression, great breadth, and unusually sharp salient angles;  $m^3$  very complex with four outer and five inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

#### D.—*rufocanus* group.

### 22. *Evotomys rufocanus* Sundevall.

(Synonymy under subspecies.)

*Type locality*.—Lappmark, Sweden.

*Range*.—Northern Europe and Asia including Japan. In Europe southwards to Dovre, Norway; in Asia to the Syansk Mountains, Lake Baikal, Mongolia, Shansi, Korea, and southwards to Sze-chwan and Hupeh. Inhabiting Saghalien and ranging throughout Japan from Hokkaido southwards to Kiushiu and Shikoku.

*Characters*.—A robust species with massive skull and heavy *Microtus*-like cheek-teeth which, however, develop roots when perfectly mature.

Size large (hind-foot 17–21 mm.; condylo-basal length of skull in adults with rooted molars 25.3–28.5 mm. or more). Tail varying in length, in different subspecies, from about one-third to about two-thirds of the length of the head and body.

Ears large and rounded. Fur soft and dense, moderately long, from 10–14 mm. long on the back. Mantle sometimes (in the typical subspecies) narrow, sharply defined and bright rufous,

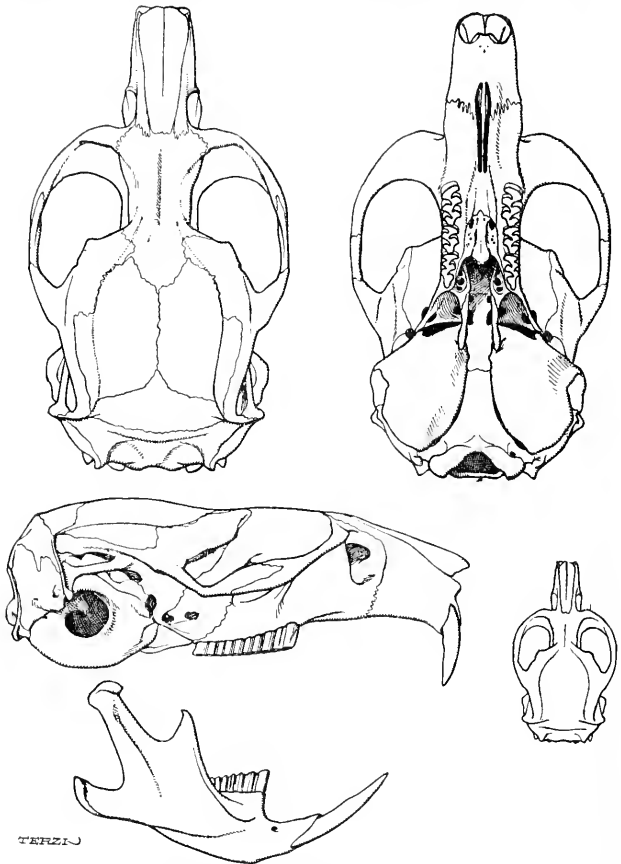


FIG. 80.—*Evotomys rufocanus rufocanus*.

Dorsal, ventral, and lateral views of skull, enlarged; the small figure represents the skull in dorsal view, natural size.

sometimes (in Far Eastern forms) diffuse and dull. Flanks and under parts more or less greyish. Hands and feet whitish or greyish above; soles rather densely haired (in adults) from the heel to the pads. Tail rather thinly or moderately clad with

hairs, the annulations usually more or less visible; provided with a thin terminal pencil, and more or less distinctly bicoloured. Mammæ,  $2 - 2 = 8$ .

Skull large and massive, resembling in these respects that of *E. casarius*, but more angular and "Microtus-like" than in that species. Zygomatic arches moderately divergent, but very light. Antorbital foramen unusually narrow. Rostrum and interorbital region rather long. Interorbital region moderately constricted, parallel-sided in adults; the superciliary ridges weak and widely separated in young adults, becoming stronger and more closely approximated in old age. Post-orbital squamosal crests large, sometimes tending to assume a peg-like form conspicuous in the dorsal view, sometimes larger, though less conspicuous, forming the entire edges of the shoulders of the braincase. Temporal ridges on braincase clearly defined, though not very salient. Braincase large and rectangular, the occiput more squarely truncated than usual in *Evotomys*. Palate usually narrow, but normal in structure; its posterior margin, however, often with a notched median projection. Choanæ narrow. Pterygoid fossæ rather short but deep, their floors distinctly dorsal (in adults) to the ventral surface of the basisphenoid. Auditory bullæ moderately large. Mandible normal; but  $m_3$  (robust and hypsodont like the other molars) more obviously displaced lingually by the shaft of the lower incisor, and more encapsuled than usual in *Evotomys*—a character giving the mandible a strong resemblance to that of *Microtus*, etc.

Cheek-teeth unusually large, heavy and tall-crowned, characterized by more perfect alternation of the inner and outer salient angles, by deeper infolds, and by tighter closure of the dentinal spaces than in other species of the genus; in these respects *E. rufocanus* makes a decided approach towards the condition found in *Microtus* and other higher genera. But, as in all other species of *Evotomys*, the cheek-teeth are of limited growth, for their enamel organs and dentinal pulps fail as old age advances, and fangs are then developed in the usual manner. While the teeth are growing, and for some considerable time after they have acquired roots, their hypsodont character is very noticeable, as their implanted portions occupy great capsules, which in the upper jaw rise considerably above the general level of the *corpus maxillaris*; the capsule of  $m^2$  is particularly conspicuous, as it forms a great mound blocking the mouth of the sphenorbital fissure, the outer surface of the mound being channelled antero-posteriorly by the infraorbital branch of the internal maxillary artery; but as age advances and as the base of each molar crown is gradually extruded from its alveolus the capsules subside and eventually disappear. In essential pattern the teeth agree with those of normal *Evotomys*;  $m^3$  is, however, in adults noticeably simplified, its posterior loop being shortened, its triangles tightly closed, and there being then only three salient angles on each

side (Fig. 81*d*); in young stages of wear the dentinal spaces are more confluent, the posterior loop longer, and there are more or less clear vestigial traces of one or two extra pairs of salient angles behind (Figs. 81*a*; 78 11*a*). In  $m_1$  the five triangles following the posterior transverse loop are usually substantially closed in adults, but the anterior or fifth triangle is sometimes narrowly confluent with the small anterior loop; in youth ephemeral complications of the anterior loop of this tooth are sometimes visible (Fig. 78, 1, 2), and the dentinal spaces are commonly more confluent with each

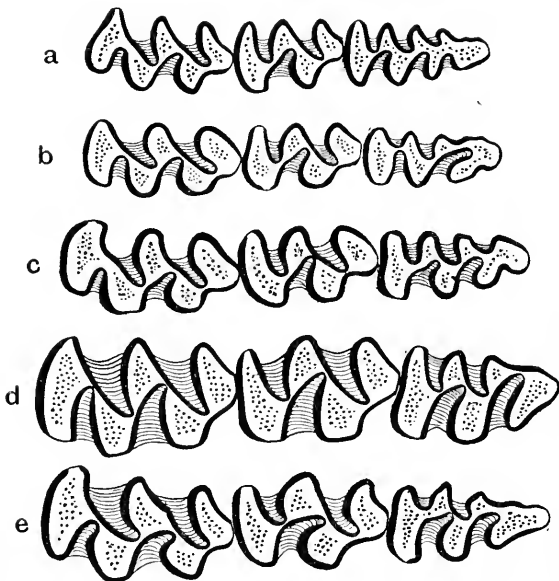


FIG. 81.—*Evotomys rufocanus* Sund. Upper Molars.

Explanation of Figs. 81 and 82: *a-d*. *E. r. smithii* (Japan); *a*, *a'*. B.M. No. 6.1.4.365, young; *b*, *b'*. 5.3.3.49, young (*type*); *c*, *c'*. 6.1.4.307, subadult

other. In  $m_2$  there is also a tendency to close two or more of the four triangles in front of the posterior loop (Fig. 82, *c'*, *d'*). Lastly, in extreme old age, when the basal parts of the crowns are exposed by wear, the pattern degenerates, the teeth acquiring again both confluent dentinal spaces and rounded salient angles similar to those of adult teeth in normal species of *Evotomys*.

*Geographical differentiation.*—A careful study of the material in the British Museum and of the literature leads me to believe that *E. rufocanus* as generally understood and all the many nominal species of "*Crascomys*" and "*Phaulomys*" that have been described in recent years from the Far East and from Central Asia must be referred to a single species. On the one hand, like

G. M. Allen, I find it, for reasons dealt with below, impossible to regard "*Crascomys shanseius*" Thomas as being more than a well-marked subspecies of *E. rufocanus*; on the other, I am unable to recognize more than a subspecific difference between *E. r. shanseius* and the forms inhabiting Korea and Japan.

In my opinion our present material warrants the recognition of only four well-marked subspecies of *E. rufocanus*, viz., *E. r. rufocanus* ranging throughout Northern Europe and Asia from Norway to Kamtschatka and southwards in Asia to the Syansk Moun-

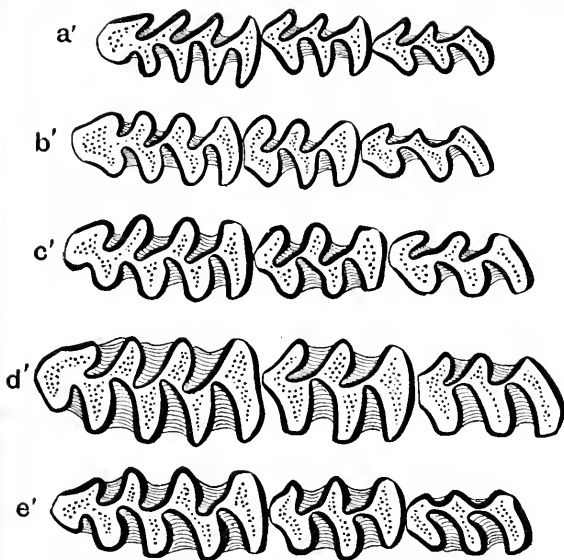


FIG. 82.—*Evotomys rufocanus* Sund. Lower Molars.

(type of "*Crascomys andersoni*"); d, d'. 6.1.4.298, adult (type of "*C. bedfordiae*"); e, e'. *E. r. rufocanus* (Irkutsk), 14.11.1.79, old.

tains and Lake Baikal; *E. r. shanseius* from China; *E. r. regulus* inhabiting Korea; and *E. r. smithii* ranging through Japan, including Saghalien. The characters distinguishing these subspecies may be "keyed" as follows:—

*Key to the subspecies of E. rufocanus*:—

- A. Mantle bright rufous, sharply defined, and conspicuously contrasted with face, flanks, and rump. Tail short, usually about one-third of head and body length. Skull with square braincase and small bullæ.

*E. r. rufocanus* Sundevall.

Northern Europe and Asia (Norway to Kamtschatka; south to Syansk Mountains and L. Baikal).

- B. Mantle dull, diffuse, not conspicuously contrasted with flanks.  
 a. Colour very pale; buffy-brown above. Tail short; skull with braincase and bullæ as in the typical form.  
*E. r. shanseius* Thomas.  
 Shansi, China.
- b. Colour dark; tail longer, usually about half length of head and body. Braincase long and narrow.  
 a<sup>1</sup>. Auditory bullæ large; palate wider.  
*E. r. regulus* Thomas.  
 Korea.
- b<sup>1</sup>. Auditory bullæ small; palate narrower.  
*E. r. smithii* Thomas.

22a. ***Evotomys rufocanus rufocanus*** Sundevall.

1846. *Hyppudæus rufocanus* Sundevall, Ofversigt af Köngl. Vetensk. Akad. Forhandl., 3, p. 122.
1847. *Lemmus rufocanus* Nilsson, Skand. Fauna. Däggdjuren, ed. 2, p. 365.
1874. *Arvicola rufocanus* Lilljeborg, Sver. og Norges Däggdjür, p. 292; Poljakov, Mém. Imp. Acad. Sci. St. Petersburg, 39, 1881, Appendix, p. 59.
1884. *Arvicola rufocanus* var. *kamtschaticus* Lataste, Ann. Mus. Civ. Storia Nat. Genova, 20, 1884, p. 284; based upon Poljakov's material from Kamtschatka preserved in the St. Petersburg Museum. Not *Arvicola kamtschatica* Poljakov, 1881.
1897. *Evotomys rufocanus* Bailey, Proc. Biol. Soc. Washington, 11, p. 122; Miller, Catal. Mamm. W. Europe, 1912, p. 648.
1898. *Microtus rufocanus* Collett, Nyt. Mag. f. Naturw., 36, p. 280; Кастченко, апрель. млекопит. ивотн. Томскаго Края. Томск, табл. 44. 1900.
1900. *Evotomys (Craseomys) rufocanus* Miller, Proc. Washington Acad. Sci., 2, p. 87.
1903. *Evotomys (Craseomys) latastei* Allen, Bull. Amer. Mus. N.H., 19, p. 145; renaming *Arvicola rufocanus* var. *kamtschaticus* Lataste.
1911. *Evotomys rufocanus* Collett, Norges Pattedyr, p. 96.
1912. *Evotomys (Craseomys) rufocanus latastei* Thomas, Ann. Mag. N.H., [8], 9, p. 397.
1924. *Evotomys (Craseomys) irkutensis* Ognev, Bull. Soc. Nat. Moscow, N.S., 31, p. 69; described from утулик, горы Хамар-Дабан, Province of Irkutsk (type an adult female, No. 3909, Mus. Zool. Univ. Moscow).
1924. *Craseomys rufocanus bargusineusis* Turov, Comptes Rendus de l'Acad. Sci. Russie, 1924, p. 110; described from the N.E. shore of Lake Baikal.

*Type*.—Stockholm Museum.

*Type locality*.—Lappmark, Sweden.

*Range*.—Northern Europe and Asia; in Europe southwards, in the mountains of Norway, to Dovre; in Asia east to Kamtschatka and south to the Syansk Mountains, the shores of Lake Baikal, and probably to the Kinghan Mountains in Northern Mantchuria.

*Characters*.—Size slightly smaller<sup>1</sup> than in Far-Eastern

<sup>1</sup> COLLETT (Norges Pattedyr, 1911, p. 96) states, however, that the total length rises to 160–170 mm. or more, of which the tail is 30–36 mm. or

subspecies; hind-foot 17-19 mm.; condylo-basal length of skull in adults with rooted molars 25.3-27.6 mm. Tail rather short, usually about one-third of the length of the head and body. Mantle sharply defined and bright rufous in adults.

Fur soft and dense, rather long, attaining a length of 12-14 mm. on the back. Mantle bright rufous in adults, narrow, sharply defined, usually conspicuously contrasted with surrounding grey parts, and extending from the interorbital region backwards, between the inner bases of the ears, to the rump. Muzzle, cheeks, flanks, and rump grey, darkened by the slaty bases of the hairs. Ears concolorous with the flanks, but the hairs of the pre-auricular and post-auricular patches with yellowish or pallid tips. Hands and feet whitish grey above; soles rather densely haired from the heel to the central pads. Tail rather thinly clad with long stiff hairs, forming a thin terminal pencil of about 10 mm. in length, but not completely concealing the annulations; bicoloured, blackish above, dirty white below.

The colour of the upper parts and the degree to which the rufous mantle contrasts with the surrounding grey tones vary considerably with individual age and with season, the tones being duller and darker in the younger, brighter in the adults, darker in summer and paler in winter. According to Collett there is also a sexual difference, females being often duller than the males. In adults the mantle varies between "hazel" and "cinnamon rufous," and is lightly lined by long black hairs, and dusky hair-tips; but in the young and adolescent it is darker, approaching a deep reddish-chestnut. The surrounding grey parts are more pallid and more sharply contrasted with the mantle in adults; deeper, richer, and less contrasted in young and adolescent individuals.

Skull slightly smaller<sup>1</sup> than in other subspecies, its condylo-basal length not or rarely exceeding 27.5 mm., the cement spaces of the molars closing when the condylo-basal length reaches about 24.5 mm. Braincase relatively short, nearly square in outline. Post-orbital crests of squamosals short, forming prominent peg-like processes in adults. Palate narrow. Auditory bullæ rather small.

Cheek-teeth of normal pattern in adults. In young stages of wear,  $m^3$  rather simpler than in some Far-Eastern forms, the fourth outer and fourth inner salient angles usually represented only by ephemeral vestiges.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—The material before me comprises a small but

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more; length of skull 28-29.5 mm. It is probable, therefore, that there is no real difference in size between *E. r. rufocanus* and the large forms of Korea and Japan.

<sup>1</sup> As already noted, considerably larger specimens (with a total length of 29.5 mm.) are recorded by Collett.

representative set of specimens from Scandinavia (including some received from Sundevall); a series from the Syansk Mountains, 100 miles west of Lake Baikal, collected by D. Carruthers; a very fine series from the neighbourhood of Lake Baikal, province of Irkutsk, collected by G. A. Burney; and three specimens from Kamtschatka obtained by Barrett-Hamilton. It thus affords topotypical material not only of Sundevall's *E. rufocanus*, but of the nominal forms *E. r. latastei* Allen, *E. irkutensis* Ognev, and *E. bargusinensis* Turov, as well. What is equally important, it represents all stages of growth, from the young with a skull of only 19.3 mm. in condylo-basal length to an aged individual with a skull measuring 27.2 mm. and cheek-teeth provided with long roots.

After carefully studying this material and the literature cited in the synonymy I can find no good reason for believing that there is more than one form of *E. rufocanus* within the vast area indicated above. For completeness' sake the following notes on the characters attributed to the nominal forms are given:—

(1) *E. r. latastei* Allen, is said to be distinguished from the typical form by its much smaller size, less angular teeth, rounder auditory bullæ, less fulvous under parts and darker grey sides. As evidence of the smaller size Allen gives the following measurements of ten "adults" from Gichiga, northern Kamtschatka:—total length 128 (120–140) mm.; tail 29 (24–33); hind-foot 19 (18–20); and for the skulls of six "adults":—total length 23.6 (22.5–25); basal length 20.5 (19–22); zygomatic breadth 13 (12–13.8); nasals 6.2 (5.7–6.5). These statements indicate, in my opinion, that Allen's material is not adult but immature; making allowance for this and for possible differences in the methods of taking the external measurements his account of *E. r. latastei* discloses no solid reason for separating this form from typical *E. r. rufocanus*. The few specimens from Kamtschatka before me are adults and they appear to agree in every respect with those from Scandinavia.

(2) *E. r. bargusinensis* Turov. Dr. Turov has kindly furnished the following diagnosis:—"Longitudo corporis minor quam in typica *E. rufocanus*, corporis longitudo 90.2–102. Planta exclusis unguibus multo minor (16.8–17.8) quam in forma typica. Cranium minus, longitudo condylo-basalis 25.4–27.6; spatium interorbitale angustum (3.6–3.8). Ossa nasalia longiora quam in forma typica (ad. 8.5). Dentium molarium series brevior (6–6.6). Color opaco-fuscus plerumque in rufum vergens vix distinguitur a forma typica colore, griseo in capitis lateribus atque corporis lateribus fulvo brunnescentibus." The facts (as distinct from the comparisons) recorded in this diagnosis, seem to me to agree perfectly with those observed in typical *E. rufocanus*; moreover Mr. Burney's fine series from the north-western shore of Lake Baikal is practically topotypical of *E. "bargusinensis,"* and I am quite unable to distinguish these specimens from those from Scandinavia.



(3) *E. irkutensis* Ognev. "Fur long and bushy, the hairs in summer coat attaining a length of 15.2 mm. Mantle rusty-brownish, narrow, the dirty buffy grey of the flanks extending far up dorsally: fore-part of head and cheeks grey yellowish-buff. Under surface dirty white with an evident buffish tint. Hind-foot with six pads. Skull smaller than that of *E. ussuriensis*; coronal suture pressed a little backwards. Cheek-teeth with the comparatively narrow enamel loops lengthened; posterior loop of  $m^3$  visibly stretched."

*Measurements*.—Head and body 88.2–117.8 mm.; tail 28.1 (subad.)–42.7; hind-foot ("w. claws") 16.7–18.6; ear 12.7 (subad.)–15.7. Skull: total length 25.5–26.5; condylo-basal (probably condylo-basilar) length 24–25.5; greatest breadth of cranium 12.7–12.9; zygomatic breadth 13.2 (subad.)–14.6–14.8 (ad.); height of "basioccipital region" 7.2–7.4; length of nasals 7.5–8.2; upper molars 6.1–6.3.

Neither in this account nor in the figures of the skull and teeth published by Ognev can I find any reason for distinguishing "*irkutensis*" from *E. r. rufocanus*. In addition Mr. Montagu has kindly examined Ognev's type in Leningrad for me, and he tells me that he could not distinguish it from *E. rufocanus*; he found the condylo-basal length of the oldest skull to be 26.4 mm., so that by "condylo-basal length" Ognev probably means the shorter "condylo-basilar" measurement.

In an account of the voles obtained by the second and third Asiatic expeditions of the American Museum, Mr. G. M. Allen<sup>1</sup> says:—"A good series [of *E. rufocanus*] was secured along the southern border of the forest at stations fifteen miles north and forty-five miles north-east of Urga, Mongolia, as well as at Sain Noin Khan to the westward. It seems to occur, therefore, in the same general localities as the smaller red-backed mouse [*E. rutilus*]. I have carefully compared this series with topotypes of *rufocanus* from Sweden and can find no tangible differences."

### 22b. *Evotomys rufocanus shanseius* Thomas.

1908. *Craseomys shanseius* Thomas, P.Z.S., 1908, p. 643; *ibid.*, 1908, 1909, p. 978.
1908. *Microtus (Eothenomys) incz* Thomas, Abstr. P.Z.S., 1908, p. 45, and P.Z.S., 1908, 1909, p. 976; *type*: B.M., No. 9.1.1.188, immature female, skin and skull, collected May 28, 1908, by M. P. Anderson, and presented by the Duke of Bedford; *type locality*: Mountains 12 miles N.W. of Ko-lan-chow, Shan-si, China. Altitude 7000 feet.
1910. *Microtus (Eothenomys) nur* Thomas, Abstr. P.Z.S., 1910, p. 26, and P.Z.S., 1910, p. 636; *type*: B.M., No. 10.5.2.79, immature male, skin and skull, collected November 29, 1909, by M. P. Anderson, and presented by the Duke of Bedford; *type locality*: Shang-chow, S.E. Shen-Si, China. Altitude 3300 feet.
1911. *Microtus (Caryomys) eva* Thomas, Abstr. P.Z.S., 1911, p. 4, and P.Z.S., 1911, p. 175; *type*: B.M., No. 11.2.1.223, immature

<sup>1</sup> Amer. Mus. Nov., No. 133, 1924, p. 3.

- male, skin and skull, collected April 3, 1910, by M. P. Anderson, and presented by the Duke of Bedford; *type locality*: Mountains, S.E. of Tau-chow, Kan-Su, China. Altitude 10,000 feet.
1911. *Microtus (Caryomys) inez* Thomas, P.Z.S., 1911, p. 176.
1911. *Microtus (Caryomys) nux* Thomas, P.Z.S., 1911, pp. 176 and 691.
1911. *Microtus (Caryomys) alcinous* Thomas, Abstr. P.Z.S., 1911, p. 50. and P.Z.S., 1912, p. 140; *type*: B.M., No. 11.9.8.136, immature male, skin and skull, collected November 24, 1910, by M. P. Anderson, and presented by the Duke of Bedford; *type locality*: Wei-ehoe, Si-ho River, W. Sze-chwan, China. Altitude 8000 to 10,000 feet.
1912. *Crasomys aquilus* G. M. Allen, Mem. Mus. Comp. Zool., Harvard Coll., 40, p. 216; *type*: Mus. Comp. Zool. Harvard, No. 7190, "adult" [immature] male, skin and skull, collected May 17, 1907, by W. R. Zappey; *type locality*: Showlungtan, Hupeh, China. Altitude 7000-9000 feet.
1923. *Caryomys inez* Hinton, Ann. Mag. N.H., [9], 11, p. 162.
1924. *Evolomys rufocanus shanseius* G. M. Allen, Amer. Mus. Nov., No. 133, p. 3.
1924. *Microtus (Caryomys) aquilus* G. M. Allen, Amer. Mus. Nov., No. 133, p. 6.

*Type*.—B.M., No. 8.8.7.85; subadult male ( $m^2$  still growing), skin and skull; collected December 4, 1907, by M. P. Anderson, and presented by the Duke of Bedford.

*Type locality*.—100 miles N.W. of Tai-Yuen-Fu, Shan-si, North China. Taken in a spruce forest at an altitude of 8000 feet.

*Range*.—Mountains of Northern, Western and Central China; extending from Shan-si eastwards towards Mongolia where it probably intergrades with both *E. r. rufocanus* and *E. r. regulus*, and southwards into the mountains of Shen-si, Kan-su, Sze-chwan and Hupeh.

*Characters*.—Size, proportions, and skull essentially as in the typical subspecies; colour of upper parts sandy in adults.

*Adult pelage* (in typical series).—Fur long, soft and loose; hairs of back (in winter coat) 12-13 mm. in length. Mantle fairly sharply defined, essentially as in *E. r. rufocanus*, but much paler, its colour a dull, pale yellowish brown (not far from "Dresden brown"), darkened inconspicuously by a sprinkling of long black hairs. Face, sides, and rump grey, without rufous suffusion, but the hairs covering ears and those of the post-auricular patches with yellowish or rufous tips. Under surface lighter, the long tips of the hairs pale cream buffy, their general effect much darkened by the slaty hair-bases. Hands and feet white above; soles rather densely haired. Tail densely clad (in winter) with stiff hairs, the annulations not visible, brown above, whitish or cream-coloured on sides and below. Adults in summer pelage (Shan-si or typical series) are slightly paler and duller with thinner coats; in them the tail is much less hairy, the annulations being distinctly visible.

Young in first pelage dusky; between this blackish coat and

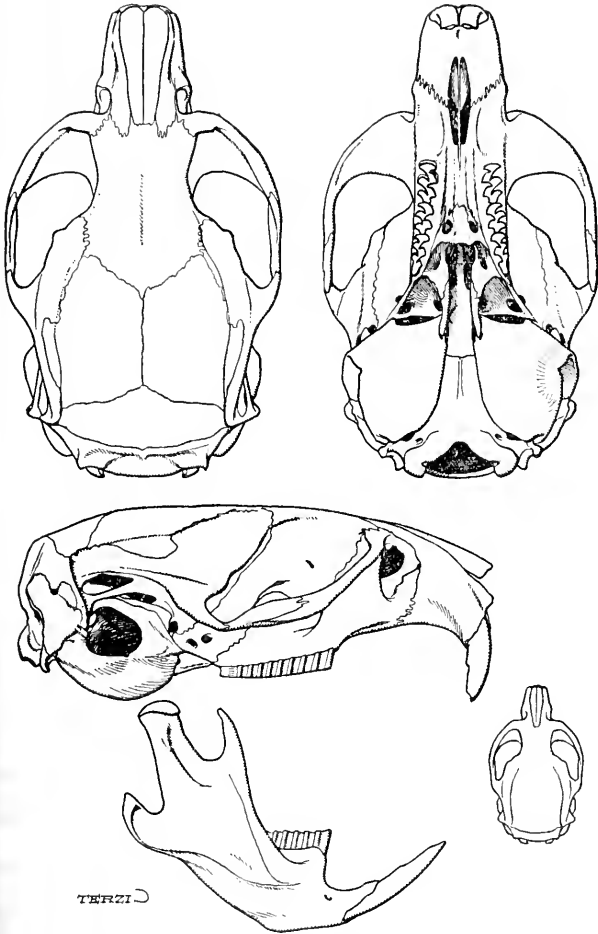


FIG. 83.—*Evotomys rufocanus shanensis* Thomas.

Young skull, one of the typical series of "*Caryomys incz.*" Dorsal, lateral, and ventral views.

the sandy dress of the fully adult animal in winter there is a long series of intermediate pelages, in the course of which the colour is gradually changed, the mantle becoming at the same time less diffuse and more evidently contrasted with the face and flanks.

Skull and teeth essentially as in *E. r. rufocanus*. The only specimen before me in which the teeth are rooted is unfortunately imperfect; in it the dental length is 15.4 mm., a dimension which indicates probably a condylo-basal length of about 25.8. On the other hand, in the three largest specimens (26.3–26.7)  $m^2$  is still growing, as it is also in equal-sized skulls of *E. r. regulus* and *E. r. smithii*, although in such equal-sized skulls of *E. r. rufocanus* as are available, the teeth are in all cases rooted (see table at p. 261).

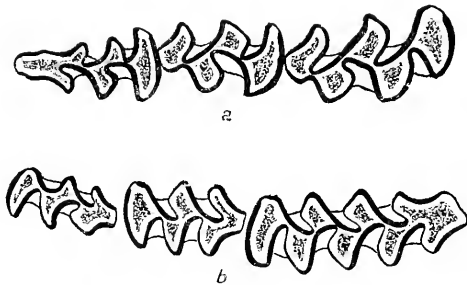


FIG. 84.—*Evotomys rufocanus shanseius* Thomas.

Cheek-teeth of young specimen, one of the typical series of "*Caryomys inez*"; a. right upper, b. left lower molars.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—As the synonymy given above indicates, "*Caryomys*" and its five species have been based upon immature specimens of *E. rufocanus* and the systematic history of this species in China thus affords an exact parallel to its systematic history in Japan (see p. 257 below), where the young were referred to a special genus "*Phaulomys*" and the adults to "*Craseomys*."

After carefully comparing all the available material representing the five nominal species of "*Caryomys*" with the long series from Japan hitherto referred to "*E. (Phaulomys) smithii*," I can find no character in either the skull or the teeth by which the one series can be distinguished from the other. The "species" of "*Caryomys*" differ from each other rather strikingly in colour, but those differences arise also from differences of age, and even the extremes find close matches in the "*smithii*" series from Southern Japan. The following details may be given:—

(1) "*Caryomys inez*":—Based on eighteen specimens collected

May 28 to June 5, 1908; hind-foot 15.5-16 mm.; condylo-basal length 19 (one skull with teeth very slightly worn) to 23.7 mm. General colour of larger specimens exactly as in *E. r. shanseius* (adults), collected at the same spot, where it was "much less common than the last," i.e., "*C. inez*"—adults usually are less common than young in early June. If further we assume that post-natal growth in "*C. inez*" enlarges the skull to the same relative degree as in other voles, then a skull with very slightly worn teeth measuring 19 mm. may be taken as indicating that a fully adult example would measure not less than 27 mm., and that is approximately the measurement of an adult skull of *E. r. shanseius*.

(2) "*Caryomys mux*":—Based upon twenty-three specimens collected in the neighbourhood of the type locality between November 20 and December 6, 1909; hind-foot 15-16 mm.; condylo-basal length 22.4-23.7 mm.; colour described as darker brown than in "*C. inez*," tail more distinctly bicoloured and averaging slightly longer. These specimens are of about the same age as those referred to *C. inez*; the differences in colour are probably seasonal; the slightly greater length of the tail is well within the limits of individual or colonial variation.

(3) "*Caryomys eva*":—Based upon four specimens collected at the type locality on April 3, 1910; eleven other specimens from the same district collected between September 13 and October 25, 1911; hind-foot 14-16 mm.; condylo-basal length 20.8-22.9 mm. Colour about as in "*C. inez*"; tail longer, 42-51 instead of 31-37 mm. These specimens are obviously a little younger than those upon which *C. inez* and *C. mux* are based; in the absence of any other character I am not inclined to attach any systematic importance to differences in the length of the tail in such young specimens; these differences are not greater than those to be observed in the specimens from Japan, referred to *E. r. smithii*.

(4) "*Caryomys alcinous*":—Based upon thirteen specimens collected at the type locality November 20-24, 1910; hind-foot 16.5-17 mm.; condylo-basal length 21.4-23.4 mm. Colour dusky, hands and feet dark brown; tail blackish above, little lighter below, long as in "*C. eva*" (48-54 mm.). These specimens are evidently still in the first pelage, and as regards colour, they can be exactly matched in the long series of "*E. (Phaulomys) smithii*" from southern Japan.

(5) "*Caryomys aquilus*":—Based upon six specimens from various localities in Hupeh. Hind-foot 17-20; tail 52-59 mm. The second largest specimen of the series is now in the British Museum (No. 13.9.13.3 female); it is obviously quite immature with a condylo-basal length of 23.3 mm., and I can find no character that will distinguish it from "*C. eva*" or "*C. mux*."

Summing up "*C. inez*" is definitely shown to be a synonym of *E. r. shanseius*; with existing materials neither "*C. mux*," "*C. eva*," "*C. alcinous*" nor "*C. aquilus*" can be distinguished satisfactorily from "*C. inez*," and for the present, they must therefore be relegated to the synonymy. But adult material from the various type localities may well show some subspecific differences, in which event one or more of these names will have to be resuscitated for subspecies.

*E. r. shanseius*, as represented by adults from the type locality and its vicinity, is a well-marked subspecies intermediate between the typical *E. r. rufocanus* and the subspecies

inhabiting Korea (*E. r. regulus*) and Japan (*E. r. smithii*), agreeing with *E. r. rufocanus* in general size, shortness of tail, extent and definition of mantle, and in the form of the skull and teeth, but approaching the Far-Eastern forms in general colour. It is thus the connecting link which prevents a specific severance of the bright-coloured, short-tailed boreal form from the dark-coloured, longer-tailed forms of Korea and Japan. Northwards from Shan-Si, it probably intergrades with *E. r. rufocanus*, eastwards with *E. r. regulus*, and to the south in Sze-chwan and Hupeh, judging from the immature specimens alone known from those provinces, it makes a near approach to *E. r. smithii* in character.

Mr. G. M. Allen says (Amer. Mus. Nov., No. 133, p. 3, 1924) that the series obtained by the Asiatic expeditions of the American Museum, "including ten from Kwei-hwa-ting, Shansi, and five from one hundred miles north-east of Peking, indicates that its range passes into that of *rufocanus* on the eastward, although separated from it on the north by the Gobi plateau and Ordos desert in Mongolia. Indeed, Thomas has referred a single specimen from sixty miles east of Peking to *regulus*, but the additional skins from that region secured by the Asiatic Expeditions . . . are quite indistinguishable from the pale form, *shanseius*. These two forms should be regarded as geographic subspecies of *E. rufocanus*"—a conclusion to which I have independently come.

#### 22c. *Evotomys rufocanus regulus* Thomas.

1907. *Craseomys regulus* Thomas, P.Z.S., 1906, p. 863; *ibid.*, 1908, p. 643.

1924. *Evotomys rufocanus regulus* G. M. Allen, Amer. Mus. Nov., No. 133, p. 3.

*Type*.—B.M., No. 6.12.6.89; subadult male (in adult pelage, but  $m^2$  still growing), skin and skull; collected November 25, 1905, by M. P. Anderson; presented by the Duke of Bedford.

*Type locality*.—Min-gyong, 110 miles south-east of Seoul, Korea. Altitude 1100–1300 feet.

*Range*.—Korea and westwards into northern China, where it may meet and perhaps intergrade with *E. r. rufocanus*.

*Characters*.—A long-tailed, short-coated, dark-coloured form with diffuse mantle and enlarged auditory bullæ.

Size as in other subspecies, hind-foot to 21 mm., condylo-basal length of skull in available material to 27.8 mm., but probably reaching 29 mm. in old age. Tail rather long, usually about 40% of the head and body length. Fur rather short and dense; in winter attaining a length of 8–9 mm. on back. Colour dark, the mantle scarcely defined. General colour of upper parts coarsely lined cinnamon-brown in most specimens, but darkening in adults to a rich and beautiful cinnamon-rufous or hazel of unusual intensity. Sides paler, without definite line of demarcation from either back or belly. Under surface broadly washed

with pinkish-buff and darkened by the slaty hair-bases. Glandular patches present on flanks, but not conspicuous. Ears well clothed with rufous hairs. Hands and feet buffy white above; soles hairy. Tail shorter than in *E. r. smithii*, well clothed with short stiff hairs which do not completely conceal the annulations; bicoloured, brown above (blackish at tip), cream buff below. Young specimens are much darker than adults.

Skull with the braincase, as in *E. r. smithii*, longer and less nearly square than in *E. r. rufocanus*; distinguished from that of all other subspecies by its rather wider palate and slightly larger auditory bullæ.

Cheek-teeth, in adult stages of wear, as in other subspecies; but as in *E. r. smithii*  $m^3$  in young stages of wear tends to be more complex than is usual in young *E. r. rufocanus* and *E. r. shanseius*, the ephemeral vestiges of the fourth inner and outer salient angles being usually clearly developed.

Size is apparently as variable in this subspecies as in others; the smallest skull with rooted teeth seen has a condylo-basal length of 25.7 mm.; on the other hand in the largest skull examined, with a condylo-basal length of 27.3 mm.,  $m^2$  is still growing. Fully mature skulls may therefore easily reach a condylo-basal length of 29 mm. or more.

For *external and cranial dimensions* see tables at end of volume.

## 22d. *Evotomys rufocanus smithii* Thomas.

1905. *Evotomys (Phaulomys) smithii* Thomas, Ann. Mag. N.H., [7], 15, p. 493; Thomas, P.Z.S., 1905, 1906, p. 355.
1905. *Evotomys bedfordiæ* Thomas, Abstr. P.Z.S., No. 23, Dec. 5, 1905; described from Shinshinotsu, near Sapporo, Hokkaido, Japan. *Type*: B.M., No. 6.1.4.298; adult male, skin and skull; collected Sept. 10, 1904, by M. P. Anderson, and presented by the Duke of Bedford.
1905. *Evotomys andersoni* Thomas, Abstr. P.Z.S., No. 23, Dec. 5, 1905; described from Tsunagi, near Morioka, Iwate Ken, North Hondo, Japan. *Type*: B.M., No. 6.1.4.307; subadult male, skin and skull, collected by M. P. Anderson, Oct. 10, 1904, and presented by the Duke of Bedford.
1906. *Evotomys (Craseomys) bedfordiæ* Thomas, P.Z.S., 1905, p. 353.
1906. *Evotomys (Craseomys) andersoni* Thomas, P.Z.S., 1905, p. 354.
1907. *Craseomys bedfordiæ* Thomas, P.Z.S., 1907, p. 413.
1909. *Craseomys niigatæ* Anderson, Ann. Mag. N.H., [8], 4, p. 317; described from Akakura, Niigata Prefecture, Hondo, Japan. *Type*: B.M., No. 8.12.1.65; young male (condylo-basal length of skull 25.4 mm., cheek-teeth still growing), skin and skull; collected by K. Kanai, Sept. 7, 1908, and presented by the Hon. N. C. Rothschild.

*Type*.—B.M., No. 5.3.3.49; immature male, skin and skull, collected February 24, 1906, and presented by R. Gordon Smith.

*Type locality*.—Kobe, Hondo, Japan.

*Range*.—Japan, including the islands of Kiushiu, Shikoku, Hondo, and Hokkaido.

*Characters*.—A long-tailed, dark-coloured form with diffuse mantle.

Size as in other subspecies, hind-foot in adults to 21 mm., condylo-basal length of skull to 28.5 mm. or more. Fur soft, moderately long and dense, attaining a length of about 10 mm. on the back. Tail relatively longer than in *E. r. rufocanus*; usually from 40 to 50% of the head and body length; thinly clothed with short stiff hairs, the annulations plainly visible in summer, nearly concealed in winter; terminal pencil very short and thin.

Colour dark, varying considerably with age, but always much less rufous above than in *E. r. rufocanus*. Mantle diffuse, covering the whole upper surface in young in post-juvenal pelage, but less extensive and rather better defined in subadult and adult specimens, although never becoming so restricted and so sharply contrasted with the surrounding parts as in the typical subspecies. In adults, although the tips of the ears are concolorous with the flanks as in *E. r. rufocanus*, the mantle extends forwards over the muzzle and invades the cheeks, instead of being confined to the area between the eyes and between the ears, and behind it fully covers the rump. In colour the mantle is yellowish—rather than reddish-brown, and more or less inconspicuously darkened by long black hairs and dusky hair-tips, its precise hue ranging between russet and dark chestnut. Some young specimens are much darker, their dorsal colour approaching dark vandyke-brown. Cheeks and flanks paler and greyer in adults; not conspicuously greyer than the back in immature specimens. Under surface not sharply defined, grey more or less heavily washed with ochraceous- or cream-buff. Hands and feet grey above, the digits sometimes whitish; soles hairy between the heel and pads. Tail more or less distinctly bicoloured, brown above, greyish or whitish below.

Skull when adult distinguished from that of *E. r. rufocanus* by its longer and narrow braincase, and by its more extensive but, in dorsal view, less conspicuously salient post-orbital squamosal crests. Skulls of young specimens (condylo-basal length 22.5–25.5 mm.) much resemble those of normal species of *Evotomys*. The superciliary ridges, if developed at all, are feeble and confined to the margins of the orbits in specimens measuring less than 24.5 mm.; in later stages they become stronger and approach each other slowly, the anterior ends of the ridges being first to show signs of approximation; later and gradually the movement affects the whole ridge on each side, so that the ridges become parallel throughout, instead of being anteriorly convergent; in the oldest skull examined (condylo-basal length 28.5 mm.) they are moderately strongly developed, parallel, and separated from each other merely by an interval of 1.9 mm.

The cement spaces of the cheek-teeth ( $m^2$ ) may show signs of closure when the condylo-basal length amounts to no more than



24.8 mm.; on the other hand, specimens already 27.1 mm. long may still have  $m^2$  in vigorous growth; but all the larger specimens examined have the cement spaces of  $m^2$  closed and the roots more or less well developed. These facts probably indicate that in this as in other subspecies individuals may vary considerably in size, the range of variation in skull length probably amounting to about 3 mm. in any given subadult or adult stage of growth.

Cheek-teeth in adult stages of wear essentially as in the typical subspecies. In young individuals  $m^3$  is much more complex than it is as a rule in equally young *E. r. rufocanus*, having four salient angles on each side with an occasional trace of a fifth outer salient angle. Very often in such young specimens the first inner infold is relatively shallow, so as to leave the first pair of triangles, following the anterior loop, more or less broadly confluent with each other. As age advances and wear exposes deeper portions of the crown upon the grinding surface, all the triangles become substantially closed, the posterior or fourth salient angles on each side die out, and the posterior loop is gradually shortened until the tooth acquires exactly the form and appearance it has in adult specimens of *E. r. rufocanus* (Fig. 82). In lower molars also the dentinal spaces of  $m_1$  and  $m_2$  are more confluent in young stages of wear than they are in middle age, when the triangles become substantially closed as in the adults of other forms of the species. Ephemeral complications of the fore-part of  $m_1$  are sometimes to be observed in the young (Fig. 78, 1, 2). In extreme old age certain of the dentinal spaces open out again and the salient angles acquire that peculiar rounding so characteristic of the adult teeth of normal species of *Evotomys*.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—A careful study of the magnificent material which the British Museum owes to the generosity of the Duke of Bedford leaves no room for doubting that *E. smithii*, *E. "bedfordiae"*, *E. "andersoni"*, and *E. "niigata"* belong to one form and if the material representing each of these nominal species had arrived on one and the same day all would, in my opinion, have been inevitably treated as one form. Voles are always difficult animals to deal with, and *E. rufocanus* is an especially difficult vole. A species in which the skull looks quite adult when the condylo-basal length measures only 23.7 mm. and then proceeds to grow to about 29 mm., its progress being marked by great changes in form as well as in size, offers a series of fine pitfalls for the energetic systematist. To make the matter more difficult, an adult pelage is acquired and sexual maturity is attained at a very early stage of growth. In these circumstances long series of specimens from single localities afford no absolute safeguard against error; indeed, as in the present case, they may help at first to mislead. In one locality where voles are breeding fast, and where there is perhaps

a suspicion of mouse plague, it is only too easy to collect a very long series of specimens, the oldest of which is scarcely adolescent. In another district, where breeding has slowed down for a time, subadults may form the great bulk of the catch. Elsewhere, after temporary cessation of breeding, the series will consist chiefly of adult and sometimes of aged animals. The result is that three separate parcels of voles come before the systematist on different days; each represents a definite locality, and each possesses a definite character of its own, the individuals in each parcel forming a very uniform series. Small wonder that the systematist hastens to describe each batch as it arrives as a new species. But on the day of revision the contents of all the parcels come together before the reviser. For a long time he struggles to make a "key" to the characters of the described forms; but the characters cannot be "keyed," and it becomes evident that there is something wrong. Throwing the lot into a heap the reviser begins by determining the relative ages of the skulls of all the specimens, and as they arrange themselves in order of length he sees at last that he is not dealing with so many distinct species and subspecies but with so many different stages of growth. That is exactly what has happened in the present case.

*E. (Phaulomys) smithii* was based upon a young male, obtained in February 1904; by accident the fifty-three specimens of the series collected in Hondo, Kiushiu, and Shikoku, by M. P. Anderson in the following year are all young too. The condylo-basal length in the largest of them is only 24.5 mm., and in all, the skull is like that of an ordinary *Evotomys*, the teeth stamped with the peculiarities of young *E. rufocanus*, and vigorously growing.

Later on Mr. Anderson collected thirteen in Hokkaido. The majority of these are adult, some even old; in size, skull form, and tooth pattern they are strikingly different from the material referred by Thomas to *E. smithii*. These were therefore described as a new species, *E. (Craseomys) bedfordiæ*. But two specimens of this original series of *E. bedfordiæ* are immature, and these are not distinguishable from the material upon which *E. smithii* was founded.

In the same paper *E. (C.) andersoni* was described, from two specimens obtained in North Hondo, as "very like *bedfordiæ* externally, but with longer tail, and much less powerful teeth." Both specimens, however, are merely large adolescents, intermediate in age between the adult material upon which *E. bedfordiæ* was established and the immature material referred to *E. smithii*—hence the less powerful teeth as compared with *E. bedfordiæ*. As regards the length of the tail, there is nothing in that; for later specimens from Hokkaido show that in *E. bedfordiæ* the tail may measure 58 mm., and it is only 54 in *E. andersoni* (as in the type of *E. smithii*). Lastly, Anderson's *E. niigata* also has been founded upon an adolescent animal; its tail, though long, averaging about 61 mm. in a series of seven, can be matched quite well in the

Total No. and range.	<i>Evotomys r. rufocanus.</i>		<i>Evotomys r. shansicus.</i>		<i>Evotomys r. regulus.</i>		<i>Evotomys r. smithii.</i>	
	(19)	(19-3-27-2 mm. Dental L. Molars. $m^2$ .)	(15)	(21-2-26-9 mm. Dental L. Molars. $m^2$ .)	(27)	(21-9-27-8 mm. Dental L. Molars. $m^2$ .)	(65)	(20-6-28-5 mm. Dental L. Molars. $m^2$ .)
C.-B.L.								
19-19-9	1	11-7	4-9	growing				
20-20-9	1	11-9	5-1	do.				
21-21-9	—	—	—	—	1	13-3	5-5	growing
22-22-9	1	13-3	5-3	growing	1	12-8	5-2	growing
23-23-9	2	13-8	5-1	growing	1	13-6	5-3	growing
		14-1	5-4		2	13-8-14	5-3-5-4	growing
24-24-9	3	14-3-14-4	5-2-5-8	growing 1 closed 2	4	14-3-15	5-7-6-1	growing
25-25-9	3	14-5-15-4	5-7-6	0 growing 1 closed 1 short 1 pro-truding	4	15-15-5	5-8-6-2	3 growing 1 rooted
26-26-9	7	15-1-15-8	5-6	6-2 all rooted (5 long roots)	3	15-7-15-9	6-2-6-3	growing
27-27-9	1	15-4	6	long roots				
28-28-9	19				15			
					6	15-3-15-8	5-5-6	4 growing 1 closing 1 rooted
					2	15-7-16-1	5-7-6	growing
					6	14-7-15-4	5-4-6	4 growing 2 rooted
					4	14-1-14-5	5-3-5-6	growing
					10	14-1-15	5-5-5-9	9 growing (2 nearly finished), 1 closed, 7 growing 1 closed.
					9	14-8-15-5	5-6-6	7 growing 1 closed.
					14	15-4-16-2	5-8-6-2	3 growing, 5 closed, 6 rooted.
					5	15-7-16-5	5-8-6-2	1 growing, 2 closed, 2 rooted.
					2	16-9-17-1	6-2-6-6	2 with long roots.
					65			
					27			

series referred to "*bedfordiæ*" and "*smithii*," and no other character can be found to give it the slightest support.

On laying out all the skulls from Japan, whether labelled as "*smithii*," "*bedfordiæ*," "*andersoni*" or "*niigataæ*," in order of age, we find that the whole series forms an exact parallel to the series formed by the skulls of *E. r. rufocanus*, *E. r. shanseius*, and *E. r. regulus* when similarly arranged. How completely the four series agree, when taken stage by stage, can be appreciated from the comparative table on p. 261.

P.S.—To the synonymy of *E. r. rufocanus* should be added:—1881. *Arvicola rufocanus* var. *sibirica* Poljakov, Mém. Imp. Acad. Sci. St. Petersburg, 39, Appendix, p. 56. I have not been able to find descriptions of *E. ussuriensis* and *E. kolymensis* described by Ognev from N.E. Asia. From Montagu's note on the type of *E. kolymensis*, it would seem that this is a synonym of *E. rufocanus*.

#### E.—American forms.

### 23. *Evotomys caurinus* Bailey.

1898. *Evotomys caurinus* Bailey, Proc. Biol. Soc. Washington, 12, p. 21; Miller, "List," 1912, p. 209; "List," 1924, p. 401.

*Type*.—U.S. Nat. Mus., No. 89460 (Biol. Survey Coll.); adult male, collected July 18, 1897, by E. A. Preble.

*Type locality*.—Lund, east shore of Malaspina Inlet, British Columbia.

*Range*.—The coastal region of British Columbia east of the Strait of Georgia and south to the Frazer River.

*Characters*.—Size small (hind-foot 18 mm.; basal length of skull 21 mm.); tail very short.

Colour dark. In *summer* mantle well defined, dark, rich, chestnut, darkened with black-tipped hairs; sides sepia grey tinged with pale buff; spots over side glands of males whitish or dusky; face clear dark grey; belly washed with whitish or rarely buffy. Ears dusky, scantily haired. Tail bicoloured, chestnut or dusky above with blackish tip, buffy below. Feet soiled whitish or slightly dusky. In *winter* mantle brighter, more rufescent than in summer; sides clearer grey. Young darker than adults, with belly, feet and tail dusky.

Skull short and wide, with spreading zygomata and very narrow nasals and rostrum. Auditory bullæ small and flattened as compared with those of *E. occidentalis* or *E. saturatus*; about as large as those of *E. wrangeli* but wider and flatter. Incisors small and slender. Cheek-teeth small and crowded longitudinally; anterior loop of  $m^2$  and of  $m^3$  usually indented.

For *external and cranial measurements*, see table at end of volume.

24. *Evotomys phæus* Swarth.

1911. *Evotomys phæus* Swarth, Univ. Calif. Publ. Zool., 7, p. 127; Miller, "List," 1912, p. 210; "List," 1924, p. 401.

*Type*.—University of California Museum Vert. Zool., No. 8742; adult male; collected June 13, 1909, by H. S. Swarth.

*Type locality*.—Marten Arm, Boca de Quadra, Alaska.

*Range*.—Coast of Alaska; known from Boca de Quadra, Chickmain River, and Bradfield Canal.

*Characters*.—Size large (hind-foot 19–20 mm.; skull length 23–25.5 mm.), tail long, about half the length of head and body.

Colour dark; mantle not very sharply defined laterally, dark brown, between chestnut and walnut brown; sides and cheeks dark Isabella colour; under surface grey (about No. 8), sharply defined from flanks. Fairly conspicuous oval patches of grey hair over the hip glands. Tail bicoloured, brownish above, yellowish below.

Skull short and broad, with wide-spreading zygomata; rostrum short; premaxillæ usually extending backwards slightly beyond nasals; frontals depressed.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Distinguished from its nearest neighbours (1) *E. wrangeli* by cranial characters and much longer tail; (2) *E. caurinus* by larger size and longer tail.

25. *Evotomys wrangeli* Bailey.

1897. *Evotomys wrangeli* Bailey, Proc. Biol. Soc. Washington, 11, p. 120; Miller, "List," 1912, p. 209; "List," 1924, p. 401.

*Type*.—U.S. Nat. Mus., No. 74724 (Biol. Surv. Coll.); adult female, collected Sept. 1, 1895, by C. P. Streater.

*Type locality*.—Wrangel, Wrangel Island, Alaska.

*Range*.—Wrangel and Revillagigedo Islands, Southern Alaska.

*Characters*.—Size large (hind-foot 20 mm.; basal length of skull 24.3 mm.); tail short, rarely twice as long as hind-foot. Fur thick and long in both young and adults collected early in September. Ears well-clothed with short hairs, distinctly rufous tipped. Sides glands well developed in one specimen of a series of eighteen.

Colour dull. Mantle dull dark chestnut with a liver-brown tone, covering whole back from eyes to base of tail, and shading gradually into the sepia grey of the sides and cheeks. Sides more or less suffused with buffy yellowish; belly dark plumbeous, washed with whitish or buffy ochraceous. Projecting part of ear and tuft of long hair in front of ear concolorous with back; no post-auricular spot. Feet dusky grey in adults, sooty in young. Tail bicoloured, blackish above, soiled buffy below;

darker and less distinctly bicoloured in immature specimens. In one adult male the white hairs covering the lateral glands form oval patches half an inch in length.

Skull long and narrow, not thick or angular; rostrum long and decurved. Zygomata smoothly arched. Nasals usually notched, rarely truncate behind, terminating in line with pre-maxillaries. Frontals slight, concave behind. Palatine bones short; lateral bridges complete before maturity. Incisors large; molar series long.

For *external and cranial measurements*, see table at end of volume.

*Remarks.*—I have seen no material representing this interesting species. Judging from Mr. Bailey's description quoted above *E. wrangeli* would seem to be analogous to the members of the European *E. nageri* group.

## 26. *Evotomys dawsoni* Merriam.

(Synonymy under subspecies.)

*Range.*—Yukon, from Finlayson River and Fort Liard west to Yakutat, and northwards along the coast to Norton Sound. Hawkins and Hinchinbrook Islands, Prince William Sound, Alaska.

*Characters.*—A robust, short-tailed, bright-coloured species (hind-foot 20 mm.; basal length of skull 22.5 mm.). Tail rarely twice as long as hind-foot, well haired, but not bristly as in *E. rutilus*. Ears prominent and well haired.

Skull large and thick-walled, relatively short, wide and angular, with the smallest and flattest auditory bullæ among American species; basioccipital unusually wide between bullæ. Nasals terminating behind in line with pre-maxillaries, pointed in immature, rounded in adult skulls, never truncate. Pterygoids strong and prominent, their ends showing in profile below the small flattened bullæ. Palatines short, rectangular, with incomplete lateral bridges except in old skulls. Posterior margin of palate with a central notch, deepest in immature specimens. Incisors large, with dark orange enamel. Molar series long and narrow.

*Geographical differentiation.*—Two subspecies are at present recognized, viz., *E. dawsoni dawsoni* of the mainland and *E. d. insularis* of Hawkins Island.

*Remarks.*—This would seem to be the representative of *E. rutilus* in north-western North America. Bailey (Proc. Biol. Soc. Washington, 11, p. 122) says:—

“The combination of large size and short tail, notched palate and small audital bullæ, while distinctly separating the species from all others south of its range in America, brings it in closer relationship with *E. rutilus*. From *rutilus*, however, it differs in longer, slenderer, less hairy tail, slenderer feet, duller colour, with less rufous on ears, and the following important cranial

characters: skull less massive; rostrum longer and slenderer; audital bullæ smaller; pterygoids more prominent; nasals sharp-tipped or rounded posteriorly instead of truncate; molar series much narrower and slenderer. In external characters it slightly resembles *E. rufocanus* of Northern Europe, but differs widely from that species in cranial characters."

Osgood<sup>1</sup> has (with Miller's approval) identified Miller's *E. alascensis*, described from St. Michael, Norton Sound, Alaska, with *E. dawsoni*. It is a little difficult, in the absence of material, to reconcile Miller's description of the bullæ in *E. alascensis* ("large, their greatest breadth considerably more than alveolar length of maxillary molar series") with the description of those of *E. dawsoni* quoted above from Bailey.

### 26a. *Evotomys dawsoni dawsoni* Merriam.

1888. *Evotomys dawsoni* Merriam, Amer. Nat., 22, p. 650; Bailey, Proc. Biol. Soc. Washington, 11, p. 121, 1897.  
 1898. *Evotomys alascensis* Miller, Proc. Acad. Nat. Sci. Philadelphia, p. 364; described from St. Michael, Norton Sound, Alaska; *type*: U.S. Nat. Mus. No.  $\frac{1}{2} \frac{4}{3} \frac{3}{5} \frac{5}{8}$ . (Identified with *dawsoni* by Osgood, N. Amer. Fauna, No. 24, p. 34, 1904.)  
 1912. *Evotomys dawsoni dawsoni* Miller, "List," p. 210; "List," 1924, p. 401.

*Type*.—U.S. Nat. Mus., collected June 23, 1887, by Dr. G. M. Dawson.

*Type locality*.—Finlayson River, a northern source of the Liard River, lat. 61° 30' N., long. 129° 30' W., Yukon, Canada. Altitude 3,000 feet.

*Range*.—From Finlayson River and Fort Liard west to Yakutat and Juneau, and north along the coast to Norton Sound.

*Characters*.—Size, general form and skull as described above under the species.

*Colour*: Mantle sharply defined, extending from just behind the eyes to the base of the tail, bright ferruginous with few dark hairs. Face, sides, and rump buffy ochraceous. Belly thinly washed with pale buff. Ears covered on inner surface of tips with short, rufous hairs; an indistinct yellowish post-auricular spot; eyes encircled by faint yellowish rings; tufts of rufous hairs fall back from in front and fill openings of ears. Tail distinctly bicoloured, clothed with a mixture of rufous and black hairs above, clear buffy ochraceous below. Feet thinly clothed with buffy and dusky hairs. A small white throat patch marks 10 out of 29 specimens. Spot covering side glands inconspicuous.

For *external and cranial measurements*, see table at end of volume.

<sup>1</sup> N. Amer. Fauna, No. 24, 1904, p. 34.

26b. *Evotomys dawsoni insularis* Heller.

1910. *Evotomys dawsoni insularis* Heller, Univ. Calif. Publ. Zool., 5, p. 339; Miller, "List," 1912, p. 210; "List," 1924, p. 401.

*Type*.—University of California Museum Vertebrate Zoology, No. 557; adult male, collected June 20, 1908, by E. Heller.

*Type locality*.—Canoe Passage, Hawkins Island, Prince William Sound, Alaska.

*Range*.—Known from the type locality and from North-East Bay, Hinchinbrook Island.

*Characters*.—Size and proportion as in *E. d. dawsoni*.

Colour: mantle ferruginous rufous from snout to base of tail; sides yellowish to level of ears; under parts and feet light greyish without any yellowish suffusion. A concealed whitish spot at base of ear. Tail bicoloured, above reddish like the back, below tawny brownish.

Skull said to be distinguished from that of *E. orca* by its greater zygomatic breadth, larger nasals, and conspicuously larger auditory bullæ.

For *external and cranial measurements*, see table at end of volume.

27. *Evotomys orca* Merriam.

1900. *Evotomys orca* Merriam, Proc. Washington Acad. Sci., 2, p. 24; Miller, "List," 1912, p. 210; "List," 1924, p. 401.

*Type*.—U.S. Nat. Mus., No. 98028; adult female, collected June 28, 1899, by A. K. Fisher.

*Type locality*.—Orca, Prince William Sound, Alaska.

*Characters*.—Size and proportions nearly as in *E. dawsoni*, but colour darker and skull with still smaller auditory bullæ.

"Dorsal area dark chestnut or hazel; sides yellowish or buffy drab, intimately mixed with black hairs and darkest on rump; face very dark, grizzled with buffy grey and black; under parts deep buffy or buffy ochraceous, the plumbeous under fur showing through; hind-feet dusky; tail above dusky from base to tip, below buffy."

Skull like that of *E. dawsoni*, with large subquadrate braincase and strongly developed post-orbital squamosal crests; auditory bullæ decidedly smaller. Upper incisors decidedly larger. Mandibular angular processes "less flaring."

For *external and cranial measurements*, see table at end of volume.

28. *Evotomys gapperi* Vigors.

(Synonymy under subspecies.)

*Range*.—Widely distributed in North America between 64° and 40° N. latitude.

*Characters*.—Essential characters of body, pelage, skull and teeth substantially as in *E. glareolus*.



No single essential character and no combination of characters can be cited as serving to distinguish all forms of *E. gapperi* from all forms of *E. glareolus*. The American species and all its geographical races might very well be treated as so many additional subspecies of *E. glareolus*. But since in most forms of *E. gapperi* the tail is relatively shorter, the hind-foot absolutely longer, and  $m^3$  often more complex than is usual in *E. glareolus*, we may take these average differences, coupled with the geographical distinction as sufficient to justify specific separation.

A considerable number of more or less well-marked subspecies of *E. gapperi* are now recognized and the descriptions given of them are summarized below.

### 28a. *Evotomys gapperi gapperi* Vigors.

1830. *Arvicola gapperi* Vigors, Zool. Journ., 5, p. 204.  
 1857. *Arvicola (Hypudæus) gapperi* Baird, Mamm. N. Amer., p. 518.  
 1877. *Evotomys rutilus* Coues, Mon. N. Amer. Rodentia, Muridæ, p. 136 (in part).  
 1885. *Evotomys rutilus gapperi* True, Proc. U.S. Nat. Mus., 7, p. 596.  
 1891. *Evotomys gapperi* Merriam, N. Amer. Fauna, No. 5, p. 119; Bailey, Proc. Biol. Soc. Washington, 11, p. 122, 1897.  
 1894. *Evotomys fuscodorialis* Allen, Bull. Amer. Mus. N.H., 6, p. 103; described from Trousers Lake, New Brunswick, Canada; type: Am. Mus. N.H. No.  $\frac{922}{273}$  adult male.  
 1912. *Evotomys gapperi gapperi* Miller, "List," p. 210; "List," 1924, p. 402.

*Type*.—Unknown.

*Type locality*.—Between York and Lake Simcoe, Ontario, Canada.

*Range*.—From Massachusetts, New Jersey, and Pennsylvania northward and from the Atlantic coast westward to the Rocky Mountains in Canada.

*Characters*.—Size medium, hind-foot about 18 mm.; condylo-basal length of skull to 24.2 mm.

Mantle in winter bright chestnut, with numerous black hairs and a slight frosting produced by the white subterminal bands of the rufous-tipped hairs. Sides bright buffy ochraceous. Under parts washed with pale buff. Hands and feet silvery grey. Tail scarcely more than twice the length of the hind-foot, about 38% of the length of the head and body, bicoloured, brownish above, becoming black at the tip, greyish-buff to the tip below.

In high pelage, a rufous stripe extends across the orbit to black spot at base of mustache on each side. Colour in summer darker. The feet and tail more dusky.

Skull essentially as in *Evotomys glareolus*. Comparing the large series in the British Museum (mainly in the Miller Collection) with skulls of *E. g. britannicus*, I can detect no tangible differences by mere inspection. Careful measurement of a series of old, and therefore fully developed, skulls of the two forms show that in *E. g. gapperi* the zygomatic breadth is a little less, the width of the

braincase and rostrum is a little greater, the distances between the condyle and  $m^3$ , and the condyle and front face of the bulla, together with the diastema and nasals, are rather longer, and the tooth-rows are distinctly shorter relatively than in *E. g. britannicus*. Such differences, however, are scarcely of more than subspecific value.

Check-teeth normal;  $m^3$  usually more complex than in *E. glareolus*, the third inner fold and fourth inner angle well developed; the third outer fold is sometimes shallow and sometimes well developed, the fourth outer salient angle being correspondingly variable; occasionally in young adults there is a fourth inner fold and still more rarely traces of a fourth outer valley and fifth outer angle—the last quite vestigial.

For *external and cranial measurements*, see tables at end of volume.

### 28b. *Evotomys gapperi ochraceus* Miller.

1894. *Evotomys gapperi ochraceus* Miller, Proc. Boston Soc. Nat. Hist., **26**, p. 193; Bailey, Proc. Biol. Soc. Washington, **11**, p. 124, 1897; Miller, "List," 1912, p. 211; "List," 1924, p. 402.

*Type*.—B.M., No. 7.7.7.2533; adult female (Miller Coll.).

*Type locality*.—Mount Washington, Coos County, New Hampshire. Altitude 5500 feet.

*Range*.—The White Mountains of New Hampshire and (probably eastward to) Nova Scotia.

*Characters*.—Like the typical form, but slightly larger (hind-foot 19 mm.; condylo-basal length of skull to 23.7 mm.), much duller and paler, with long lax fur.

Mantle faintly defined, pale dull rusty rufous, with no black hairs. Sides buffy. Under parts plumbeous, lightly washed with dirty white. Feet grey. Tail brownish above, buffy below; the upper surface of the pencil blackish. Ears well haired, their upper edges pale fulvous.

Skull and teeth nearly as in the typical form. The oldest among seventeen skulls in the Miller Collection examined by me (twelve from Mount Washington, five from Digby, Nova Scotia) have the pterygoid fossæ and nasals relatively a little shorter than in equal-aged skulls of *E. g. gapperi*.

For *external and cranial measurements*, see tables at end of volume.

### 28c. *Evotomys gapperi rhoadsii* Stone.

1893. *Evotomys gapperi rhoadsii* Stone, Amer. Nat., **27**, p. 55; Bailey, Proc. Biol. Soc. Washington, **11**, p. 125, 1897; Miller, "List," 1912, p. 211; "List," 1924, p. 402.

*Type*.—Stone Collection No. 160; adult male, collected December 2, 1892.

*Type locality*.—May's Landing, Atlantic County, New Jersey.

*Range*.—Known only from the type locality.

*Characters*.—Resembling typical *E. gapperi*, but with slightly darker ("plain chestnut") mantle, less buffy sides, slightly shorter tail and larger hind-foot, the general body measurements and those of the skull being as in the typical form.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Bailey says: "The slight shortness of the tail compared with that of typical *gapperi* is entirely within the range of individual variation and discrepancies in the methods of taking measurements. If a more extensive series of specimens should prove the colour and foot characters inconstant, the subspecies will have to be given up. With the material in hand I prefer to retain it, though other more marked forms remain unnamed."

Regarded by Miller (Bull. N.Y. State Mus., 8, p. 111, 1900) as a distinct species.

#### 28d. *Evotomys gapperi loringi* Bailey.

1897. *Evotomys gapperi loringi* Bailey, Proc. Biol. Soc. Washington, 11, p. 125; Miller, "List," 1912, p. 211; "List," 1924, p. 402.

*Type*.—U.S. Nat. Mus., No. 75795 (Biol. Surv. Coll.); adult male, collected Nov. 22, 1895, by J. Alden Loring.

*Type locality*.—Portland, Traill County, North Dakota.

*Range*.—Timbered valleys along edge of plains in Minnesota and eastern North and South Dakota.

*Characters*.—The smallest member of the genus occurring in America, hind-foot averaging 17.9 mm.

Colour bright. Mantle in winter sharply defined, extending from anterior base of ears to rump, pale reddish-hazel, scarcely darkened with black hairs and frosted by the subterminal hair-bands. In some specimens, with the maximum of white, the back is fairly hoary, in others the chestnut predominates and conceals the white zone.

Face, sides and rump, bright greyish-ash more or less washed with buff. Belly pure white, rarely creamy. Feet pure white. Tail sharply bicoloured, dusky above, whitish below; pencil black above with a few white hairs below. Adult males with large whitish spots over lateral glands. In summer mantle dark rich chestnut. Sides and face pale bistre, more or less suffused with yellowish. Belly thinly washed with white or whitish. Feet dusky. Tail darker and less sharply bicoloured. Ears brownish. Side spots in old males sooty grey.

Skull smaller, narrower and more slender than in the typical form; not ridged or angular even in old age. Posterior edge of palate straight or with a slight median projection. Auditory bullæ less rounded and inflated.

*Remarks*.—This is described by Bailey as intergrading with typical *E. gapperi*. He regards *E. g. loringi* as a development

of the latter, produced as it "reached out on the dryer, more open region along the edge of the prairies. . . . The extremes of the form come from the furthest outlying localities."

For *external and cranial measurements*, see table at end of volume.

28e. ***Evotomys gapperi athabascæ*** Preble.

1908. *Evotomys gapperi athabascæ* Preble, N. Amer. Fauna, No. 27, p. 178; Miller, "List," 1912, p. 211; "List," 1924, p. 402.

*Type*.—U.S. Nat. Mus., No. 109945; adult male, collected June 27, 1901, by E. and A. Preble.

*Type locality*.—Fort Smith, Slave River, Mackenzie, Canada.

*Range*.—Throughout the region to the north of Great Slave Lake, Canada.

*Characters*.—Size as in *E. g. gapperi*; with longer fur, greyer face, lighter sides and under surface.

Mantle in colour like that of the typical subspecies, but ending rather abruptly a short distance in front of ears; face much clearer grey; sides greyer and less ochraceous; lower parts white and very rarely tinged with creamy.

For *external and cranial measurements*, see table at end of volume.

28f. ***Evotomys gapperi galei*** Merriam.

1890. *Evotomys galei* Merriam, N. Amer. Fauna, No. 4, p. 23.

1897. *Evotomys gapperi galei* Bailey, Proc. Biol. Soc. Washington, 11, p. 126; Miller, "List," 1912, p. 211; 1924, p. 402.

*Type*.—U.S. Nat. Mus., No.  $\frac{5}{6} \frac{6}{3} \frac{8}{5} \frac{5}{2}$ ; adult female, collected July 13, 1889, by D. Gale.

*Type locality*.—Ward, Boulder County, Colorado. Altitude 9500 feet.

*Range*.—Boreal zone of mountains of Colorado and northwards along eastern ranges of Rocky Mountains to Northern Montana.

*Characters*.—Distinguished from the typical subspecies by its slightly longer tail, lighter colour, and the prominent development of the superciliary ridges in old skulls.

Mantle, in winter pelage, sharply defined, reddish-chestnut with a few black hairs. Sides and face buffy grey. Belly and feet whitish or yellowish-grey. Tail bicoloured, blackish or buffy grey above, whitish below, the upper side of pencil black. Ears faintly tinged with chestnut. In spring and early summer the mantle darkens to warm hazel, the sides to rich buffy grey. In full summer pelage, the mantle is chestnut, slightly darkened with black hairs; the sides and face clearer grey than in winter; feet grey. Spot covering lateral glands in old males whitish or grey. Young in August are darker than adults, with ears strongly tipped with chestnut, the feet dusky and the tail not sharply bicoloured.

Skull in adults narrower than in *E. g. gapperi*; interorbital region

sharply concave with prominent superciliary ridges. Zygomata not abruptly spreading. Auditory bullæ small and globose.

For *external and cranial measurements*, see table at end of volume.

28g. **Evotomys gapperi saturatus** Rhoads.

1894. *Evotomys gapperi saturatus* Rhoads, Proc. Acad. Nat. Sci. Philadelphia, p. 284; Bailey, Proc. Biol. Soc. Washington, **11**, p. 128; Miller, "List," 1912, p. 211; "List," 1924, p. 403.

*Type*.—Rhoads Collection, No. 483; adult female, collected August 17, 1892.

*Type locality*.—Nelson, British Columbia; on the Kootenai River, 30 miles north of the northern boundary of Washington.

*Range*.—The Blue Mountains of Oregon, mountains of northern Idaho, and northwards into British Columbia to Cariboo Lake (near Kamloops).

*Characters*.—Larger and longer-tailed than the typical form with larger ears and stouter hind-feet.

Mantle bright and rather light-reddish chestnut, closely matching that of *E. g. gapperi* from Ontario and Western New York, but beginning further behind the eyes. Sides, face, and lower rump dark grey, with less ochraceous wash than in *E. g. gapperi*. Belly washed with almost pure white. A white throat patch frequently present. Ears large, protruding well out of fur, slightly tipped with rufous. Feet grey. Tail indistinctly bicoloured, dark grey above, light grey below.

Skull larger, wider, and more angular than in *E. g. gapperi*. Pterygoids longer and more slender. Auditory bullæ slightly larger.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Mr. Bailey says the name *saturatus* is misleading, this subspecies being scarcely darker than *E. g. gapperi* and much lighter-coloured than *E. obscurus*, *E. californicus*, *E. occidentalis*, *E. wrangeli*, *E. dawsoni*, or *E. carolinensis*.

29. **Evotomys brevicaudus** Merriam.

1891. *Evotomys gapperi brevicaudus* Merriam, N. Amer. Fauna, No. 5, p. 119.

1897. *Evotomys brevicaudus* Bailey, Proc. Biol. Soc. Washington, **11**, p. 129; Miller, "List," 1912, p. 212; "List," 1924, p. 403.

*Type*.—U.S. Nat. Mus., No.  $\frac{4}{5} \frac{507}{142}$ , Merriam Coll.; adult male, collected July 21, 1888, by Vernon Bailey.

*Type locality*.—Three miles north of Custer, Black Hills, Custer County, South Dakota. Altitude about 6000 feet.

*Range*.—Boreal cap of Black Hills in South Dakota.

*Characters*.—Size as in *E. gapperi*, with rather larger hind-foot and much shorter tail.

Colour in summer pelage paler than in *E. g. gapperi* and *E. g.*

*loringi*, with black hairs more conspicuous; sides ash grey, strongly suffused with buffy; belly creamy white; side spots dusky grey.

Skull similar to that of *E. g. gapperi* in large size and broad braincase; zygomatic arches low and flaring out, so that the inner instead of the outer side shows in a top view; palate approximately straight edged; pterygoids wide, flat, and close together. Auditory bullæ as large as in *E. g. gapperi*, but less rounded. Incisors slender and pale yellow; molars large.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Mr. Bailey says that the skulls show that the two specimens known are “not fully adult, though probably full grown. Though based on so scanty material, the characters distinguishing the species are fairly pronounced. Its range is isolated, and widely separated from that of any other members of the genus by open prairie country and a wide belt of the Transition Zone. There seems to be no valid reason for considering it a subspecies. It is even difficult to decide to which form it is most nearly related.”

### 30. *Evotomys carolinensis* Merriam.

1888. *Evotomys carolinensis* Merriam, Amer. Journ. Sci., [3], 36, p. 460; Bailey, Proc. Biol. Soc. Washington, 11, p. 130; Miller, “List,” 1912, p. 212; 1924, p. 403.

*Type*.—U.S. Nat. Mus., No. 3660; adult female, collected August 11, 1887.

*Type locality*.—Roan Mountain, Mitchell County, North Carolina. Altitude 6000 feet.

*Range*.—Boreal parts of Allegheny Mountains of North Carolina, Tennessee, and West Virginia [also Virginia and Maryland].

*Characters*.—Size large, hind-foot 20 mm. or more; tail long. Colour dark and rich. Molars larger than in any other American species.

*Summer pelage*: dark chestnut above, blending gradually with bistre of sides, face, and rump; darkened everywhere above with numerous black hairs; belly varying from white to buffy ochraceous, the under fur showing through. Ears dusky. Feet greyish brown. Tail indistinctly bicoloured, blackish above and at tip, grey below. Side glands of males covered by inconspicuous spot of slightly darker fur. *Winter pelage*: paler and brighter; back brighter ferruginous, belly averaging whiter; sides buffy ochraceous; ears slightly rufous tipped. Young darker than adults.

Skull larger, wider and more angular than in *E. gapperi*; with relatively smaller, flatter and more elongated auditory bullæ and wider basioccipital. Cheek-teeth larger, wider and heavier. Enamel of upper incisors darker yellow.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Readily distinguished from all other Eastern forms by its larger size and darker coloration. Specimens in the same pelage should be used for comparison, as the lightest phase of winter pelage in *E. carolinensis* matches the darkest summer phase of *E. gapperi*.

### 31. *Evotomys limitis* Bailey.

1913. *Evotomys limitis* Bailey, Proc. Biol. Soc. Washington, **26**, p. 133; Miller, "List," 1924, p. 203.

*Type*.—U.S. Nat. Mus., No. 141335; adult male, collected October 27, 1906, by V. Bailey.

*Type locality*.—Willow Creek, a branch of the Gilita, Mogollon Mountains, Socorro County, New Mexico. Altitude 8500 feet.

*Characters*.—Compared with *E. gapperi galei*, size slightly larger (hind-foot 20 mm.; basal length of skull 24.5 mm.); colour duller, greyer and less buffy; skull and dentition heavier.

Winter pelage with chestnut dorsal area less extensive; general colour less yellowish and greyer; sides, face, and feet clear grey; belly whitish; tail bicoloured, whitish below, dark grey above, its pencil blackish. Summer pelage much darker chestnut, with dark grey sides and face.

Skull larger, heavier, and conspicuously more ridged; auditory bullæ large and especially deep. Dentition heavy throughout.

For *external and cranial measurements*, see table at end of volume.

### 32. *Evotomys ungava* Bailey.

1897. *Evotomys ungava* Bailey, Proc. Biol. Soc. Washington, **11**, p. 130; Miller, "List," 1912, p. 212; "List," 1924, p. 403.

*Type*.—U.S. Nat. Mus., No.  $\frac{5471}{8152}$ , Merriam Coll.; adult male, collected May 12, 1883, by L. M. Turner.

*Type locality*.—Fort Chimo, Ungava, Canada.

*Characters*.—Size as in *E. gapperi*; tail and feet slender; ears very small, not projecting beyond fur.

Colour dull (skinned from spirit). Mantle not sharply defined, dull brownish-chestnut; sides and face buffy grey, finely lined with blackish hairs; belly dark plumbeous, heavily washed with buffy. Feet dusky grey. Tail indistinctly bicoloured, brownish above, soiled buffy below.

Skull compared with that of *E. gapperi* long and slender; braincase narrower; zygomata less spreading; rostrum longer and straighter; lateral bridges of palate incomplete. Auditory bullæ longer, flatter and less rounded. Incisors slender. Enamel pattern normal.

*Remarks*.—Type alone known.

For *external and cranial measurements*, see table at end of volume.

33. **Evotomys idahoensis** Merriam.

1891. *Evotomys idahoensis* Merriam, N. Amer. Fauna, No. 5, p. 66; Bailey, Proc. Biol. Soc. Washington, 11, p. 131; Miller, "List," 1912, p. 212; "List," 1924, p. 403.

*Type*.—U.S. Nat. Mus., No.  $\frac{24283}{31687}$ ; adult female, collected October 4, 1890.

*Type locality*.—Sawtooth (or Alturas) Lake, east base of Sawtooth Mountains, Blaine County, Idaho. Altitude 7200 feet.

*Range*.—Mountains of south central Idaho, between Snake River and the Salmon.

*Characters*.—Size medium (hind-foot 20 mm.); tail longer than in *E. gapperi*.

Mantle well defined, pale hazel, somewhat darkened by black hair-tips; face, sides and rump clear ash grey; belly washed with white or whitish. Ears sooty grey, without rufous tips. Feet grey. Tail bicoloured, blackish above, grey below.

Skull long, narrow and smooth, convex interorbitally; zygomatic arches very oblique; rostrum long; posterior margin of palate straight; pterygoids long and slender, longer, straighter and further apart than in *E. g. saturatus*. Auditory bullæ long and laterally compressed, the basioccipital wide between them. Incisors pale yellow.

For *external and cranial measurements*, see table at end of volume.

34. **Evotomys mazama** Merriam.

1897. *Evotomys mazama* Merriam, Proc. Biol. Soc. Washington, 11, p. 71; Bailey, *ibid.*, p. 132; Miller, "List," 1912, p. 212; "List," 1924, p. 404.

*Type*.—U.S. Nat. Mus., No. 79913; adult male, collected August 15, 1896.

*Type locality*.—Crater Lake, Mount Mazama, Klamath County, Oregon. Altitude 7000 feet.

*Range*.—Crest of the Cascade Mountains in Oregon.

*Characters*.—Size large (hind-foot 18.7 mm.; basal length of skull 23.3 mm.), tail long, about half length of head and body.

Colour bright, ears not rufous. Mantle extending from front of ears to base of tail, cinnamon rufous or hazel, shading gradually into buffy grey of sides and face; belly washed with buffy white. Oval spot covering side glands in adult males slaty grey, more or less frosted with white-tipped hairs. Feet greyish-white. Tail sharply bicoloured, blackish above, whitish below.

Skull broad and angular, with unusually flat top; long straight rostrum, and abruptly spreading zygomata; pterygoids prominent, wide and inflated at tips; palate with a median posterior projection. Auditory bullæ large. Enamel of incisors orange.

For *external and cranial measurements*, see table at end of volume.



*Remarks.*—Bailey states that this species differs conspicuously in colour from the dark-coloured coast species, but needs careful comparison with *E. obscurus*. Judging from the description quoted above *E. mazama* may be an American representative of the *E. rufocanus* group; the non-rufous ear and angular skull appear to support such a suggestion.

### 35. *Evotomys obscurus* Merriam.

1897. *Evotomys obscurus* Merriam, Proc. Biol. Soc. Washington, 11, p. 72; Bailey, *ibid.*, p. 133; Miller, "List," 1912, p. 212; "List," 1924, p. 404.

*Type.*—U.S. Nat. Mus., No. 80413; adult male, collected August 29, 1896, by E. A. Preble.

*Type locality.*—Prospect, Upper Rogue River, Valley, Jackson County, Oregon. Altitude about 2600 feet.

*Range.*—West slope of the Southern Cascade Range and northern Sierra Nevada in southern Oregon and northern California.

*Characters.*—Size medium (hind-foot 17 mm.; basal length of skull 21.8), tail nearly half the length of the body.

Upper parts olive grey, with an ill-defined mantle of cinnamon rufous, obscured by black hairs; lower flanks and face clear grey; belly washed with dull buff. Ears dusky, not rufous tipped. Feet dusky grey. Tail bicoloured. Side glands inconspicuous but present.

Skull "less angular and abruptly spreading than that of *E. mazama* and with a more arched dorsal line; rostrum short, decurved, with lower outline well arched; anterior palatal foramina short and wide. Palate and auditory bullæ as in *E. mazama*."

For *external and cranial measurements*, see table at end of volume.

*Remarks.*—Bailey says that in both geographic position and specific character this species lies between *E. mazama* of the summit of the Cascade Mountains and *E. californicus* of the coastal region. There is no evidence of intergradation with *E. mazama*, although the two species may come in contact; but some slight approach towards *E. californicus* is shown by specimens from Carberry Ranch, California.

### 36. *Evotomys californicus* Merriam.

1890. *Evotomys californicus* Merriam, N. Amer. Fauna, No. 4, p. 26; Bailey, Proc. Biol. Soc. Washington, 11, p. 133, 1897; Miller, "List," 1912, p. 213; "List," 1924, p. 404.

*Type.*—U.S. Nat. Mus., No.  $\frac{17011}{23920}$ ; adult male, collected June 3, 1889, by T. S. Palmer.

*Type locality.*—Eureka, Humboldt County, California.

*Range.*—Coast strip of Oregon and northern California.

*Characters*.—Size large (hind-foot 21 mm.; basal length of skull 22.8 mm.), tail long, nearly half the length of head and body, colour dark.

Upper parts dark bistre or sepia, becoming dusky on rump, and dull, dark chestnut on back; mantle indistinct, shading gradually into colour of sides; belly pale buffy or soiled whitish darkened by under fur. Lateral glands conspicuous in old males, covered by oval patches of slightly contrasted dense fur. Ears dusky, with no rufous or light-coloured hairs. Feet whitish or but slightly dusky. Tail sharply bicoloured, blackish above and at tip, whitish below.

Skull thick and heavy, with short stout decurved rostrum; zygomatic arches bent well down and not abruptly spreading; palatines usually triangular in outline, instead of U-shaped as in other species, and with a triple or single-pointed posterior projection. Auditory bullæ and pterygoids both relatively and absolutely larger than in any other species.

Cheek-teeth wide and heavy; enamel folds crowded longitudinally and irregular;  $m^3$  short with posterior loop very small or, in four specimens out of six, absent.

For *external and cranial measurements*, see table at end of volume.

### 37. *Evotomys occidentalis* Merriam.

1890. *Evotomys occidentalis* Merriam, N. Amer. Fauna, No. 4, p. 25; Bailey, Proc. Biol. Soc. Washington, 11, p. 134, 1897; Miller, "List," 1912, p. 213; "List," 1924, p. 404.

1894. *Evotomys pygmaeus* Rhoads, Proc. Acad. Nat. Sci. Philadelphia, p. 284; described from the mouth of the Nisqually River, Pierce County, Washington; *type*: Rhoads Collection No. 247; young female.

*Type*.—U.S. Nat. Mus., No.  $\frac{17447}{21351}$ ; adult male, collected August 16, 1889, by T. S. Palmer.

*Type locality*.—Aberdeen, Chehalis County, Washington.

*Range*.—Coast and Puget Sound region of Washington and southern British Columbia.

*Characters*.—Size considerably less than in *E. californicus*; dorsal area ill defined, sometimes indistinct, varying from dull burnt amber to dark chestnut, darkened by numerous black-tipped hairs. Sides dusky grey with a buffy suffusion, an oval darker patch over lateral glands. Belly salmon buff, darkened by hair bases. Ears concolorous with back, nearly naked, not large, but conspicuous above short summer fur. Feet dusky. Tail almost concolorous, blackish.

Skull thin and light, without prominent angles and processes, relatively narrow and slender, with gently arching zygomata; palatines with a rounded or notched posterior projection; pterygoids flat, thin, and much perforated at base. Auditory bullæ much inflated, crowding close together over basioccipital.

Cheek-teeth normal. Enamel of incisors orange, not pale yellowish as in *E. g. saturatus*.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Bailey says: "This species is peculiar to the low, moist coast and sound region—the 'Webfoot country'—where its dark colour blends with the shadows of dense vegetation." Possibly it intergrades with *E. californicus* to the south, and with *E. g. saturatus* of the mountains further east. *E. pygmaeus* Rhoads was based upon the young of this species.

### 38. *Evotomys nivarius* Bailey.

1897. *Evotomys nivarius* Bailey, Proc. Biol. Soc. Washington, **11**, p. 136; Miller, "List," 1912, p. 213; "List," 1924, p. 404.

*Type*.—U. S. Nat. Mus., No. 66203 (Biol. Surv. Coll.); adult female, collected July 9, 1894, by C. P. Streater.

*Type locality*.—North-west slope of Mount Ellnor, Olympic Mountains, Mason County, Washington. Altitude 4000 feet.

*Range*.—Mount Ellnor and probably other high peaks in the Olympic Mountains.

*Characters*.—Size and proportions about as in *E. occidentalis*, but colour lighter and brighter, with skull more angular. Fur long and lax; ears small or scantily haired; tail and feet slender, well covered with short hair.

Mantle well defined, extending from anterior bases of ears to base of tail, dull light chestnut, sides dark grey, with little buffy suffusion; belly thinly washed with soiled whitish, darkened by under fur. Ears dusky; post-auricular patches whitish. Feet dirty white. Tail bicoloured, dusky above, dirty white below.

Skull short, wide, angular and flat; zygomatic processes of maxillæ projecting at right angles to long axis of skull: frontals deeply concave post-orbitally; temporal ridges of frontals and parietals prominent; posterior border of palate straight; pterygoids slender. Auditory bullæ large, as in *E. occidentalis*. Tooth pattern variable [no details given]. Enamel of incisors as in *E. occidentalis*.

For *external and cranial measurements*, see table at end of volume.

*Remarks*.—Bailey says that this species may intergrade with *E. occidentalis* at the eastern base of the Olympic Mountains.

### 39. *Evotomys proteus* Bangs.

1897. *Evotomys proteus* Bangs (in Bailey), Proc. Biol. Soc. Washington, **11**, p. 137; Bangs, *ibid.*, p. 239; Miller, "List," 1912, p. 213; "List," 1924, p. 404.

*Type*.—Collection of E. A. and O. Bangs, No. 4081; old female, collected Aug. 27, 1895, by C. H. Goldthwaite.

*Type locality*.—Hamilton Inlet, Labrador.

*Characters*.—Size very large and colour very variable. Adults usually yellowish or greyish above, with a darker (often sooty) dorsal stripe. Red-backed individuals are in a small minority, and even these have the face grey. In the type (representing the colour phase that seems to be most usual), the sides, flanks, cheeks, and face are smoke grey, somewhat shaded with yellowish and drab, darkening on back into a broad dorsal stripe of sepia, and paling off on under parts to light smoke grey. Hands and feet dull grey. Tail indistinctly bicoloured, dusky above, dull grey below; both it and the feet hairier than in *E. gapperi*.

Skull larger than that of *E. gapperi* (including *E. g. ochraceus*), the braincase more angular, the interorbital constriction deeper, and the post-orbital squamosal processes much more strongly marked. Dentition normal.

No skull measurements recorded.

For *external measurements*, see table at end of volume.

*Remarks*.—Mr. Bangs (Proc. Biol. Soc. Washington, 11, p. 239) describes this as the commonest small mammal about Hamilton Inlet, and says: "Several times while walking through the forest Mr. Goldthwaite discovered one sitting upon a spruce branch 'like a squirrel.' I have never known of this arboreal habit in other species. The range of individual colour variation . . . is simply astounding, and it seems incredible that extremes from the series can belong to the *same* species, yet any specimen picked out can be graded by the most delicate steps into any of the other extremes." The plate, illustrating Mr. Bangs' paper, is said to show "admirably a few of the most pronounced colour phases."

### Genus: 6. ASCHIZOMYS Miller.

1898. *Aschizomys* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1898, p. 368; Hinton, Ann. Mag. N.H., [9], 11, 192, p. 147 (genus).

*Genotype*.—*Aschizomys lemminus* Miller.

*Range*.—Known only from Plover Bay, Behring Strait, Siberia.

*Characters*.—General outward form lemming-like. Tail very short, the caudal vertebræ shorter than the hind-foot and but slightly longer than the terminal hair-pencil. Plantar tubercles 6. Mammary formula unknown.

Skull essentially as in *Evotomys*, broad, depressed, lightly built, smooth and rounded, with the palatal structure of typical *Evotomys*; alveolar capsule of  $m^2$  forming a conspicuous hump at the mouth of the sphenorbital fissure.

Mandible with the  $m_3$  displaced lingually by the shaft of the incisor and encapsuled as in *E. rufocanus* and *Microtus*.

Cheek-teeth persistently growing, but with the general pattern and rounded salient angles of typical *Evotomys*;  $m^3$  small and weak with well-developed fourth outer angle.

*Remarks.*—So far as our present knowledge goes *Aschizomys*, represented by a single specimen, the type of *A. lemminus*, "is apparently a most remarkable descendant from some old species of *Evotomys*. In skull and in the pattern and lightness of the cheek-teeth it is practically identical with *Evotomys*. But living in the high north, it has acquired the outward form of a lemming; and subsisting apparently upon a diet which rapidly wears away the crowns of the cheek-teeth, the latter have become hypsodont and rootless as in the higher voles." Since I wrote the passage just quoted my studies have shown that "*Phaulomys*" and "*Caryomys*," reputed generic groups with cranial and dental characters exactly like those of *Aschizomys*, are based upon immature individuals of *E. rufocanus*, and I now suspect that *Aschizomys lemminus* will prove to be a member of the *E. rufocanus* group, although sharply distinguished as a species from *E. rufocanus* by its external peculiarities. It is to be hoped that further material will be forthcoming from the neighbourhood of Plover Bay.

### 1. *Aschizomys lemminus* Miller.

1898. *Aschizomys lemminus* Miller, Proc. Acad. Nat. Sci., Philadelphia, 1898, p. 369.

*Type.*—U.S. Nat. Mus. No.  $\frac{9911}{37299}$ ; "adult" in alcohol, collected by C. W. Baxter.

*Type locality.*—Kelsey Station, Plover Bay, Behring Strait, N.E. Siberia.

*Range.*—Known only from the type locality.

*Characters.*—Size medium. Ears broad and rounded, longer than fur immediately in front of their bases. Hands large, palms naked, with five prominent tubercles; claws short and stout; thumb vestigial with a convex compressed nail. Feet broad; soles with six pads, of which five are subequal and one much smaller, posteriorly densely haired between heel and hindermost tubercle, anteriorly granular and clothed with a considerable number of short white hairs interspersed among the granules; claws moderately developed, overhung with white hairs. Tail club-shaped. Whiskers long, reaching to shoulders.

Fur dense, soft and silky, about 10 mm. long on back, nearly as long on belly, slate-grey at base. Dorsal surface clothed with a uniform fine grizzle of sepia and yellowish-brown; no indication of a darker dorsal area, but the shading is slightly heavier across the lumbar region than elsewhere. An indistinct tuft of whitish hairs in front of each ear. Sides, belly, limbs and paws, together with the under surface of the tail, light straw yellow, sharply contrasted with the colour of the dorsal surface. Miller says that this description of the colour "can be only approximately correct, since it is taken from the skin which had been immersed in alcohol for many years. Before

skinning, the tail was club-shaped, and in its present condition it retains a trace of this form. For a short distance at its base it is covered with short loose hairs, similar in texture to those of the body. Near the middle of the tail, the hairs become abruptly much elongated, stiffened and directed backwards. The pencil thus formed is nearly as long as the tail vertebræ. It is distinctly flattened from above. The general appearance of the tail is much like that of *Dicrostonyx*, but it is even more bushy than in average specimens of any lemming."

Skull and teeth as described under the genus;  $m^3$  "remarkably long with four distinct salient angles on each side."

*Measurements* recorded by Miller: Total length 99 mm.; head and body 85; tail vertebræ 16; caudal pencil 14; hind-foot 17.5; ear from meatus 11.5.

Skull: greatest length 25.4 mm.; basal length 23.8; basilar length 22; zygomatic breadth 14.8; interorbital breadth 4; mastoid breadth 12.6; occipital depth 7; fronto-palatal depth 7; length of nasals 3 [*sic* probably misprint for 8]; incisive foramina 4.6; upper molars (alveolar) 6; mandible 15; lower molars (alveolar) 6.

#### Genus: 7. EOTHENOMYS Miller.

1871. *Arvicola* Milne-Edwardes, *Nouv. Arch. Mus.*, 7, Bull., p. 93; *Recherches hist. nat. Mamm.*, 1, p. 284, 1874. Not of Lacepède, 1799.
1881. *Neodon* "section of *Arvicola*," Blanford, *J. Asiat. Soc. Bengal*, 50, pp. 110, 114. Not of Hodgson, 1849.
1891. *Microtus* Blanford, *Fauna of British India, Mammalia*, p. 434 (in part). Not of Schrank, 1798.
1896. *Eothenomys* Miller, *N. Amer. Fauna*, No. 12, p. 45 (subgenus of *Microtus*).
1923. *Eothenomys* Hinton, *Ann. Mag. Nat. Hist.*, (9), 11, p. 145 (genus).

*Genotype*.—*Arvicola melanogaster* M.-Edw.

*Range*.—Southern China (W. Sze-chwan, N.W. Fokien, and Hupeh), the Highlands of Yunnan, and westwards into Assam and Burma.

*Characters*.—General outward form nearly as in *Evotomys*. Fur soft and dense, slightly modified.

Colour usually dark, the back with peculiar metallic reflections. Ears well developed, provided with a naked meatal valve. Hands and feet normal; fore-claws shorter than hind-claws; thumb small, with a small flattened nail; palmar tubercles 5; plantar tubercles 6; soles hairy behind pads. Tail from one-fourth to one-half length of head and body, clothed with stiff hairs forming a very short and thin terminal pencil, the annulations not completely concealed.  $Mammæ\ 0 - 2 = 4$ .

Skull essentially similar to that of *Evotomys* in form and

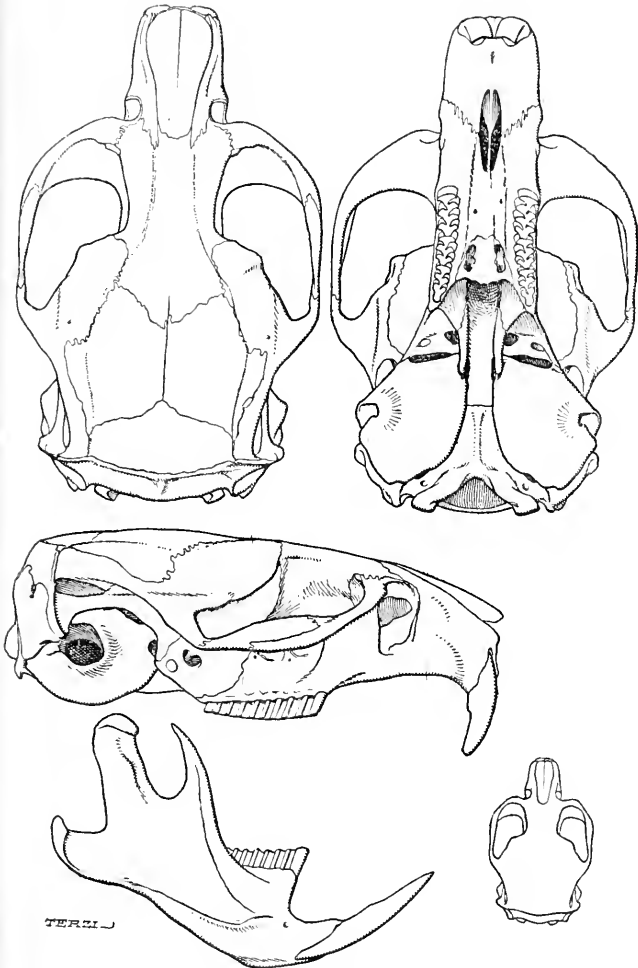


FIG. 85.—*Eothenomys melanogaster melanogaster*.

Dorsal, ventral, and lateral views of skull; the small figure represents the skull in dorsal view, natural size.

structure. Temporal ridges feebly developed, and widely separated in the interorbital region. Post-orbital squamosal crests weak or moderate. Palate much like that of *Evotomys*, ending behind in a simple transverse shelf, which is, however, sometimes furnished with a weak median process; post-palatal lateral pits well developed, their inner edges effecting a junction with the dorsal surface



Fig. 1a



Fig. 2a

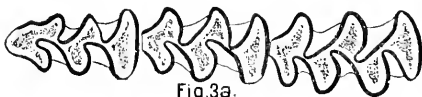


Fig. 3a.



Fig. 4a.



Fig. 5a

FIG. 86a.

a. Right upper molars of *Eothenomys* (the corresponding lower molars are shown in Fig. 86b).

1. *E. melanogaster confinii* Hinton. (Type.)
2. *E. fidelis* Hinton. (Type.)
3. *E. melanogaster columnus* Thomas. (B.M., No. 98.11.1.27.)
4. *E. olitor* Thomas. (B.M., No. 11.9.8.123.)
5. *E. proditor* Hinton. (Type.)

of the palatal shelf far forwards and under cover of the shelf. Pterygoid fossæ moderately large and deep, their floors very slightly dorsal to the ventral surface of the basisphenoid. Auditory bullæ simple, without internal spongy tissue; stapedia artery not enclosed in a bony tube.

Mandible normal;  $m_3$  displaced lingually by the shaft of the incisor.

Dentition. Incisors normal. Cheek-teeth rootless and rather



tall-crowned, the alveolar capsule of  $m^2$  moderately protuberant in the floor of the sphenorbital fissure; enamel about equal in thickness on convex and concave sides of prisms; salient angles opposed rather than alternating, the dentinal spaces tending to be transversely confluent in consequence. Enamel pattern peculiar and complex;  $m^1$  with well-developed fourth inner or postero-internal salient angle,  $m^2$  with well-developed third inner salient angle in most forms, but in others these structures are reduced and  $m^1$  and  $m^2$  have a more normal form;  $m^3$  variable,



Fig. 1b.



Fig. 2b.



Fig. 3b.



Fig. 4b.



Fig. 5b.

FIG. 86b.

Lower molars of *Eothenomys* (1-3 and 5 left; 4 right).

when most complex with four salient angles on each side, when somewhat reduced with three outer and four inner salient angles, and when most reduced with three salient angles on each side, the precise form of this tooth being a very constant feature in most of the species and subspecies now recognized. Enamel pattern of lower molars much less variable;  $m_1$  with four outer and five inner angles, the general form of its anterior loop "nivaloid" (Fig. 86b);  $m_2$  and  $m_3$  each with three salient angles on each side; the opposition of the inner and outer salient angles is most evident in the lower molars, where the dentinal spaces throughout form a series of transverse loops or lozenges.

In this genus the size of the cheek-teeth seems to stand in inverse proportion to the size of the auditory bullæ, forms with large bullæ having small light molars and those with small bullæ large heavy molars.

*Remarks.*—The relationships of *Eothenomys*, which seems to be an offshoot from some primitive *Evotomys*-like stock, are discussed in the Introduction. Twelve or thirteen forms are now known from South-Eastern Asia, and these I have recently referred to four species. The characters of these forms may be “keyed” as follows:—

*Key to the species and subspecies of Eothenomys:—*

- A. Anterior upper cheek-teeth complex;  $m^1$  with four,  $m^2$  with three salient angles on the inner side.
- a.  $m^3$  with four inner salient angles.
- a<sup>1</sup>.  $m^3$  with four outer salient angles; auditory bullæ small, cheek-teeth heavy. Colour bright.  
*E. melanogaster cachinus* Thomas.  
Kachin Province, W. Burma.
- b<sup>1</sup>.  $m^3$  with three outer salient angles.
- a<sup>2</sup>. Size normal; condylo-basal length to 26 mm.; hind-foot to 19 mm.
- a<sup>3</sup>. Bullæ large, molars light.
- a<sup>4</sup>. Colour darker . . . . . *E. m. eleusis* Thomas.  
Yunnan.
- b<sup>4</sup>. Colour brighter . . . . . *E. m. aurora* Allen.  
Hupeh.
- b<sup>3</sup>. Bullæ small, molars heavy.
- a<sup>4</sup>. Skull strongly bowed dorsally. Colour rather brighter . . . . . *E. m. miletus* Thomas.  
W. of Yang-pi, Yunnan.
- b<sup>4</sup>. Skull normal, not bowed dorsally. Colour rather darker . . . . . *E. m. confinii* Hinton.  
Kiu-chiang-Salween Divide.
- b<sup>2</sup>. Size large; condylo-basal length 28 mm.; hind-foot 20 mm. Colour bright . . . . . *E. fidelis* Hinton.  
Li-chiang Range.
- b.  $m^3$  with three inner and three outer salient angles.
- a<sup>1</sup>. Bullæ large, molars light.
- a<sup>2</sup>. Colour darker, bullæ slightly larger.  
*E. m. melanogaster* M.-E.  
W. Sze-chwan.
- b<sup>2</sup>. Colour brighter, bullæ slightly smaller.  
*E. m. colurnus* Thomas.  
N.W. Fokien.
- b<sup>1</sup>. Bullæ small, molars heavy. Colour very dark.
- a<sup>2</sup>. Larger (hind-foot 19 mm.), with broad braincase.  
*E. m. mucronatus* Allen.  
W. Sze-chwan.
- b<sup>2</sup>. Smaller (hind-foot 17 mm.), with narrow braincase.  
*E. m. libonotus* Hinton.  
Mishmi Hills.
- B. Anterior upper cheek-teeth more or less simplified;  $m^1$  with only three inner salient angles.

- a. Small (condylo-basal length to 24 mm.);  $m^2$  normal, with three inner salient angles;  $m^3$  complex, with four salient angles on each side . . . . . *E. olitor* Thomas.  
Chao-tung-fu, Yunnan.
- b. Large (condylo-basal length to 27.5 mm.);  $m^2$  with the third inner salient angle vestigial;  $m^3$  with its first outer infold shallow (*Allicola*-like), and with the fourth inner and fourth outer salient angles vestigial. Colour bright.  
*E. proditor* Hinton.  
Li-chiang Range.

*E. bonzo* from Fuchow, described by Cabrera (Bol. Real Soc. Españ. Hist. Nat., 22, 1922, p. 168) is probably a synonym of *E. m. colburnus*.

### 1. *Eothenomys melanogaster* Milne-Edwardes.

(Synonymy under subspecies.)

*Range*.—Southern China and Northern Yunnan, westwards into Northern Burma and Assam.

*Characters*.—Essential characters as described under the genus; colour and size varying with the subspecies.

Skull normal, not especially narrow, massive, or strongly ridged. Anterior upper cheek-teeth,  $m^1$  and  $m^2$ , always complex,  $m^1$  with four and  $m^2$  with three well-developed salient angles on the inner side;  $m^3$  with three or four salient angles on each side according to the subspecies. Auditory bullæ and molar teeth differing in different forms, large bullæ being correlated with small molars, and large molars with small bullæ.

*Geographical differentiation*.—Nine subspecies of *E. melanogaster* are at present recognized.

#### 1a. *Eothenomys melanogaster melanogaster* Milne-Edwardes.

1871. *Arvicola melanogaster* Milne-Edwardes, Nouv. Arch. Mus., 7, Bull. p. 93; Rech. Mamm., p. 284, pls. xlv.

1891. *Microtus melanogaster* Blanford, Fauna British India, Mammalia, p. 434.

1896. *Microtus (Eothenomys) melanogaster* Miller, N. Amer. Fauna, No. 12, p. 46.

1923. *E[iothenomys] m[elanogaster] melanogaster* Hinton, Ann. Mag. N.H., (9), 11, p. 149.

*Type*. Paris Museum.

*Type locality*.—Moupin, Western Sze-chwan, China.

*Characters*.—Size normal, hind-foot 17 mm.; condylo-basal length to 25 mm.

Colour very dark; upper parts clove brown, very finely peppered by the short tawny subterminal bands of the longer hairs; under surface blackish. Feet light brown. Tail obscurely bi-coloured, dusky above, brownish white below.

Skull normal, with relatively large auditory bullæ and light cheek-teeth;  $m^3$  with three salient angles on each side.

For *external and cranial measurements*, see tables at end of volume.

1b. **Eothenomys melanogaster cachinus** Thomas.

1921. *Microtus (Eothenomys) cachinus* Thomas, J. Bombay N.H.S., 27, p. 504.  
 1923. *Eothenomys melanogaster cachinus* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—B.M., No. 20.8.7.14; adult female, collected June 29, 1919, by Mr. F. Kingdon Ward, and presented by the Bombay Natural History Society.

*Type locality*.—Imaw Bum, Kachin Province, Northern Burma. Altitude 9000 feet.

*Range*.—Known only from the type locality.

*Characters*.—A bright-coloured form, with small auditory bullæ, heavy cheek-teeth and complex  $m^3$ .

Size rather large (hind-foot 19 mm.; condylo-basal length of skull 25.9 mm.).

Colour as in *E. m. eleusis* or slightly paler. Ears and feet as in that form, but tail rather longer.

Skull larger and heavier than in *E. m. eleusis*; interorbital region longer and more parallel-sided. Anterior palatal foramina narrowed in their posterior third. Auditory bullæ decidedly smaller than in *E. m. eleusis*, in antero-posterior diameter (parallel with the middle line of the skull) 6 instead of 6.7 mm.

Cheek-teeth markedly heavier than in *eleusis*, and  $m^3$  slightly more complex than in latter form;  $m^1$  with four,  $m^2$  with three salient angles on inner side;  $m^3$  with four inner and four outer salient angles.

For *external and cranial measurements*, see tables at end of volume.

1c. **Eothenomys melanogaster eleusis** Thomas.

1911. *Microtus (Eothenomys) melanogaster eleusis* Thomas, Abstr. P.Z.S., 1911, p. 50; P.Z.S., 1912, p. 139.  
 1923. *Eothenomys melanogaster eleusis* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—B.M., No. 11.9.8.111; adult male, collected March 13, 1911, by Malcolm Anderson; presented by the Duke of Bedford.

*Type locality*.—East of Chao-tung-fu, Northern Yunnan. Altitude 5800 feet.

*Range*.—Known only from the type locality.

*Characters*.—Size normal (hind-foot 19 mm.; condylo-basal length of skull to 26 mm.). Distinguished from *E. m. melanogaster* by its longer tail and more complex  $m^3$ .

Colour dark nearly as in *E. m. melanogaster*, but back averaging rather more greyish-brown. Tail decidedly longer, usually 46–48 mm. instead of 34–36 mm., but an isolated example of each of the two forms in each case measures 43 mm.

Skull nearly as in *E. m. melanogaster*, the auditory bullæ being

relatively large and the cheek-teeth light;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

1d. ***Eothenomys melanogaster aurora*** Allen.

1912. *Microtus (Eothenomys) aurora* G. M. Allen, Mem. Mus. Comp. Zool. Harvard Coll., 40, p. 211.

1923. *Eothenomys melanogaster aurora* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—Mus. Comp. Zool. Harvard Coll., No. 7788; male, skin and skull, collected February 2, 1909, by W. R. Zappey.

*Type locality*.—Changyanghsien, Hupeh, China.

*Range*.—Hupeh, China.

*Characters*.—Size normal, hind-foot to 18.5 mm.; condylo-basal length 25.8 mm.

Colour of upper parts bright, near "tawny" of Ridgway, with peculiar bright-yellow brassy reflections; muzzle grizzled grey without tawny. Flanks scarcely lighter than back, the colour grading insensibly into that of ventral surface. Under parts grey washed conspicuously, except on thighs and throat, with ochraceous buff, darkened by slaty bases of hairs, but not to the extent seen in *E. m. melanogaster*. Feet and ears clothed with short brown hairs, with greyish reflections. Tail indistinctly bicoloured, blackish above, greyish below.

Skull large and heavy with more prominent ridges and angles than in the typical form. Auditory bullæ large; cheek-teeth light. Enamel pattern of molars nearly typical, but  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

1e. ***Eothenomys melanogaster miletus*** Thomas.

1914. *Microtus (Eothenomys) melanogaster miletus* Thomas, Ann. Mag. N.H., [8], 14, p. 474.

1923. *Eothenomys melanogaster miletus* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—B.M., No. 14.10.23.32; adult male, collected February 28, 1914, by F. Kingdon Ward; presented by the Hon. N. C. Rothschild.

*Type locality*.—10 miles W. of Yang-pi, Western Yunnan. Altitude 7000 feet.

*Range*.—Known only from the type locality.

*Characters*.—Size normal (hind-foot 19 mm.; condylo-basal length of skull 25.3 mm.). General external characters, including colour and the greater length of tail, as in *E. m. eleusis*; size, however, somewhat greater. Colour rather brighter than in *E. m. confinii*.

Skull markedly larger and heavier than that of *E. m. eleusis*, strongly bowed dorsally, with small auditory bullæ and heavy cheek-teeth;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

1f. ***Eothenomys melanogaster confinii*** Hinton.

1923. *Eothenomys melanogaster confinii* Hinton, Ann. Mag. N.H., [9], 11, p. 151.

1924. *Microtus (Eothenomys) melanogaster confinii* G. M. Allen, Amer. Mus. Nov., No. 133, p. 3.

*Type*.—B.M., No. 22.12.1.1; adult male, collected July 25, 1921, by Mr. G. Forrest; presented by Colonel Stephenson R. Clarke, C.B., D.S.O.

*Type locality*.—Kin-chiang—Salween Divide in latitude 28° N., at an altitude of 11,000 feet.

*Range*.—Mountains of Southern Yunnan at altitudes from 6000 feet (Salween Basin) to 12,000 feet on the Kiu-chiang—Salween Divide, and to over 10,000 feet on the Pei-tai Mountain, south of Chung-tien.

*Characters*.—Most closely resembling *E. m. miletus*, but with more normal skull. Size (hind-foot 19 mm.; condylo-basal length of skull 25.2 mm.) and external proportions as in *E. m. miletus*. Colour a trifle darker with blackish slaty belly; many of the long hairs on sides and belly have burnished tips.

Skull with dorsal contour less convex than in *E. m. miletus*; interorbital region flatter, with distinct though weak temporal ridges along its margins; auditory bullæ slightly smaller and cheek-teeth slightly larger. Cheek-teeth as in *E. m. miletus* and *E. m. eleusis*;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Externally the likeness to *E. m. miletus* is striking, but the more normal skull is of very different appearance. Allen notes that "a series secured by the Second Asiatic Expedition [American Museum] includes two which, as noted by the collector, contained on February 8, 1917, one and two embryos respectively, a number correlated, no doubt, with the reduced number of mammæ."

1g. ***Eothenomys melanogaster colurnus*** Thomas.

1911. *Microtus (Eothenomys) melanogaster colurnus* Thomas, Ann. Mag. N.H., [8], 7, p. 209.

1923. *Eothenomys melanogaster colurnus* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—B.M., No. 0.5.8.38; adult male, collected October 24, 1899, and presented by C. B. Rickett, Esq.

*Type locality*.—Kuatun, N.W. Fokien.

*Range*.—N.W. Fokien.

*Characters*.—Differing from *E. m. melanogaster* by its much brighter colour and perhaps by its shorter tail (properly measured specimens not available).

General colour of upper parts rather darker and richer than "hazel," instead of being between "bistre" and "mummy brown" as the typical subspecies.

Skull with relatively large auditory bullæ (but these rather smaller than in *E. m. melanogaster*) and light cheek-teeth. As in the typical form  $m^3$  has only three salient angles on each side.

For *external and cranial measurements*, see tables at end of volume.

### 1h. *Eothenomys melanogaster mucronatus* Allen.

1912. *Microtus (Eothenomys) mucronatus* G. M. Allen, Mem. Mus. Comp. Zool., Harvard Coll., 40, p. 214.

1923. *Eothenomys melanogaster mucronatus* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—Mus. Comp. Zool., Harvard Coll., No. 7789; adult female, skin and skull, collected August 11, 1908, by W. R. Zappey.

*Type locality*.—Tachiao, Western Sze-chwan. Altitude 12,000 feet.

*Range*.—Known only from the type locality.

*Characters*.—Size normal, hind-foot 19 mm., condylo-basal length 26 mm. Ears relatively large. Fur long and soft.

General colour above near "mummy brown," produced by a fine grizzle of blackish hairs and hairs with cinnamon rufous tips. Under parts dark slate, with a very slight buffy wash on chest. Feet and tail covered with short hair-brown hairs; those of the tail slightly paler ventrally.

Skull with broad braincase and more bowed zygomata than in the typical form; palate boldly sculptured, its posterior edge with distinct median spinous process. Auditory bullæ small, cheek-teeth heavy. Enamel pattern of molars essentially as in *E. m. melanogaster*;  $m^3$  with three salient angles on each side.

For *external and cranial measurements*, see tables at end of volume.

### 1i. *Eothenomys melanogaster libonotus* Hinton.

1923. *Eothenomys melanogaster libonotus* Hinton, Ann. Mag. N.H., [9], 11, p. 151.

*Type*.—B.M., No. 21.12.5.54; adult male, collected June 20, 1921, by Mr. H. W. Wells; presented by the Bombay Natural History Society.

*Type locality*.—Dreyi, Mishmi Hills, Assam. Altitude 5140 feet.

*Range*.—Known only from the type locality.

*Characters*.—Closely resembling *E. m. mucronatus*, but smaller. Size rather small (hind-foot 17 mm.; condylo-basal length of skull 24.9 mm., instead of 19 and 26 respectively, as in *mucronatus*).

Colour dark and rich. Upper parts near "clove brown" of Ridgway, brightened by dull golden or rufous hair-tips. Under surface slaty grey. Feet above scarcely lighter than upper surface of tail.

Skull with small auditory bullæ and large teeth as in *E. m. mucronatus*; distinguished from that of the latter by its smaller size and narrower braincase. Cheek-teeth as in *E. m. melanogaster*;  $m^3$  with only three outer and three inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

## 2. *Eothenomys fidelis* Hinton.

1923. *Eothenomys fidelis* Hinton, Ann. Mag. N.H., [9], 11, p. 150; Thomas, *t.c.*, p. 661.

1924. *Microtus (Eothenomys) fidelis* G. M. Allen, Amer. Mus. Nov., 133, p. 4.

*Type*.—B.M., No. 22.12.1.8; adult female, collected Nov. 1921, by Mr. G. Forrest, and presented by Colonel Stephenson R. Clarke, C.B., D.S.O.

*Type locality*.—Li-chiang Range, N.W. Yunnan; in latitude  $27^{\circ} 30' N.$ , at altitudes between 13,000 and 14,000 feet.

*Range*.—The flanks of the Li-chiang Mountains and other parts of Yunnan. (See remarks quoted from G. M. Allen below.)

*Characters*.—A bright-coloured species, differing from *E. melanogaster* chiefly by its larger size and long narrow skull. Size large (hind-foot about 20 mm.; condylo-basal length of skull to about 28 mm.). Essential external characters as in *E. melanogaster*.

Colour nearly as in the brighter subspecies of *E. melanogaster* (e.g., *colurnus* and *miletus*). Upper parts dark brown (near "mummy brown"), brightened by rufous hair-tips; under surface slate grey, with a hoary tinge. Feet and tail dusky above.

Skull very large, long and narrow; with the temporal ridges and post-orbital squamosal crests strongly developed. Auditory bullæ relatively small, teeth relatively large, their relations about as in *E. m. libonotus* and *E. m. miletus*. Cheek-teeth (Fig. 86a and b, 2) normal;  $m^1$  with four,  $m^2$  with three inner salient angles;  $m^3$  with three outer and four inner salient angles.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This is the largest known member of the genus, a very reddish-looking vole with large skull and hind-foot. Allen states that "a fine series was secured from the same area [Li-chiang Mountains] by the Second Asiatic Expedition [American Museum], as well as others from Chunglu, Siao-ke-la, Chiangwei, and Yangtsien, on the Mekong River between altitudes of 6000-



9000 feet; Ha-pa (north of Taku) 10,000 feet; Yang-pi River (Tengyneh Road) at 5000 feet; Tali Lake, 6500 feet; and other localities. The entire series is very uniform in its characters. In two cases, three embryos were found in specimens captured the first week in October, and two in a female taken October 30, 1916. These are not only late litters but, as in the case of the preceding species [i.e., *E. melanogaster*], indicate a correlation between the small number of young per litter and the reduced number (four) of mammæ. It is possible also that the breeding season extends over a longer period than in some other *Microtines*."

### 3. *Eothenomys proditor* Hinton.

1923. *Eothenomys proditor* Hinton, Ann. Mag. N.H. [9], 11, p. 152; Thomas, *l.c.*, p. 661.

1924. *Microtus (Eothenomys) proditor* G. M. Allen, Amer. Mus. Nov., 133, p. 4.

*Type*.—B.M., No. 22.12.1.10; adult male, collected by Mr. G. Forrest, May 27, 1921, and presented by Colonel Stephenson R. Clarke, C.B., D.S.O.

*Type locality*.—Li-chiang Range, N.W. Yunnan; in lat. 27° 30' N. Altitude 13,000 feet.

*Range*.—Known only from the Li-chiang Mountains between 9000 and 13,000 feet.

*Characters*.—A bright-coloured, short-tailed, medium-sized species, with highly modified cheek-teeth. Size medium (hind-foot 16–18 mm.; condylo-basal length of skull to 27.3 mm.). Tail short, usually between 28 and 38 mm. Soles with six pads; hairy from heel to pads. Mammæ 0 — 2 = 4.

Colour of upper parts dark brown, but noticeably brighter than in *E. fidelis*; belly usually with well-marked yellowish suffusion. Feet dark above, concolorous with the upper surface of the tail. Tail dusky above, paler below.

Skull normal, rather smaller than that of *E. fidelis*; auditory bullæ rather large, teeth rather light. Check-teeth (Fig. 86a and b, 5) much reduced in pattern;  $m^1$  with three inner salient angles only;  $m^2$  with only a very slight vestige of the third inner angle (cusp  $n$ );  $m^3$  with the first outer infold shallow, as in *Alticola* and some other voles, and with vestigial fourth outer and fourth inner salient angles. Lower cheek-teeth normal; the outer angles of  $m_3$  well developed.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This species is very sharply distinguished from *E. fidelis*, which also inhabits the Li-chiang Range, by its smaller general size, shorter tail, and especially by its peculiar teeth. The latter in character approach those of *Antelionomys* and *Alticola*. It is noteworthy that no member of the genus *Neodon* is known to accompany *E. fidelis* and *E. proditor* upon the Li-chiang

Mountains and it seems probable that the place of *Neodon* is supplied by one or other of these two species of *Eothenomys*.

Allen states that "the series of ten specimens brought back by the Second Asiatic Expedition is from the same range, at the following localities: Ssu-shan-chong, 9000 feet; Peswi, 10,000 feet; Ssu-shan (Snow Mountain), 12,000 feet; timber-line 13,000 feet. Evidently it is a species of high levels."

#### 4. *Eothenomys olitor* Thomas.

1911. *Microtus (Eothenomys) olitor* Thomas, Abstr. P.Z.S., 1911, p. 50; P.Z.S., 1912, p. 139; Allen, Amer. Mus. Nov., 133, p. 4.

1923. *Eothenomys olitor* Hinton, Ann. Mag. N.H., [9], 11, p. 149.

*Type*.—B.M., No. 11.9.8.122; adult female, collected by Malcolm P. Anderson, March 19, 1911; presented by the Duke of Bedford.

*Type locality*.—Chao-tung-fu, Yunnan. Altitude 6700 feet.

*Range*.—Western Yunnan.

*Characters*.—A small greyish-brown species, with simplified  $m^1$  and complex  $m^3$ . Size small (hind-foot 16 mm.; condylo-basal length to 24 mm.).

General colour less warm brown than in other species. Upper parts greyish-brown, near sepia; under parts dark slaty grey (rather more smoky than "grey No. 5"). Hands and feet brown. Tail dark brown above, little lighter below.

Skull in general form like that of *E. melanogaster* but smaller, with the auditory bullæ relatively a little smaller.

Check-teeth;  $m^1$ , as in *E. proditor*, with only three inner salient angles;  $m^2$  with its third inner salient angle normally developed;  $m^3$  quite unreduced with four salient angles on each side, its first outer infold often shallow, imparting an *Alticola*-like appearance to the anterior loop;  $m_3$  with third outer angle more reduced than is usual in *Eothenomys*. Other teeth normal.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Mr. Allen says that three specimens were obtained by the American Museum Asiatic Expedition at an elevation of 7000 feet on the Mucheng-Salween Divide, Western Yunnan, and he remarks that the species is apparently the least common of the members of the genus in Yunnan.

#### Genus: 8. ANTELIOMYS Miller.

1896. *Anteliomys* Miller, N. Amer. Fauna, No. 12, p. 47; subgenus of *Microtus*; G. M. Allen, Amer. Mus. Nov., No. 133, 1924, p. 5.

1923. *Anteliomys* Hinton, Ann. Mag. N.H., [9], 11, p. 146 (genus).

*Genotype*.—*Microtus chinensis* Thomas.

*Range*.—Southern China and Yunnan.

*Characters*.—Externally nearly as in *Evotomys*. Ears large,

provided with a well-developed naked meatal valve. Hands and feet normal; claws of hind-foot slightly the longer; thumb small, furnished with a flattened nail. Palmar pads 5; plantar

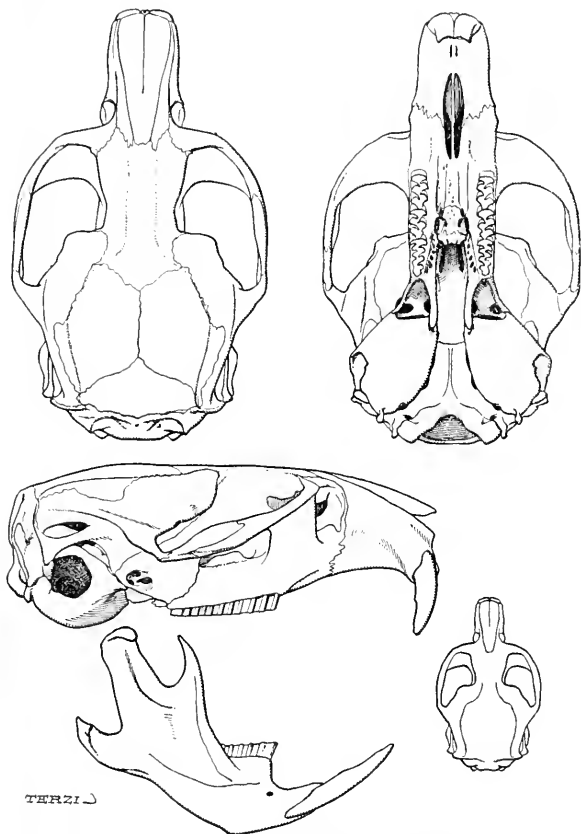


FIG. 87.—*Antelionomys wardi* Thomas.

Dorsal, lateral, and ventral views of skull; the small figure shows the skull in dorsal view, natural size.

pads 6, all well developed; sole hairy between heel and pads. Tail from one-third to about one-half the length of the head and body; well clothed with stiff hairs, forming a thin and short terminal pencil, but leaving the scaly annulations plainly visible. Mammæ 0 — 2 = 4.

Fur dense, very soft and fine although not specially modified. Colour more or less rufous brown, sometimes with metallic reflections.

Skull long and narrow, rather strongly built. Rostrum long and slender, the nasals ending anteriorly nearly flush with the incisors. Zygomata normal, the greatest zygomatic breadth falling in the glenoid region. Interorbital region relatively narrower in adults than in *Eothenomys*. Braincase long and narrow, smooth, the ridges not conspicuous in the material

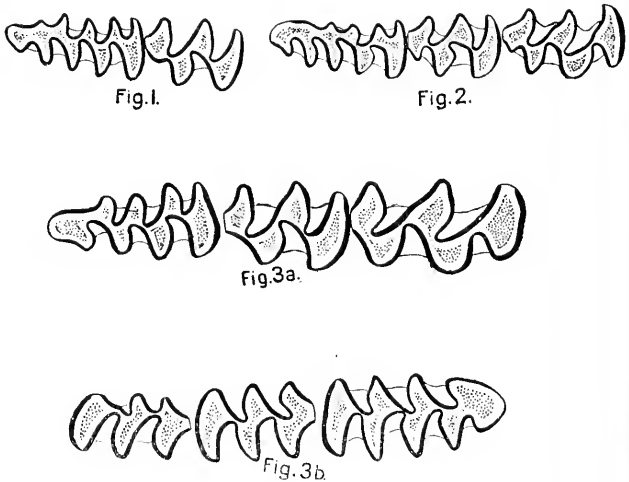


FIG. 88.—Cheek-teeth of *Antelionomys*.

1. *A. chinensis* (B.M., No. 11.2.1.215). Right  $m^2$  and  $m^3$  juv.
2. *A. custos* (B.M., No. 12.3.18.6). Right  $m^1$ ,  $m^2$ , and  $m^3$
3. *A. chinensis tarquinius* (B.M., No. 11.2.1.209). a. Right upper, b. left lower molars.

available. Temporal ridges tending to fuse, and in old age probably fusing to form a median interorbital crest; diverging behind, these ridges have a normal course, following the squamosoparietal suture on the fore-part of the braincase, and then crossing successively the lateral wing of each parietal, and the lateral extremities of the interparietal. Post-orbital crests of squamosals moderately developed, anterior squamosal encroachment incipient; upper border of jugal gently convex. Anterior palatal foramina large. Posterior portion of palate essentially as in *Evotomys*, but its posterior border in adults produced to form a median spine. Pterygoid fossæ large, their floors distinctly

though slightly dorsal to the ventral surface of the basisphenoid. Auditory bullæ simple, without spongy tissue internally; stapedia artery not enclosed in a bony tube.

Mandible without special peculiarities;  $m_3$  displaced lingually by the shaft of the lower incisor.

Dentition. Incisors normal; upper incisors strongly curved, slightly "opisthodont." Cheek-teeth hypsodont and rootless, the capsule of  $m^2$  noticeably obstructing the mouth of the sphen-orbital fissure; enamel about equally thick on convex and concave sides of prisms; dentinal spaces of mandibular molars and usually of maxillary molars more or less confluent; re-entrant folds with cement. Enamel pattern (Figs. 88, 89);  $m^1$  and  $m^2$  nearly normal, the triangles following the anterior loop in each tooth sometimes substantially closed, often more or less confluent; a vestigial trace of the fourth inner angle in  $m^1$  and of the corresponding third inner angle in  $m^2$  often present;  $m^3$  very complex

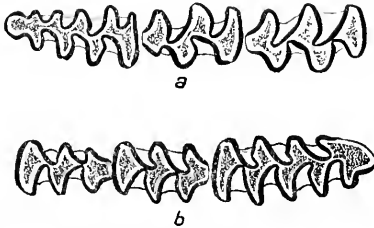


FIG. 89.—Cheek-teeth of *Anteliomys wardi* Thomas.  
 a. Right upper, b. left lower molars.

and peculiar, usually with four or five salient angles on the outer side and five or six salient angles on the inner side; in one form (*A. chinensis tarquinius*) the number of salient angles is usually reduced to four on each side by suppression of some of the posterior elements of the tooth; in normal forms the anterior loop is followed by seven or eight alternating triangles, the first outer infold is shallow leaving the first triangle confluent with the anterior loop as in *Alticola* and some other genera, the second outer fold is deep substantially closing off the second triangle (second inner angle), while the third and fourth outer folds are very shallow leaving all parts of the tooth behind the second triangle more or less confluent with each other. In *A. c. tarquinius* the outer folds of  $m^3$  are deeper so that four or five of the triangular dentinal spaces, including the first outer triangle, behind the anterior loop are substantially closed. The mandibular molars do not differ in any essential respect from those of *Eothenomys*.

Remarks.—*Anteliomys* differs from its closest ally *Eothenomys*, chiefly by the tendency to approximation in the interorbital

region shown by the temporal ridges and the anterior portions of the squamosals, characters which betoken increased development of the anterior portions of the temporal muscles; and by the greater size and complexity of the  $m^3$ . In the confluence of the dentinal spaces of the teeth most of the species agree with *Eothenomys*; but one form (*A. c. tarquinius*) shows in this respect a tendency towards the condition characteristic of *Evotomys rufocanus*.

*Species*.—Five forms, all very closely related structurally and geographically, are now known, and they are currently referred to three species; viz., *A. chinensis* and *A. wardi* which are large forms, and *A. custos* which is smaller. The differences between these species, though apparently constant, are of little moment, and not improbably all, at some future date, will be regarded as subspecies of *A. chinensis*. It is to be hoped that efforts will be made to collect further material; for although the series now available are tolerably long they include very few if any specimens which I should be inclined to regard as fully developed.

*Key to the species and subspecies of Antelionomys* :—

- A. Tail about two-thirds the length of the head and body. Ears relatively large. Colour darker.
- a. Skull with large, lofty and convex braincase; auditory bullæ large.
- a<sup>1</sup>. Cheek-teeth normal; upper molars with confluent dentinal spaces;  $m^3$  complex with five inner salient angles . . . . . *A. chinensis chinensis* Thomas.  
W. Sze-chwan.
- b<sup>1</sup>. Cheek-teeth modified; upper molars with dentinal spaces substantially closed;  $m^3$  simpler, with four inner salient angles . . . . . *A. c. tarquinius* Thomas.  
W. Sze-chwan.
- b. Skull with braincase small, depressed and flattened above. Auditory bullæ very small . . . . . *A. wardi* Thomas.  
N.W. Yunnan.
- B. Tail less than half the length of the head and body. Ears shorter. Colour paler.
- a. Upper parts less rufous, under surface browner. Hands and feet greyish white . . . . . *A. custos custos* Thomas.  
Mekong-Yangtze Divide.
- b. Upper parts redder, under-surface greyer. Hands and feet dusky . . . . . *A. c. rubellus* G. M. Allen.  
Li-chiang Range.

1. ***Antelionomys chinensis*** Thomas.

(Synonymy under subspecies.)

*Range*.—Mountains of Western Sze-chwan.

*Characters*.—Size large; hind-foot 20–23 mm.; condylo-basal length 28 mm. Fur soft and dense, about 12 mm. long on back.

General colour dark; upper surface dark brown, near “Prouts”

brown," with a slight reddish tinge produced by the brighter hair-tips; under parts bluish-grey, rather heavily washed on chest and belly with wood brown. Ears large and prominent, coloured like the back. Tail very long, about two-thirds the length of the head and body; indistinctly bicoloured, dark brown or blackish above, greyish-white below. Hands and feet dusky.

Skull with relatively large and lofty braincase, its upper surface well arched. Auditory bulke large, the basioccipital correspondingly narrow in front.

*Geographical differentiation.*—Two subspecies distinguished by slight average differences in the form of the  $m^3$  have been described by Thomas.

**1a. *Anteliumys chinensis chinensis* Thomas.**

1891. *Microtus chinensis* Thomas, Ann. Mag. N.H., [6], 8, p. 117.

1896. *Microtus (Anteliumys) chinensis* Miller, N. Amer. Fauna, No. 12, p. 48; Thomas, P.Z.S., 1911, p. 175.

*Type.*—B.M., No. 91.5.11.3; adult female.

*Type locality.*—Kia-ting-fu, Western Sze-chwan, China.

*Range.*—Western Sze-chwan. Known from the type locality, and from Omi-San.

*Characters.*—External and cranial characters as described above under the species. Cheek-teeth as usual in the genus;  $m^3$  normally with five salient angles on the inner side; dentinal spaces of upper teeth relatively confluent (for details see account of *A. c. tarquinius* below, and Fig. 88).

For *external and cranial measurements*, see tables at end of volume.

**1b. *Anteliumys chinensis tarquinius* Thomas.**

1911. *Microtus (Anteliumys) chinensis* Thomas, P.Z.S., 1911, p. 175 (in part).

1912. *Microtus (Anteliumys) chinensis tarquinius* Thomas, Ann. Mag. N.H., [8], 9, p. 517.

*Type.*—B.M., No. 11.2.1.207; adult male, collected June 15, 1910, by M. P. Anderson, and presented by the Duke of Bedford.

*Type locality.*—23 miles S.E. of Ta-t sien-lu, Western Sze-chwan. Altitude 10,000 feet.

*Range.*—Known only from the neighbourhood of the type locality.

*Characters.*—External and cranial characters as in the typical form.

Cheek-teeth somewhat more specialized, the dentinal spaces of upper molars more tightly closed and  $m^3$  somewhat reduced; usually with only four salient angles on its inner side (in 7 out of 8 specimens; a fifth inner angle present in 8 out of 9 specimens of *A. c. chinensis*). With regard to the greater confluency of the dentinal spaces, Thomas records that the triangles of the first

pair following the anterior loop in  $m^1$  are closed in 5 out of 8 specimens of *A. c. tarquinius*, open in all 9 of *A. c. chinensis*; that the second and third triangles (second inner, third outer angles) of  $m^3$  are closed in 6 out of 8 specimens of *A. c. tarquinius*, open in 7 out of 9 of *A. c. chinensis*. The first outer infold of  $m^3$  is also normally deeper than in *A. c. chinensis*, the first outer triangle being as a rule substantially shut off from the anterior loop instead of broadly confluent with it as usual in this genus and in *Alticola* and some other forms.

For *external and cranial dimensions*, see tables at end of volume.

## 2. *Antelionomys wardi* Thomas.

1912. *Microtus (Antelionomys) wardi* Thomas, Ann. Mag. N.H., [8], 9, p. 516; Thomas, Ann. Mag. N.H., [8], 14, p. 473.

1923. *Antelionomys wardi* Hinton, Ann. Mag. N.H., [9], 11, p. 154.

*Type*.—B.M., No. 12.3.18.15; skull of male, collected by F. Kingdon Ward, and presented by the Duke of Bedford.

*Type locality*.—Chamutong, Upper Salween drainage-area, W. of A-tun-tsi, North-Western Yunnan. Altitude 13,000 feet.

*Range*.—Widely distributed in the high Alpine meadows of North-Western Yunnan, at altitudes of from 8000–14,000 feet.

*Characters*.—Size, external form, and colour as in *A. chinensis*.

Skull slightly smaller and noticeably more depressed than in *A. chinensis*. Braincase relatively small, low, and flattened above. Anterior palatal foramina narrow throughout. Auditory bullæ very small, the basioccipital correspondingly broad anteriorly.

Cheek-teeth essentially as in *A. c. chinensis*;  $m^2$  usually with a vestigial trace of the third inner angle;  $m^3$  complex.

For *cranial and external measurements*, see tables at end of volume.

## 3. *Antelionomys custos* Thomas.

(Synonymy under subspecies.)

*Range*.—Mountains of North-Western Yunnan; on the divide between the Mekong and Yangtse-kiang rivers from A-tun-tsi south-eastwards along the Li-chiang Range, at altitudes of from 9000–13,000 feet.

*Characters*.—Size small; hind-foot 16.5–18.5 mm.; condylo-basal length 25 mm. Fur long and soft; hairs of back about 11 mm. in length. General colour of upper surface rusty brown, noticeably paler than in *A. chinensis*. Ears slightly shorter and less prominent than in other forms. Hands and feet normal. Tail relatively short, less than half the length of the head and body.

Skull essentially as in other forms; <sup>1</sup> auditory bullæ rather small, though slightly larger relatively than in *A. wardi*.

<sup>1</sup> Thomas describes his type as an "old male," and says of the skull of this species: "upper surface smooth, rounded, without marked ridges,



Cheek-teeth as in other species.

*Geographical differentiation.*—Two subspecies, viz., the typical form from the neighbourhood of A-tun-tsi, and *A. c. rubelius* Allen from the Li-chiang Range further south, are at present recognized. These forms are distinguished by slight differences of colour.

### 3a. *Antelionmys custos custos* Thomas.

1912. *Microtus (Antelionmys) custos* Thomas, Ann. Mag. N.H., [8], 9, p. 517; Thomas, Ann. Mag. N.H., [8], 14, 1914, p. 474; G. M. Allen, Amer. Mus. Nov., No. 133, 1924, p. 5.

*Type.*—B.M., No. 12.3.18.19; adult male, collected May 28, 1911, by F. Kingdon Ward, and presented by the Duke of Bedford.

*Type locality.*—A-tun-tsi, North-Western Yunnan. Altitude 11,500–12,500 feet.

*Range.*—Mountains of North-Western Yunnan, at altitudes of from 9000–13,000 feet.

*Characters.*—Hind-foot 17 mm.; condylo-basal length 25 mm.

General colour above rather warmer than "broccoli brown"; head more greyish brown. Under surface paler brown, the hairs of the belly washed with wood brown, but those of the throat, chest, and axilla with greyish tips. Ears brown, like the back. Hands and feet greyish-white above. Tail dark brown above, greyish below.

Skull with nasals ending posteriorly between and noticeably in advance of the ends of the ascending branches of the pre-maxillaries.

For *external and cranial dimensions*, see tables at end of volume.

### 3b. *Antelionmys custos rubelius* G. M. Allen.

1924. *Microtus (Antelionmys) custos rubelius* G. M. Allen, Amer. Mus. Nov., No. 133, p. 5.

*Type.*—American Mus. N.H., No. 44001; adult female, skin and skull, collected October 13, 1916, by R. C. Andrews and Edmund Heller.

*Type locality.*—Ssu-shan (Snow Mountain), Li-chiang Range, Yunnan. Altitude 13,000 feet, at timber line.

*Range.*—Known only from the Li-chiang Range.

*Characters.*—Similar in general to *A. c. custos*, but slightly more reddish above, the belly clearer grey, lacking the decided brownish wash, although sometimes with a very faint brownish

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the interorbital region broad, short, its edges rounded and its middle line flat or concave, without tendency to form a median crest." As a result of my special studies of the Microtine skull, and after examination of all the skulls of *Antelionmys* available, I am of opinion that neither the type nor any of the other skulls of *A. custos* can be regarded as fully mature.

wash on the chest. Feet and tail dusky above; the tail paler (greyish) below.

In his description of this form Allen describes the nasals as falling considerably short of the premaxillaries behind, believing the converse condition to obtain in *A. c. custos*. But the type of *A. c. custos* and our other skulls of the typical form agree perfectly with Allen's description of *A. c. rubellus* in this respect.

For *external and cranial dimensions*, see tables at end of volume.

Genus: **9. ALTICOLA** Blanford.

1881. *Alticola* Blanford, J.A.S. Bengal, **50**, pt. 2, p. 96 (proposed as a section of the genus *Arvicola*).  
 1891. *Alticola* Sclater, Catal. Mamm. Ind. Mus., pt. 2, p. 89 (in part; subgenus of *Arvicola*).  
 1891. *Microtus* Blanford, Fauna Brit. India, Mamm., p. 429 (in part).  
 1896. *Alticola* Miller, N. Amer. Fauna, No. **12**, p. 52; Proc. Acad. Nat. Sci. Philadelphia, **1899**, p. 291; Wroughton, "Summary," J. Bombay N.H.S., **27**, p. 59, 1920 (subgenus of *Microtus*).  
 1912. *Alticola* Thomas, Ann. Mag. N.H., [8], **9**, p. 400; Miller, Proc. Biol. Soc. Washington, **25**, 1912, p. 59 (genus).

*Genotype*.—*Arvicola stoliczkanus* Blanford.

*Range*.—The genus has a wide distribution in the mountains of Central Asia, where its members are found living at high altitudes (6000–18,500 feet). The known range extends from Kumaon and Lahul northwards to beyond the Thian Shan Mountains (Bogdo-Ola Mountains) and from the Hissar Mountains, east of Samarkand, eastwards to Mount Everest. In this area the genus is known to be represented by fifteen forms; but others probably remain to be discovered. On the other hand, owing to the lack of satisfactory material, it is not possible to determine the precise status of some of the forms that have been described.

*Characters*.—Size small or medium (hind-foot ranging between 16 and 20 mm.; condylo-basal length of skull rarely exceeding 29 mm.).

Fur full and soft, its length variable. Eyes moderately large. Ears simple and rounded, of moderate size, though often failing to overtop the long fur, furnished with an antitragus. Tail from less than one-fifth to more than one-half of the combined length of the head and body, clothed more or less densely with long stiff hairs which partly or wholly conceal the scaly annulations and form a terminal pencil of variable length. Hands and feet normal; claws rather short but sharp, those of the foot slightly longer than those of the hand; thumb vestigial, with or without a minute flattened nail. Palmar tubercles 5; plantar tubercles 6; palms and soles more or less densely haired behind the pads;

spaces between the pads sometimes naked, sometimes clothed with short hair. Mammary formula  $2-2=8$ .

Skull in palatal structure and other essential respects as in

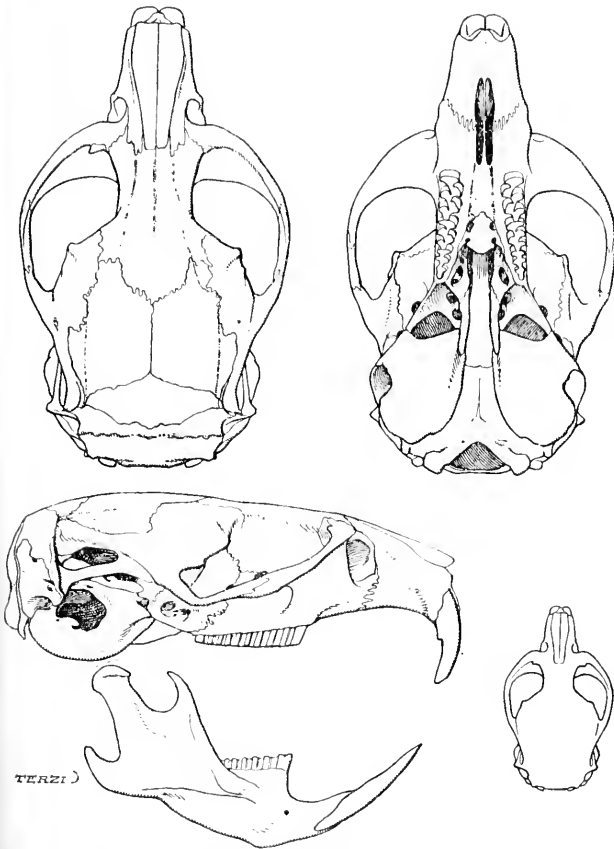


FIG. 90.—*Alticola roylei* Gray.

Dorsal, lateral, and ventral views of skull; the small figure shows the skull in dorsal view, natural size.

*Evotomys*. Temporal ridges, in adults, widely separated in the interorbital region and on the braincase; post-orbital squamosal crests often slightly more salient than is usual in *Evotomys*; no, or very slight, squamosal encroachment upon the fore-part of



Fig. 4.



Fig. 1a.



Fig. 5.



Fig. 2a.



Fig. 6.



Fig. 3a.



Fig. 7.



Fig. 1b.



Fig. 8.



Fig. 2b.



Fig. 9.

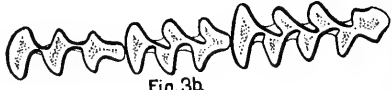


Fig. 3b.



Fig. 10.



Fig. 14.



Fig. 17.



Fig. 11.



Fig. 15.



Fig. 18.



Fig. 12.



Fig. 16.



Fig. 19.



Fig. 13.



Fig. 20.

FIG. 91.—Cheek-teeth of *Alticola*.  
(For explanation see opposite page.)

## EXPLANATION OF FIG. 91.

- FIG. 1. *A. phasma*. 1a right upper, 1b left lower molars. (B.M., No. 12.4.1.116).  
 2. *A. stracheyi*. 2a right upper, 2b. left lower molars. (B.M., No. 6.12.3.19.)  
 3. *A. (Platycranius) strelzowi*. 3a. right upper, 3b. left lower molars. (B.M., No. 8.11.6.8.)  
 4. *A. worthingtoni*. Left  $m^3$ . (B.M., No. 12.4.1.190.)  
 5. *A. worthingtoni*. Left  $m^3$ . (B.M., No. 12.4.1.115.)  
 6. *A. worthingtoni*. Left  $m^3$ . (B.M., No. 5.12.4.9.)  
 7. *A. worthingtoni*. Left  $m^3$ . (B.M., No. 12.4.1.188.)  
 8. *A. blanfordi*. Left  $m^3$ . (B.M., No. 1.8.4.10.)  
 9. *A. roylei*. Left  $m^3$ . (B.M., No. 14.7.10.225.)  
 10. *A. roylei*. Left  $m^3$ . (B.M., No. 14.7.10.222.)  
 11. *A. roylei*. Left  $m^3$ . (B.M., No. 14.7.10.220.)  
 12. *A. montosa* ("imitator"). Left  $m^3$ . (B.M., No. 12.11.26.18.)  
 13. *A. blanfordi lahulius*. Left  $m^3$ . (H. W. W. 2722.)  
 14. *A. albicauda*. Left  $m^3$ . Skardu (B.M., No. 5.10.8.5.)  
 15. *A. stracheyi*. Left  $m^3$ . (B.M., No. 7.9.6.7.)  
 16. *A. stracheyi*. Left  $m^3$ . (H. W. W. 2721.)  
 17. *A. roylei*. Right  $m_1$ . (B.M., No. 14.7.10.225.)  
 18. *A. albicauda*. Right  $m_1$ . (B.M., No. 5.10.8.5.)  
 19. *A. worthingtoni*. Right  $m_1$ . (B.M., No. 5.12.4.9.)  
 20. *A. blanfordi*. Right  $m_1$ . (B.M., No. 1.8.4.10.)

the braincase. Auditory bullæ well developed, often considerably inflated, invariably simple, thin-walled, and lacking any trace of spongy bone-tissue within. Mandible normal; lower incisor displacing  $m_3$  lingually, and ascending into the condylar process to about the level of the alveolar margin of the ramus.

*Cheek-teeth* rootless, growing from persistent pulps; a small quantity of cement present in the re-entrant folds; enamel more or less well differentiated, as in the higher voles. Enamel pattern of  $m^1$ ,  $m^2$ ,  $m_2$ , and  $m_3$  essentially as in normal voles, and lacking traces of additional vestigial angles behind ( $m^1$ ,  $m^2$ ) or in front ( $m_2$ ,  $m_3$ );  $m_1$  (Fig. 91, 1b-3b, 17-20) with a posterior loop, followed by five alternating and more or less completely closed triangles, and terminated by an anterior loop of variable form, which is more or less confluent posteriorly with the fifth triangle, the tooth showing in most species four outer and five inner salient angles. The last upper molar,  $m^3$ , varies much in form in different species. When most complex (Fig. 91, 1a) this tooth has an anterior transverse loop, followed by six alternating triangles, of which, however, only the second and third are substantially closed, and is terminated by a short posterior loop. When most reduced (Fig. 91, 15, 16)  $m^3$  has an anterior loop, followed by three alternating triangles only, and is terminated by a posterior loop of variable length and form; sometimes the posterior loop is very long and narrow, forming more than half the length of the entire crown; sometimes it is short and broad, forming less than half the length of the crown. According to its degree of reduction, the number of salient angles present in the  $m^3$  in this genus varies

from five inner and five outer to three outer and two inner angles. In all species the first outer infold of  $m^3$  is shallow, so that the anterior loop and the first or small external triangle behind it are more or less widely confluent with each other. In this respect *Alticola* agrees with many of the species of *Eothenomys*, *Antelionomys*, *Hyperacrius* and some other genera.

*Subgenera*.—Two subgenera are now recognized, namely, *Alticola*, comprising the great majority of the species, characterized by its normal skull; and *Platycranius*, comprising one or two species with remarkably depressed skulls.

Subgenus : **Alticola** Blanford.

(Synonymy under the genus above.)

*Range and characters* as described under the genus.

*Interrelationships of the species*.—By searching the known forms for the most primitive expressions of each character subject to variation in the genus, it is possible to arrive at a sum which must express the highest degree of specialization possible for the common ancestor of the living members of the genus. In that ancestor the fur was probably short and overtopped by the moderately large ears; the colour must have been at least as dark as in *A. roylei roylei*, dark brown above with the lower surface dingy and not contrasted; the hands, feet, and tail must have been dusky above. In the hands and feet the claws were short and not covered by long hairs growing upon the dorsal surfaces of the digits; the vestigial thumb bore a small nail or claw; the palms and soles were not very densely haired behind the pads, and the spaces between the pads were naked. The tail, as in *A. argurus*, must have been longer than half the length of the head and body, very imperfectly clothed, its short hairs not concealing the scaly annulations and scarcely forming a terminal pencil (cf. *A. r. roylei*). As in all known species the under surface of the tail is whitish, in the ancestor the tail was probably already bicoloured. Other ancestral characters, common to all the species of the genus, are the possession of five palmar and six plantar tubercles and the mammary formula  $2-2=8$ .

The skull was probably lightly and delicately built, much as in *A. blanfordi*, with the temporal ridges widely separated throughout, and the auditory bullæ and the cheek-teeth of moderate size. The enamel pattern of  $m^3$  and  $m_1$  must have been as complex as in *A. phasma*; but the other cheek-teeth had already acquired the reduced form which characterizes them in most of the higher voles.

The living species of *Alticola* are all very closely related to each other. Although they vary considerably in external appearance, they are all much alike in skull and dentition. Their skulls differ only in small details correlated with slight differences in the development of the anterior portions of the temporal muscles, in the size

of the teeth, and in the size and form of the auditory bullæ. By the differences in the structure of  $m^3$  the species fall into two rather natural groups, viz., one, the *roylei* group, in which  $m^3$  remains comparatively complex, always possessing at least three well-developed salient angles on the inner side; and the other, the *stracheyi* group, in which  $m^3$  has been considerably reduced, possessing in adults normally only two salient angles upon the inner side, although a vestige of the third angle is commonly present as an ephemeral complication in immature teeth. Broadly speaking, the external characters also follow this dental division between the two groups; thus in the *roylei* group, side by side with the more primitive  $m^3$ , we find in one species or another the most primitive external characters (darkest colour; barest feet; longest, least clothed, or most distinctly bicoloured tail) known in the genus; whereas in the *stracheyi* group, in association with the highly specialized  $m^3$ , we find that all the forms show in their pallid adult coloration, booted feet, very short, heavily clothed and entirely white tails, a high degree of external specialization. But although the members of the *roylei* group are on the whole more primitive than those of the *stracheyi* group, many of them are so highly specialized in one or other external character that as regards that particular character they approach or even rival the members of the higher group. No hard and fast line can be drawn between the two groups save that which depends upon the structure of the  $m^3$ ; that even this is quite an arbitrary distinction is evident when we consider that the reduction of that tooth from species to species, or from youth to age (in the *stracheyi* group) proceeds by very gentle gradations. As in other Microtinæ the progressive reduction of this tooth has proceeded apparently from behind forwards, the three posterior (viz. one outer, two inner) of the six triangles primitively intervening between the anterior and the posterior loops successively dwindling in size until, losing their independence, they have become completely blended with the posterior loop, thus producing the peculiar form of  $m^3$  so characteristic of *A. stracheyi* and its nearest relatives. Finally the posterior loop, now a compound of the loop proper and the three atrophied triangles, has been shortened from behind, thus resulting in the form of  $m^3$  found in *A. stoliczkanus*, somewhat similar to that so characteristic of the genus *Hyperacrius*.

If we examine the various species of *Alticola* critically we find that it is impossible to bring them into any linear sequence if attention be paid to more than one character at a time; for each species shows its own peculiar blend of archaic and progressive features. Differences of altitude and latitude (probably by their influence upon humidity, temperature, light intensity, food and the other factors which constitute an environment) appear to exercise a direct control over the outward habit of these animals and to be the chief causes of the external differentiation of the species. In some degree too, by controlling the nature of

the food supply, they probably influence the dentition and the correlated cranial characters; but their control in this direction is less peremptory and direct; for what food shall be available to *Alticola* in any given district must obviously depend upon the presence or absence there of competing genera as well as upon the physical conditions of the station.

*Key to species and subspecies of Alticola* :—

- A.  $m^3$  in adults with at least three well-developed salient angles on the inner side. Tail always longer than hind-foot. Palms and soles naked between pads, more or less densely haired posteriorly.
- a. Tail imperfectly clothed, its scaly annulations more or less apparent. Claws not hidden by long dorsal hairs of digits.
- $a^1$ . Tail very long (54% of head and body length), wholly white, with a thin terminal pencil of about 7 mm. in length. Colour very pale, ecru drab above, white below;  $m^3$  with third triangle closed behind.  
*A. argurus* Thomas.  
Hissar Mts. (9500 feet).
- $b^1$ . Tail shorter, not exceeding half the length of the head and body; distinctly bicoloured in all except *A. albicauda*. Colour darker.
- $a^2$ . Skull long, narrow and delicately built;  $m^3$  with third outer fold well developed, the third triangle substantially closed behind. Tail long (40–50% of head and body length), with a long but thin terminal pencil . . . . . *A. blanfordi* Scully.
- $a^3$ . Colour darker, yellowish-brown above, whitish or faintly buffy below. Auditory bullæ smaller;  $m^3$  with a distinct though small fourth outer angle.  
*A. blanfordi lahulius* Hinton.  
Labul (10,000–14,000 feet).
- $b^3$ . Colour paler, light greyish-brown above, greyish-white below. Auditory bullæ larger;  $m^3$  with the fourth outer angle vestigial.  
*A. blanfordi blanfordi* Scully.  
Gilgit (9000–10,000 feet).
- $b^2$ . Skull broader and more heavily built.
- $a^3$ .  $m^3$  with third triangle substantially closed behind. Auditory bullæ larger; cheek-teeth lighter.
- $a^4$ . Tail longer (about 40% of head and body length), its terminal pencil very short. Colour darker; dark greyish-brown above, silvery-grey below.  
*A. montosa*, True.  
Central Kashmir (11,000 feet).
- $b^1$ . Tail shorter (about 35% of head and body length). Colour lighter; light brownish-grey above, greyish-white below. . . . . *A. glacialis* Miller.  
Baltistan (11,000 feet).
- $b^3$ .  $m^3$  with third outer infold reduced, the third triangle more or less confluent with the posterior loop.
- $a^4$ . Tail longer (averaging 33–36% of the head and body length), distinctly bicoloured; its terminal



pencil very short and thin. Colour dark; rich dark brown above. Auditory bullæ small; cheek-teeth robust . . . . . *A. roylei* Gray.

*a*<sup>5</sup>. Under parts with an ochraceous wash.  
*A. roylei roylei* Gray.  
[Kumaon (10,000-13,000 feet).]

*b*<sup>5</sup>. Under parts silvery-grey.  
*A. roylei cautus* Hinton.  
Lahul (8500-9200 feet).

*b*<sup>1</sup>. Tail shorter (28-30% of head and body length), wholly white or with a very faint brown tinge above; better clothed, and with a long terminal pencil. Colour pale; reddish- or yellowish-grey above, white below . . . . . *A. albicauda* True.

Baltistan (12,000 feet).

*b*. Tail completely clothed, its annulations concealed; wholly white; usually between 30 and 40% of head and body length. Claws partly hidden by the long dorsal hairs of the digits.

*a*<sup>1</sup>. *m*<sup>3</sup> more complex (Fig. 91, 1*a*); auditory bullæ very large; anterior palatal foramina longer, terminating behind between the tooth-rows. Colour pallid, yellowish-brown above, white below; terminal pencil of tail about 13 mm. long . . . . . *A. phasma* Miller.

Kara Korum Mts. (9000-10,000 feet).

*b*<sup>1</sup>. *m*<sup>3</sup> somewhat simpler (Fig. 91, 4-7); auditory bullæ smaller; anterior palatal foramina shorter terminating behind in advance of the tooth-rows. Colour darker and greyer; terminal pencil of tail shorter, about 5 mm. long . . . . . *A. worthingtoni* Miller.

*a*<sup>2</sup>. Under parts white . . . . . *A. w. worthingtoni* Miller.

Thian Shan Region (6000-9000 feet).

*b*<sup>2</sup>. Under parts pale pinkish buff.

*a*<sup>3</sup>. Skull and teeth smaller (condylo-basal length 25.1 mm.) . . . . . *A. w. sublutus* Thomas.

Thian Shan, Semiretschensk.

*b*<sup>3</sup>. Skull and teeth larger (condylo-basal length to 28.7 mm.) . . . . . *A. w. semicanus* Allen.

Central Mongolia.

*B. m*<sup>3</sup> in adults with only two salient angles on the inner side. Tail very short, rarely exceeding the hind-foot in length, completely clothed, and wholly white. Palms and soles more or less hairy between the pads; densely haired behind. Claws usually concealed by long dorsal hairs of digits.

*a. m*<sup>3</sup> less reduced, its form most peculiar, the posterior loop long and narrow and forming fully half the length of the crown. Colour pallid, light yellowish-brown or brownish-grey above, white below.

*a*<sup>1</sup>. Braincase small; auditory bullæ less inflated.

*A. stracheyi* Thomas.

E. Kashmir, W. Tibet (14,500-18,500 feet).

Everest (17,300 feet).

*b*<sup>1</sup>. Braincase larger and deeper; auditory bullæ larger and more swollen . . . . . *A. lama* Barrett-Hamilton.

W. Tibet (16,000-17,800 feet).

- b. m*<sup>3</sup> more reduced but more normal in appearance; the posterior loop short and broad forming less than half of the length of the crown.
- a*<sup>1</sup>. Tail longer, hind-foot shorter (25 and 16 mm. respectively). Colour darker, bright ferruginous brown above, white below . . . . . *A. stoliczkanus* Blanford.  
Kuenlun Mts., N. Ladak.
- b*<sup>1</sup>. Tail shorter, hind-foot longer (18.6 and 19 mm., respectively). Colour paler, pinkish-buff above, white below.  
*A. acrophilus* Miller.  
Kara Korum Pass (17,000 feet).

### 1. *Alticola argurus* Thomas.

1909. *Microtus (Alticola) argurus* Thomas, Ann. Mag. N.H., [8], 3, p. 264.

*Type*.—B.M., No. 9.4.3.100; sub-adult female, skin and skull, collected June 14, 1908, and presented by D. Carruthers.

*Type locality*.—Hissar Mountains, 100 miles east of Samarkand. Altitude 9500 feet. Trapped in juniper forest.

*Range*.—Known only from the type locality.

*Characters*.—A pallid species with an unusually long white tail.

Fur fine and soft; hairs of back (in summer pelage) about 7-8 mm. in length. General colour above "ecru drab"; under surface white, the slaty bases of the hairs showing through; a line of cream-buff marking the junction of the upper and lower colours on the sides. Hands and feet white. Tail unusually long (about 54% of the head and body measurement), thinly haired (in summer), lightly pencilled, wholly white above and below; hairs not completely concealing the annulations; terminal hairs project about 7 mm. Mammæ 2-2 = 8.

Skull too young to show definite characters, but apparently not unlike that of *A. worthingtoni*.

Cheek-teeth normal; *m*<sup>3</sup> nearly as in *A. blanfordi*.

For *external and cranial measurements*, see tables at end of volume.

### 2. *Alticola blanfordi* Scully.

(Synonymy under subspecies.)

*Range*.—North-west Himalayas, the limits of range being at present unknown. Found in the vicinity of Gilgit at altitudes of from 9000-10,000 feet, and in Lahul at altitudes of from 10,000-14,000 feet.

*Characters*.—Size medium (hind-foot 17-20 mm.; condylo-basal length of skull up to about 27.5 mm.). Tail from two-fifths to about half the length of the head and body; well haired, although traces of the scaly annulations are visible under a lens, with a thin terminal pencil 5 to 8 mm. in length.

Fur moderately dense and rather short (about 10 mm. long on the middle of the back). Colour intermediate between that

of the darkest and lightest members of the genus. Upper parts (according to the subspecies) either a rather light greyish-brown, or else a warmer reddish-brown. Under parts whitish. Feet white. Tail more or less distinctly bicoloured. Palmar tubercles 5, plantar tubercles 6; soles clad rather densely with stiff white hairs behind the pads; claws as in *A. roylei*. Mammæ 2-2 = 8.

Skull rather long and narrow, delicately built with moderately developed or rather large auditory bullæ. Dentition (Fig. 91, 8, 13, 20) as in other members of the *roylei* group;  $m^3$  normally either with a distinct vestige of the fourth outer angle, or else with that angle rather well developed.

### 2a. *Alticola blanfordi blanfordi* Scully.

1880. *Arvicola blanfordi* Scully, Ann. Mag. N.H., [5], 6, p. 399, and P.Z.S., 1881, p. 206; Blandford ["section *Alticola*"], J.A.S., Bengal, 50, pt. 2, 1881, p. 104.

1891. *Arvicola (Alticola) blanfordi* Selater, Catal. Mamm. Ind. Mus., pt. 2, p. 91.

1891. *Microtus blanfordi* Blandford, Fauna Brit. Ind. Mamm., p. 432.

1896. *Microtus (Alticola) blanfordi* Miller, N. Amer. Fauna, No. 12, p. 54; Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 292; Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 60.

*Co-types*.—Two in British Museum (Nos. 81.3.1.22 and 8.3.9.17) and two in the Indian Museum, Calcutta (Nos. *a* and *b*). Of these Thomas has selected B.M., No. 8.3.9.17, an adult male, skin and skull, as the "lectotype" (J. Bombay N.H.S., 25, 1918, p. 371).

*Type locality*.—Gilgit, at altitudes between 9000 and 10,000 feet.

*Range*.—At present known only from the vicinity of the type locality.

*Characters*.—Upper parts rather light greyish-brown, with a very slight rufous tinge; under parts greyish-white darkened by the slaty hair bases; no sharp line of demarcation along the flanks. Feet white. Tail brown above, dirty white below, its terminal pencil about 5 mm. long.

Skull long, narrow, and depressed, with a slender rostrum and moderately large auditory bullæ; characters not fully appreciable from the available material. Distinguished from that of the next subspecies by its longer and relatively narrower nasals and rather larger bullæ. Dentition (Fig. 91, 8, 20):  $m^3$  with the fourth outer angle represented usually by a vestige.

For *external and cranial measurements*, see tables at end of volume.

### 2b. *Alticola blanfordi lahulius* subsp. n.

*Type*.—B.M., No. 26.3.9.1, original No. 2676; young adult male, skin and skull, collected July 30, 1922, by H. W. Wells

(Mammal Survey of India); presented by the Bombay Natural History Society.

*Type locality*.—Kyelang, Lahul. Altitude 10,380 feet.

*Range*.—Known from various places in the neighbourhood of the type locality in Lahul, at altitudes ranging from 10,000–14,000 feet.

*Characters*.—Distinguished from *A. b. blanfordi* by its darker colour, shorter nasals, and less inflated auditory bullæ.

Upper parts yellowish-brown, produced by a fine mixture of ochraceous subterminal bands and dark brown and blackish hair-tips. Under parts whitish or faintly buffy, darkened by the slaty hair-bases. No sharp line of demarcation along the flanks. Feet greyish-white above. Tail distinctly though not sharply bicoloured; dark brown to dusky above, dirty white below; terminal pencil about 8 mm. in length.

Skull with shorter and relatively broader nasals than in *A. b. blanfordi* and with the auditory bullæ slightly smaller and less inflated. Cheek-teeth normal; but  $m^3$  (Fig. 91, 13) usually with a distinct though small fourth outer salient angle.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This well-marked subspecies, distinguished from *A. b. blanfordi* by its darker colour, shorter nasals, less developed bullæ, and slightly less reduced  $m^3$ , would appear to be a slightly more primitive animal than the typical subspecies. Mr. Wells collected a long series of specimens in Lahul in the months June to September 1922, but unfortunately very few of the available skulls can be regarded as being fully developed. In old adults the condylo-basal length probably reaches 27.5 mm., but in most of those before me it ranges between 25 and 25.5 mm. In these the nasals measure  $7-7.8 \times 3-3.2$  as against  $8.3 \times 3$  in a similar-sized skull of *A. b. blanfordi* from the Nultar Valley, Gilgit. Good skulls of both subspecies of *A. blanfordi* are badly needed for further work upon the relationships of the members of this most difficult genus.

### 3. *Alticola roylei* Gray.

(Synonymy under subspecies.)

*Range*.—Western Himalayas, but the details of its distribution unknown. It occurs in Kumaon at altitudes between 10,000 and 13,000 feet; and in the Kulu Valley, Lahul, at altitudes between 8500 and 9200 feet.

A specimen in the Calcutta Museum collected by Theobald in 1853 at the "Bala Pass" (probably Babeh Pass in Spiti) was referred by Blyth (J.A.S. Bengal, 32, 1863, p. 89) to this species; but a little later Blyth (Catal. Mamm. Mus. As. Soc., 1863, p. 125) gave the locality of this specimen as "Pind Dadun Khan in the Punjab." According to Sclater (Catal. Mamm. Ind. Mus., pt. 2, 1891, p. 91) Blyth's identification is erroneous, for in this

specimen  $m^3$  possesses only two and not three internal angles, and its thumb is distinctly clawed, characters which suffice to distinguish it from *A. roylei* and to indicate that it should be referred to some species of *Hyperacrius*.

Jerdon (Mammals of India, 1867, p. 216) referred specimens which he obtained "in Kunawar, near Chini, at an elevation of nearly 12,000 feet, and again on the south side of the Barendo Pass, at about the same height" to this species; he stated further that he had "observed it in the Pir Punjal pass." The voles at the latter locality were no doubt *Hyperacrius fertilis*, a species described much later by True; those that he collected at the other localities named most probably belonged to other species and not to *A. roylei*.

Lastly in 1916 Wroughton (J. Bombay N.H.S., 24, p. 491) referred the voles collected in Sikkim by Crump for the Bombay Natural History Society's Mammal Survey to this species. But these specimens are, I find, all referable to *Neodon sikimensis*.

*Characters*.—*A. roylei* is characterized by its dark colour; moderately short, imperfectly clothed, and bicoloured tail; strongly built skull; small auditory bullæ; and heavy cheek-teeth, in which  $m^3$  always possesses a well-developed third inner angle. Size medium; hind-foot 18–20 mm.; condylo-basal length of skull up to 27.3 mm.

Fur soft and full, though rather short; measuring about 13 mm. in length on centre of back. General colour of upper parts a rich dark brown, resulting from a fine mixture of dark brown and blackish hair-tips and ochraceous subterminal hair-bands; under parts grey, darkened by the slaty bases of the hairs, and (according to the subspecies) with or without a well-marked rusty suffusion; no sharp division between dorsal and ventral surfaces along the flanks. Tail about one-third of the length of the head and body, dark brown above, greyish-white below; clothed with a comparatively scanty growth of rather short stiff hairs, which leave the scaly annulations plainly visible and form only a short and thin terminal pencil. Hands and feet greyish-white above; palms with 5, soles with 6 tubercles; soles behind pads hairy, though not very densely so; hairs on dorsal surfaces of digits comparatively short and sparse, not concealing the short claws. Mammæ, 2 — 2 = 8.

Skull, when fully adult, strongly built, moderately ridged and angular. Zygomatic arches rather widely bowed, the zygomatic breadth sometimes exceeding 60% of the condylo-basal length. Temporal ridges diverging rather slowly behind the coronal suture, so that in adult skulls a considerable antero-external portion of each parietal bone is included in the corresponding temporal fossa. Anterior palatal foramina moderately large, extending backwards almost to the plane of the molars. Post-molar region rather short. Auditory bullæ small and rounded.

Dentition heavy. Enamel of incisors pale yellow. Cheek-teeth robust, the tooth-rows relatively long, and the individual teeth with tall, massive crowns; the alveolar capsule of  $m^2$  forms a conspicuous mound, obstructing the mouth of the sphenorbital fissure;  $m^3$  (Fig. 91, 9-11) with at least three salient angles on each side, the third inner angle being always well developed, and often with more or less evident traces of a fourth angle on the inner, the outer, or both sides;  $m_1$  (Fig. 91, 17) with four outer and five inner salient angles.

*Remarks.*—The relationships of *A. roylei* and reasons for regarding it as one of the most primitive members of the genus have been discussed above (p. 304). That we are now able to give a tolerably complete account of the species is entirely due to the enterprise of the Bombay Natural History Society and the zeal of the late Mr. R. C. Wroughton. Before the work of the Mammal Survey, the only specimen representing the species in the national collection was the type, which fortunately possesses a very good skull.

Two subspecies of *A. roylei* are now known, namely, one inhabiting Kumaon, characterized by its shorter tail and ears and rusty-tinged belly; the other found in the Kulu Valley, Lahul, with a longer tail, larger ears, and silvery under parts. After a direct comparison with what is left of the skin of Gray's type I do not feel able to dispute Wroughton's conclusion arrived at before the discovery of the Lahul animal, that Kumaon should be regarded as the type locality of *A. roylei*. The type, after a long immersion in alcohol, naturally differs a good deal in colour from the beautiful series of fresh skins collected in Kumaon by Mr. Crump and from the corresponding series collected in Lahul by Mr. Wells. But on the whole it agrees better with the Kumaon series than with those from Lahul; therefore the Kumaon animals may be treated as representing *A. roylei roylei*, and the form from Lahul as a subspecies, *A. r. cautus*.

#### 4. *Alticola roylei roylei* Gray.

1842. *Arvicola roylei* Gray, Ann. Mag., N.H., 10, p. 265; Wagner, Schreber's Säugth. Suppl., 3, p. 587, 1843; Giebel, Säugthiere, p. 613, 1859; Jerdon, Mammals of India, p. 216, 1867 (in part); Blandford, J.A.S., Bengal, 50, pt. 2, p. 102; 1881 (section *Alticola*).
1891. *Arvicola (Alticola) roylei* Sclater, Catal. Mamm. Ind. Mus., pt. 2, p. 91.
1891. *Microtus roylei* Blandford, Fauna Brit. Ind., Mamm., p. 430.
1896. *Microtus (Alticola) royliei* Miller, N. Amer. Fauna, No. 12, p. 54 (misprint).
1899. *Microtus (Alticola) roylei* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 292; Wroughton, J. Bombay, N.H.S., 23, 1914, p. 299; and "Summary," *ibid.*, 27, 1920, p. 60 (in part).

*Type.*—B.M., No. 2002; a defective skin (from alcohol) with skull, collected before 1839, by Dr. J. F. Royle.

*Type locality*.—Kumaon (*vide* Wroughton); given as "India (Cashmere)" by Gray.

Wroughton (J. Bombay N.H.S., 23, p. 299) has given reasons for believing that Kumaon and not Kashmir is the real type locality of *A. roylei*. He says: "Gray's Indian localities . . . are very often erroneous. A good deal of collecting has been done in recent years in Kashmir, notably by Colonel Ward, [but] no specimen representing *roylei* has been found. The common vole of Kashmir is *M. montosa* True (*imitator* Bonhote). . . . Dr. Royle, who was Superintendent of the Botanical Gardens at Saharanpur, and after whom the species was named, published a book entitled 'Illustrations of the Botany and other branches of the Natural History of the Himalaya Mountains and of the Flora of Cashmere' (1839). Though he gave his attention to Botany, he also made a collection of Mammals. Mr. Ogilvy, in an appendix . . . wrote a note on the distribution of the Mammals of the Himalayas, based chiefly on this Collection. He . . . refers to an extremely short-tailed rat occurring in the higher ranges of Kumaon, which it seems to me can be no other than our present species, and Gray's type specimen most probably was from the same locality. The type was originally in spirits, and was skinned out comparatively recently; it is now in very poor condition, but measurements and skull characters correspond very fairly with our present series" [*i.e.*, those collected in Kumaon by the Mammal Survey]. As stated above I am not prepared to differ from this conclusion of my late friend, notwithstanding the recent discovery of a representative of *A. roylei* in Lahul on the verge of the Kashmir border.

*Characters*.—As described above under the species. Under parts with a strong rusty or dull ochraceous suffusion. Tail and ears shorter than in *A. r. cautus*. Hands and feet less white above.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Mr. Crump (J. Bombay N.H.S., 23, p. 299) records that this species was "trapped on the same ground as *Apodemus*; both were frequently taken under the same small rock. In Kashmir I observed that *Microtus* and *Apodemus* were invariably found on the same ground."

*Material examined*.—Thirty-six.

#### 4a. *Alticola roylei cautus* subsp. n.

*Type*.—B.M., No. 26.3.9.2, original No. 2384; adult male, skin and skull, collected June 6, 1922, by Mr. H. W. Wells, for the Mammal Survey of India; presented by the Bombay Natural History Society.

*Type locality*.—Rahla, Kulu Valley, Lahul.

*Range*.—Known only from the vicinity of the type locality. Altitudes 8500-9200 feet.

*Characters*.—Distinguished from *A. r. roylei* by its longer tail and ears and by its hoary under parts.

Under parts hoary, the tips of the hairs silvery grey, and usually without any trace of the ochraceous tinge so constantly present in *A. r. roylei*. Upper surfaces of hands and feet and lower surface of tail whiter than in the typical form. Tail and ears both absolutely and relatively longer; the tail measurement ranging between 36 and 44 mm. (instead of 33–39 mm.) and averaging 36·5% (instead of 33·3%) of the head and body length; the ear measurement ranging between 14 and 15·5 mm. (instead of 11–13 mm.).

For *external and cranial measurements*, see tables at end of volume.

### 5. *Alticola albicauda* True.

1894. *Arvicola albicauda* True, Proc. U.S. Nat. Mus., 17, p. 12.

1896. *Microtus* [*Alticola*] *albicauda* Miller, N. Amer. Fauna, No. 12, p. 54, and Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 294; Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 59.

*Type*.—U.S. Nat. Mus., No.  $\frac{20}{3} \frac{20}{8} \frac{20}{14}$ ; adult female, skin and skull, collected, Dec. 19, 1891, by Dr. W. L. Abbott.

*Type locality*.—Braldu Valley, Baltistan.

*Range*.—Baltistan; at present known only from the Braldu Valley and the Nahr Nullah, Skardu, at an altitude of about 12,000 feet.

*Characters*.—General external appearance much as in *A. blanfordi*, but readily distinguished by its much shorter, entirely or almost entirely white tail, and its peculiarly modified *m*<sup>3</sup>.

Fur moderately dense and about 15 mm. long upon the back. Colour of upper parts pale reddish-grey, the hairs dark plumbeous at the base, with a subterminal ring of pale yellow, and brown tips, the peculiar pale tint of the back being produced by the mingling of these three colours. Under parts (together with the upper lip) pure white, the hairs with grey bases. Ears clothed with long hairs, those of the margin pale orange brown. Tail short, its length equal to 28–30% of the head and body measurement; more closely haired than in *A. blanfordi*, pure white (in the type) above and below, and with a terminal pencil 12 mm. in length. Hands and feet pure white; thumb with a "rudimentary" claw; soles densely haired behind the pads.

In three specimens from the Nahr Nullah, Skardu, collected in August, the backs are dull yellowish-grey; the under parts are white, darkened by the slaty bases of the hairs, and sharply contrasted with the flanks; the tail, clothed with long stiff hairs, which form a moderately thick terminal pencil of about 10 mm. in length but do not quite conceal the annulations, shows a feeble trace of bicoloration, its upper surface being very faintly tinged with brown. In all other respects these specimens agree



closely with the accounts of the type of *A. albicauda* published by True and Miller.

Skull, judging from the measurements and figures given by Miller, with the zygomatic breadth relatively greater than in *A. blanfordi*; about as in *A. roylei*; auditory bullæ considerably larger than in the latter, larger even than in *A. worthingtoni* according to Miller. The skulls from Nahr Nullah before me are defective; but in them the rostral and palatal portions are as in *A. blanfordi*, the nasals being, however, rather shorter and broader.

Cheek-teeth characterized by the somewhat peculiar form of  $m^3$ . In this tooth (Fig. 91, 14 and fig. 4a, Miller, 1899) there are three outer and three inner salient angles; the third outer infold is so reduced that the third triangle is rather broadly confluent with the somewhat shortened posterior loop, instead of being substantially shut off from the latter as is usual in most other species of *Alticola*. In this respect it agrees with *A. roylei* in which, however, the posterior portion of the tooth is less reduced.

For *external and cranial measurements* see tables at end of volume.

*Remarks.*—Only four specimens of this vole are at present known, viz., the type from the Braldu Valley and three examples in the British Museum collected by Mr. C. H. T. Whitehead in the Nahr Nullah, Skardu. One of the latter (B.M., No. 5.10.8.5), a male, is of interest, since it shows the beginning of the autumn moult; on parting the hairs over the rump the pale tips of the developing winter coat are seen rising up among the slaty bases of the summer hairs. The slight differences in colour which appear to exist between these Skardu specimens and the type of *A. albicauda* are not improbably seasonal.

## 6. *Alticola montosa* True.

1894. *Arvicola montosa* True, Proc. U.S. Nat. Mus., **17**, p. 11.

1899. *Microtus (Alticola) montosus* Miller, Proc. Acad. Nat. Sci. Philadelphia, **1899**, p. 293; Wroughton, "Summary," J. Bombay N.H.S., **27**, p. 59, 1920.

1905. *Microtus imitator* Bonhote, Ann. Mag. Nat. Hist., [7], **15**, p. 97; described from Tullian, Kashmir; *type*: B.M., No. 5.1.5.12, adult male. Altitude 11,000 feet.

*Type.*—Half-grown male (skin and skull) U.S. National Museum, No.  $\frac{2}{3} \frac{0}{5} \frac{1}{5} \frac{4}{6} \frac{7}{8}$ ; collected by Dr. W. L. Abbott, October 4, 1891.

*Type locality.*—Central Kashmir. Altitude 11,000 feet.

*Range.*—Known only from Kashmir at elevations between 8000 and 13,000 feet.

*Characters.*—Distinguished from *A. roylei* by its relatively longer tail, silvery-grey and better contrasted under parts, and much larger auditory bullæ.

Fur soft and full, about 12 mm. long on middle of back.

Upper parts dark as in *A. roylei*, but rather greyer; under parts silvery grey, darkened by the slaty basal portion of the fur, but without any marked buffy suffusion; flank contrast between upper and lower surfaces much sharper than in *A. roylei*. Tail longer, its length rather more than two-fifths of the head and body measurement, bicoloured, dusky above, whitish below; clothed with short stiff hairs, more numerous than in *A. roylei* but too few and too short to conceal the annulations completely; terminal pencil very short. Hands and feet essentially as in *A. roylei*; creamy white or greyish above. Ears moderate, rounded, and clothed with short hairs similar in colour to the upper parts.

Skull rather longer, narrower and flatter than in *A. roylei*, with the braincase noticeably depressed posteriorly. The temporal ridges pursue a slightly less elevated course upon the forepart of the braincase, following the squamoso-parietal suture, so that no substantial portion of each parietal is included in the temporal fossa; post-orbital squamosal crests slightly weaker. Anterior palatal foramina somewhat shorter, ending behind distinctly in advance of the tooth-rows. Bullæ considerably larger, transversely widened rather than lengthened.

Dentition somewhat lighter. Enamel of incisors stained a deeper yellow. Cheek-teeth narrower than in *A. roylei* and not so tall-crowned, the alveolar capsule of  $m^2$  making a much less marked protuberance in the mouth of the sphenorbital fissure. Enamel pattern of the teeth essentially similar (Fig. 91, 12).

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—Although with the material at present available Bonhote's *A. imitator* must be treated as a synonym of True's *A. montosa*, it is not at all unlikely that further work in the field will lead to the recognition of several distinct subspecies in Kashmir. Certain of the skulls before me differ rather markedly from those of the good series of "*imitator*" in the collection. It is possible also that intergradation with *A. roylei* will eventually be proved; but all the specimens from Kashmir at present known have the large bullæ and the external characters described above as distinguishing *A. montosa* from its ally in Kumaon.

### 7. *Alticola glacialis* Miller.

1913. *Alticola glacialis* Miller, Proc. Biol. Soc., Washington, 26, p. 197.

*Type.*—Adult female, skin and skull. U.S. Nat. Mus., No. 176071; collected by Dr. W. L. Abbott, August 23, 1912.

*Type locality.*—Chogo Lungma Glacier, Baltistan. Altitude 11,000 feet.

*Range.*—Known only from the type locality.

*Characters.*—Like *A. montosa* from which it is distinguished by its shorter tail and more pallid dorsal colour.

Upper parts a moderately light grey, with a faint brownish suffusion along the back. The individual hairs are slate-coloured through the greater part of their length, then dull ivory yellow for about 3 mm., their tips black. Under parts between pallid mouse grey and white, the contrast with colour of sides noticeable, but line of demarcation not sharply defined. Tail greyish-white below, the upper surface brownish at the tip; the dark area sometimes extends to the base, but is rarely so well defined as in average specimens of *A. montosa*.

Skull and teeth like those of *A. montosa*.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—This species is only known to me from Miller's description based upon forty-six specimens collected in Baltistan by Dr. W. L. Abbott. Miller says that it is readily distinguishable from *A. montosa* by its shorter tail and lighter colour. "In *montosa* the general appearance is that of an ordinary brownish vole, while in *glacialis* it begins to approach that of the characteristic members of the genus. The colour is practically identical with that of *A. worthingtoni* of the Thian Shan Mountains, except that the tail is never entirely white." Judging from the description *A. glacialis* must be very like its geographical neighbour *A. blanfordi*, a species, however, in which the skull apparently has marked peculiarities, and in which the tail is still shorter.

### 8. *Alticola phasma* Miller.

1912. *Alticola phasma* Miller, Proc. Biol. Soc. Washington, 25, p. 59.

*Type.*—B.M., No. 12.4.1.120; adult male, skin and skull, collected Oct. 13, 1911, and presented by D. Carruthers.

*Type locality.*—Eastern side of the Kara Korum Mountains, Chinese Turkestan, at an altitude of between 9000 and 10,000 feet, where it was "trapped among rocks on barren mountains."

*Range.*—Known only from the type locality.

*Characters.*—A pallid species, with a moderately long and completely clothed white tail, greatly inflated auditory bullæ, and very complex *m*<sup>3</sup>.

Fur soft and full, about 13 mm. long on back. Colour pallid. Upper parts (in October) clad in a mixture of wood brown and olive buff, inconspicuously lined with dark brown, becoming clearer below to form a narrow streak of deep olive-buff which extends along the lower edges of the flanks. Under parts and the cheeks white; the snow-white ventral surface is sharply contrasted against the flanks, though here and there considerably darkened by the underlying slaty bases of the hairs. Feet and tail creamy white. Tail equal to about 40% of the head and body measurement, densely clothed with stiff white hairs, which completely conceal the annulations and form a terminal pencil of about 13 mm. in length. Digits clothed dorsally with long white hairs, which

conceal the claws; claws not lengthened; thumb with a minute nail. Soles with 6 pads, densely hairy behind.

Skull with well-arched dorsal contour, the braincase deeper and less angular, and the temporal ridges (in adults) rather more closely approximated posteriorly (near the interparietal) than in other species. Anterior palatal foramina long and narrow, extending backwards to terminate between the front edges of the anterior cheek-teeth, instead of in advance of the tooth-rows as usual. Auditory bullæ very large and globular.

Cheek-teeth remarkable for the complexity of  $m^3$ . Measured at the grinding surface this tooth is in antero-posterior length about equal to  $m^1$  and considerably longer than  $m^2$ . In its most complex condition the crown of  $m^3$  in this species has an anterior loop, followed by six alternating triangles and terminated by a small posterior loop (Fig. 91, 1a); and it has four salient angles on each side. Of the triangles the posterior three vary in development in different individuals and also in the degree to which they are confluent with each other and with the posterior loop behind. When most reduced the tooth resembles that of *A. blanfordi lahulius* and possesses 4 outer and 3 inner salient angles (Fig. 91, 13).

The enamel of the incisors is pale yellow.

For *external and cranial measurements*, see tables at end of volume.

### 9. *Alticola worthingtoni* Miller.

(Synonymy under subspecies.)

*Range*.—Central Asia between latitudes 42° and 44° N. and longitudes 80° and 88° E. Typical subspecies known from the Thian-Shan Mountains (Koksu 9000 feet; Kapkak 8000 feet; and S. Muzart 7000 feet) and from the Bogdo-ola Mountains, South-East Dzungaria, at an altitude of 6000 feet. A second subspecies, *A. w. subluteus*, occurs in Djarkent, Semiretschensk.

*Characters*.—Externally this species resembles *A. phasma*, but is distinguished by its less pallid dorsal coloration and shorter tail pencil, the latter measuring about 5 mm. instead of 13 mm. in length. The skull is distinguished by its shorter and broader incisive foramina, slightly smaller bullæ, and less complex  $m^3$ .

Fur soft and full, about 10 mm. long on back. General colour of upper parts a light yellowish-grey, much greyer and less yellow than in *A. phasma*; under parts pure white or "pale pink buff," irregularly clouded by the slaty bases, and not so sharply contrasted with the flanks as in *A. phasma*; white not extending so far upon the cheeks. Tail from a third to about two-fifths of the head and body measurement, densely clothed, the hairs completely concealing the annulations and forming a short terminal pencil of about 5 mm. in length. Claws more or less concealed by the long hairs clothing the dorsal surfaces of the digits; soles hairy behind the pads.

Skull rather lighter and narrower than in *A. roylei* and *A. montosa*. Anterior palatal foramina short and broad, terminating considerably in advance of the tooth-rows. Cheek-teeth small and light, the capsule of  $m^2$  not obstructing the mouth of the sphenorbital fissure. Auditory bullæ large and globular, much larger than in *A. roylei* though less inflated than in *A. phasma*, and somewhat deeper though not quite so wide as in *A. montosa*.

Cheek-teeth:  $m^3$  with three well-developed salient angles on each side; its posterior loop shut off from the third triangle, usually rather long and bearing more or less evident vestigial traces of the fourth and fifth outer and the fourth inner salient angles (Fig. 91, 4-7, 19).

Enamel of incisors yellow, the tint deeper than in *A. roylei*.

*Remarks*.—Three subspecies are at present recognized, viz., the typical form *A. w. worthingtoni*, described from the Thian-Shan Mountains, characterized by its pure white under parts and white tail and feet; *A. w. subluteus*, described from Djarkent, distinguished by the pale pinkish-buff tinge which pervades its under parts, feet and tail; and the recently described *A. w. semicanus* from Central Mongolia, a form with buffy under parts and larger skull.

**9a. *Alticola worthingtoni worthingtoni* Miller.**

1906. *Alticola worthingtoni* Miller, Ann. Mag. N.H., [7], 17, p. 372.

*Type*.—B.M., No. 5.12.4.11; adult female, skin and skull, collected Sept. 30, 1904, by A. B. Bayley Worthington.

*Type locality*.—Thian-Shan Mountains (Koksu). Altitude 9000 feet.

*Characters*.—Essential external characters, skull and teeth as described above under the species. Under parts pure white.

Colour of upper parts finely blended smoke grey and black, with a faint suffusion of pale ochraceous buff, particularly on the sides. The individual hairs are blackish-slate throughout the greater part of their length, then smoke grey darkening to ochraceous, which is succeeded by a blackish tip. Under parts white, the dark bases of the hairs appearing irregularly at the surface. Feet white, with a faint creamy tinge. Tail light cream-buff, with a faint brownish tinge in the pencil.

For *external and cranial measurements*, see tables at end of volume.

**9b. *Alticola worthingtoni subluteus* Thomas.**

1914. *Alticola worthingtoni subluteus* Thomas, Ann. Mag. N.H., [8], 13, p. 570.

*Type*.—B.M., No. 14.5.10.186; slightly immature female, skin and skull, collected July 20, 1913, by W. Rückbeil.

*Type locality*.—Djarkent, Semiretschensk, Central Asia ("In die Schlucht Tischkan").

*Range*.—Known only from the type locality.

*Characters*.—Like *A. w. worthingtoni* in all essential characters, but the pure white of the end of the hairs of the lower surface replaced by "pale pinkish buff" (Ridgway, 1912). Hands, feet, and tail also with a slight buffy tinge.

Skull and teeth as in *A. w. worthingtoni*.

For *external and cranial measurements*, see tables at end of volume.

9c. ***Alticola worthingtoni semicanus*** G. M. Allen.

1924. *Microtus (Alticola) worthingtoni semicanus* G. M. Allen, Amer. Mus. Nov., No. 133, p. 6.

*Type*.—American Museum N.H., No. 57805; adult male, skin and skull, collected June 5, 1922, by the Third Asiatic Expedition.

*Type locality*.—Sain Noin Khan, Mongolia.

*Range*.—Central Mongolia. Altitude 6000–7000 feet.

*Characters*.—Hind-foot 19 mm.; condylo-basal length 28.7 mm.

General colour above buffy grey slightly darkened with scattered black hairs. Sides of nose, front and back of ears nearly "pinkish buff." Under parts buffy white, the hairs with dark bases. The mixed grey of the back is sharply defined at the sides of the head and body and the buff is here clearer and brighter, forming an indistinct "pinkish buff" lateral line.

Skull larger throughout than in typical form, with longer tooth-rows;  $m^3$  with well-defined first outer infold;  $m_1$  with posterior loop, four completely closed triangles and an anterior trefoil.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—Distinguished from the typical subspecies by its buffy instead of clear white under surface and by its larger skull and longer tooth-rows.

10. ***Alticola stoliczkanus*** Blanford.

1875. *Arvicola stoliczkanus* Blanford, J.A.S. Bengal, 44, pt. 2, p. 107; Sci. Res. Second Yarkand Mission, Mammalia, p. 42, pl. viii, fig. 1, pl. xb, fig. 2, 1879; J.A.S. Bengal, 50, pt. 2, p. 97, 1881 (section *Alticola*).

1881. *Arvicola stoliczkana* Thomas, Ann. Mag. N.H., [5], 6, p. 333.

1891. *Arvicola (Alticola) stoliczkanus* Sclater, Catal. Mamm. Ind. Mus., pt. 2, p. 89.

1891. *Microtus stoliczkanus* Blanford, Fauna Brit. India, Mamm., p. 430.

1896. *Microtus (Alticola) stoliczkanus* Miller, N. Amer. Fauna, No. 12, p. 52; Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 292; Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 60.

*Co-types*.—Indian Museum, Calcutta, Nos. *a* and *b*. Sclater (Catal. Mamm. Ind. Mus., pt. 2, p. 89) gives the following

particulars: "Only known from the two specimens mentioned below from the Kuenlun Mountains in Northern Ladak.

a. Skin, skull. Aktagh, Yarkand River, 13-10-73. F. Stoliczka.

b. Skin. Nubra Valley. Dr. Bellew.

[Co-types of *A. stoliczkanus* Blanford.]

*Type locality*.—Kuenlun Mountains, Northern Ladak.

*Range*.—Known only from the vicinity of the type locality.

*Characters*.—A brown-backed, short-tailed species, with reduced  $m^3$ .

Fur soft, and rather woolly. General colour bright ferruginous brown above, white below, the two colours sharply divided. Fur dark leaden-grey at base; the terminal fourth of the shorter hairs on the back rufous white, tipped with dark rufous. With these are intermixed numerous rather longer hairs with dark rufous-brown tips. Ears small, completely concealed in the fur; clothed with short, bright rufous hair towards the margin inside and with longer and paler hair outside. Feet and tail white. Feet small, armed with long compressed claws, which are much concealed by long white hairs; thumb vestigial and clawless; palms and soles hairy, with a few hairs between the digital pads. Tail short, about one-fourth of the length of the head and body, covered with stiff fulvescent-white hair, which extends for half an inch beyond the tail-tip.

Skull rather large (condylo-basal length about 29 mm.), its special characters unknown. Incisors deep yellow in front; the upper pair described as having a very shallow groove down the centre, but this is probably an individual peculiarity.

Cheek-teeth generally as in the genus;  $m^3$  reduced, much as in *A. stracheyi*, but with the posterior loop "much less than half the length of the tooth, with three outer and two inner salient angles, and some slight trace of a fourth outer angle behind."

For *external and cranial measurements*, see tables at end of volume.

### 11. *Alticola stracheyi* Thomas.

1851. *Cricetus songarus* Horsfield, Catal. East Ind. Mus., p. 145. Not of Pallas.
1880. *Arvicola stracheyi* Thomas, Ann. Mag. N.H., [5], 6, p. 332; Blanford, J.A.S. Bengal, 50, pt. 2, 1881, p. 98 (section *Alticola*).
1891. *Arvicola (Alticola) stracheyi* Sclater, Catal. Mamm. Ind. Mus., pt. 2, p. 90.
1891. *Microtus stracheyi* Blanford, Fauna Brit. India, Mamm., p. 431.
1896. *Microtus (Alticola) stracheyi* Miller, N. Amer. Fauna, No. 12, p. 54; Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 292; Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 60.
1899. *Microtus cricetus* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 294 [subgenus *Alticola*]; described from Tso-Kyun, Ladak; altitude 16,000 feet (*type*: U.S. Nat. Mus., No. 84043).

1920. *Microtus (Alticola) cricetulus* Wroughton, "Summary," J. Bombay N.H.S., 27, p. 61.

*Type*.—B.M., No. 60.5.4.113; subadult, skin and skull (both defective), collected by Captain R. Strachey.

*Type locality*.—"Kumaon" = Ladak.

"Kumaon" is given as the type locality by Thomas on the authority of an old label written by Horsfield and attached to the skin; but Wroughton (J. Bombay N.H.S., 27, p. 59) points out that Horsfield (in his Catal. E.I. Mus., p. 145) distinctly states that the specimen is "From Capt. R. Strachey's Collection in Ladak."

*Range*.—Eastern Kashmir and Western Tibet, from the Upper Suttlej and Lahul northwards to the Dipsang Plains, Northern Ladak, and the Massimik Pass, Western Tibet. In this region it is widely distributed over the highest ground at altitudes between 14,500 feet and 18,500 feet. Exact limits of range unknown, but to the north it is replaced by the closely related *A. acrophilus* Miller, and the more distinct *A. stoliczkanus* Blanford. In Tibet it probably intergrades with *A. lama* Barrett-Hamilton. Lastly a member of the same group, imperfectly known from a single young specimen, and at present not distinguishable from *A. stracheyi*, has been discovered upon the eastern slope of Mount Everest,<sup>1</sup> Tibet, at an elevation of 17,300 feet.

*Characters*.—A short-tailed, pallid species with reduced *m*<sup>3</sup>. Size medium (hind-foot in adults 18–20 mm., condylo-basal length of skull up to 28 mm.).

Fur very soft, fine, and dense but rather short (10–14 mm. long on the back). Upper parts pale yellowish-brown, inconspicuously lined by longer blackish hairs; the shorter hairs, composing the great mass of the body fur, slate-coloured for nearly three-fourths of their length, and thence brownish-yellow to their tips. Under parts and upper lip white, sharply though rather irregularly contrasted with the upper surface along the flanks. Hairs of the under surface with slaty bases and pure white tips. Ears rather short, scarcely showing above the fur, and thickly clothed with hair resembling that of the back in colour. Feet and tail pure white or cream-coloured. Palms with five, soles with six pads; densely haired behind, the region between the pads being also clothed with short white hairs; dorsal surfaces of digits well clothed with rather long white hairs, which overlap and partly conceal the claws; thumb vestigial, armed with a minute flattened nail. Tail about as long as hind-foot, densely clothed above and below with long creamy-white hairs, which completely conceal the annulations and form a terminal pencil up to half an inch in length.

Young specimens have the upper parts much darker and greyer than in adults. The darkest specimen seen is that from

<sup>1</sup> Listed as "*Microtus (Alticola)* sp." by Thomas and Hinton, Ann. Mag. N.H., [9] 9, p. 183, 1922.



Mount Everest; this example is very different in colour from adult animals from Ladak and Lahul, but it is closely approached by the immature (though slightly older) specimens from Lahul.

Skull differing from those of all the species of the first group (*i.e.*, those possessing a more complex  $m^3$ ) by its relatively shorter, smaller, and more nearly square braincase, the interorbital region appearing correspondingly longer. Post-orbital squamosal crests quite weak, but appearing to be a little more salient in adults than in adults of other species. Auditory bullæ of moderate size.

Cheek-teeth characterized by the reduction and peculiar form of  $m^3$  (Fig. 91, 2a, 15, 16). In this tooth in adults there are three outer and only two inner salient angles; the third triangle, forming the third outer angle, opens behind into the posterior loop; the latter is extremely narrow and long, continued straight backwards and forming (with the triangle at its base) about half the length of the entire tooth. In young specimens a vestige of the third inner angle is present, but this dies out in the deeper portions of the crown brought to the surface by wear in adult stages of growth (Fig. 91, 15, 16). In  $m_1$  the anterior loop is short and there are four outer and four or five inner salient angles (Fig. 91, 2b).

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—With the limited material at present at our disposal no attempt to work out the geographical variation of this striking species can succeed. Direct comparison of one of the three specimens upon which Miller based his *A. cricetus* with the type of *A. stracheyi* and with the other material in the Museum from Ladak shows that *A. cricetus* must be treated as a synonym of *A. stracheyi*. When Miller published his description the last-named species was believed to have come from Kumaon, and besides the somewhat immature and defective type only one other specimen, from the Massimik Pass, Tibet, and that without proper measurements, existed in the collections of Europe and America. The area represented by the material now available is a large one, and having regard to our experience with other species of *Alticola*, which seem to have quite restricted ranges, it is surprising that this material should show so little sign of any definite geographical variation. In spite of a very close scrutiny I can find nothing upon which to base subspecies; but long series of specimens from different localities will probably be more instructive. Probably the more uniform conditions of the higher altitudes at which this species lives have a good deal to do with its constancy of character. It lives at a greater elevation than any other member of the genus; and its outward form, pelage, colour and dentition are all stamped with a high degree of specialization.

Sclater (Catal. Mamm. Ind. Mus., pt. 2, p. 90) refers a male (in alcohol) collected at Dharmsala, Kangra, in the Punjab Himalayas, at an altitude of 16,000 feet, to this species. He states that

the under surface is brown like the back, and that there are only five tarsal pads, statements which seem to indicate that the specimen represents a species of *Hyperacrius*.

### 12. *Alticola lama* Barrett-Hamilton.

1900. *Microtus (Alticola) lama* Barrett-Hamilton, P.Z.S., 1900, p. 196.

*Type*.—B.M., No. 97.1.21.3; adult skin and skull (defective), collected Aug. 1896, and presented by Captain H. H. P. Deasy.

*Type locality*.—Twenty-five miles S.E. of Lake Arucho. Western Tibet. Altitude 16,000 feet.

*Range*.—Western Tibet; known only from the vicinity of the type locality at altitudes of 16,000 and 17,800 feet.

*Characters*.—Outwardly quite like *A. stracheyi*, from which it is distinguished chiefly by its larger and deeper braincase and larger auditory bullæ. Hind-foot 18 mm.

*Cheek-teeth*.—In the type,  $m^3$  on each side possesses a rather well-developed third inner angle; but this is possibly only an individual abnormality. In a second skull from the type locality  $m^3$  is exactly as in many examples of *A. stracheyi*, its third inner angle being obsolete and represented by no more than a vestigial bulge on the inner side of the long posterior loop. A third specimen from a slightly higher locality is younger and its  $m^3$  shows the minute vestige of a third inner angle commonly found in young specimens of *A. stracheyi*.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—The status of *A. lama* will remain doubtful until further material has been obtained. The specimens upon which it is based are in poor condition without proper measurements and with broken skulls. Not improbably it will turn out to be no more than a subspecies of *A. stracheyi*, intergrading near the western frontier of Tibet with the typical form.

### 13. *Alticola acrophilus* Miller.

1899. *Microtus acrophilus* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 296 (subgenus *Alticola*).

1920. *Microtus (Alticola) acrophilus* Wroughton, J. Bombay N.H.S., 27, p. 59.

*Type*.—U.S. Nat. Mus. No. 62162; adult female, skin and skull, collected July 25, 1893, by Dr. W. L. Abbott.

*Type locality*.—Ladak side of the Karakorum Pass. Altitude 17,000 feet.

*Range*.—Known only from the type locality.

*Characters*.—Closely related to *A. stoliczkanus*, from which it is readily distinguishable by its shorter tail and much paler colour.

Fur full and soft, about 15 mm. long on middle of back. Basal two-thirds of hair slaty plumbeous, slightly paler than in *A. albicauda* and *A. "cricetulus"* (= *stracheyi*). On the dorsal surface the plumbeous basal area is followed by a broad band of pinkish-buff which gives the general tone to the pelage. Throughout the dorsal area the fur is sprinkled with longer dark brown hairs, but these are nowhere conspicuous. The buff is brightest on the head and lumbar region, paler and greyer across the shoulders, along the sides, and on the rump. Belly snowy white, much clouded by the plumbeous under fur. Feet and tail dirty white. Ears about as long as in *A. "cricetulus,"* but less conspicuous owing to the longer fur. Palms with five, soles with six tubercles; all the tubercles very large. Soles densely haired behind pads. Mammæ, 2 - 2 = 8.

Skull in general form like those of *A. albicauda* and *A. "cricetulus,"* but slightly longer than either and much more massively built. Zygomatic arches shorter and rostrum broader and deeper than in either of the cited species. Nasal branches of premaxillaries narrow, scarcely reaching posterior edge of nasals. Mandible larger than in *A. "cricetulus,"* but with much more slender angular process.

Incisors pale yellow as in *A. "cricetulus."*

Cheek-teeth heavier than in *A. "cricetulus,"* but enamel pattern exactly similar ( $m_1$  imperfectly known). The salient angles are, however, less acute, and the terminal loop of  $m^3$  forms less than half of the length of the crown instead of slightly more than half as in *A. albicauda* and *A. "cricetulus."*

For *external and cranial measurements*, see tables at end of volume.

*Material examined.*—None. The type is the only specimen so far known.

*Remarks.*—Apparently most closely related to *A. stracheyi*.

#### Subgenus: **Platycranius** Kascenko.

1901. *Platycranius* Kascenko Ann. Mus. Zool. Acad. Imp. Sci. St. Petersburg, 6, p. 199 (subgenus of *Microtus*).  
 1908. *Alticola* Miller, Ann. Mag. N.H., [8], 1, p. 97.

*Genotype.*—*Microtus strelzowi* Kascenko.

*Range.*—Altai Mountains, Central Asia.

*Characters.*—Skull remarkably broad and flat; postero-lateral palatal bridges slender but usually complete. Other essential characters as in normal *Alticola*.

The subgenus *Platycranius* seems to be an offshoot from the genus *Alticola*, which has become specialized for life in the crevices of bare rocks; and in this habit and the correlated cranial characters it affords a parallel to *Gliriscus*, a similar offshoot from *Grafiurus*, the great African genus of Dormice.<sup>1</sup>

<sup>1</sup> THOMAS and HINTON, P.Z.S., 1925, p. 232.

Two species are at present recognized—*Alticola* (*Platycranius*) *strelzowi* Kaschenko and *A. (P.) alliarus* Pallas; but the differences between these forms are very slight and in all probability both will eventually have to be treated as subspecies of *A. (P.) alliarus*.

### 1. *Alticola* (*Platycranius*) *strelzowi* Kaschenko.

1840. *Arvicola alliarum* Eversmann, *Естест. Исторія Оренбургс. Края*, **1**, p. 168. Not *Mus alliarus* Pallas, 1779.  
 1900. *Microtus strelzowi* Kaschenko, *Bull. Imp. Tomsk Univ.*, **16**, p. 50.  
 1901. *Microtus (Platycranius) strelzowi* Kaschenko, *Ann. Mus. Zool. Acad. Imp. Sc. St. Petersburg*, **6**, p. 201.  
 1901. *Microtus strelzowi desertorum* Kaschenko, *Ann. Mus. Zool. Acad. Imp. Sc. St. Petersburg*, **6**, p. 206 (*nom. nov.* for *Arvicola alliarum* Eversmann); *type*: *Zool. Mus. Acad. Sc. Russia (Leningrad)*, No. 1471.

*Co-types*.—*Zool. Mus. Acad. Sc. Russia (Leningrad)*, Nos. 13261–3, and perhaps in the Museum of Tomsk University.

*Type locality*.—Altai.

*Range*.—Altai Mountains, Central Asia. Limits of distribution unknown.

Eversmann's specimen (Leningrad, No. 1471) is reputed to have come from the Orenburg district; for this reason Kaschenko, regarding it as representing a "semi-hypothetical steppe subspecies," has renamed Eversmann's "*Arvicola alliarum*," as indicated above in the synonymy. But no other trace of such an animal has been found in the Orenburg district; and neither Kaschenko nor Montagu (who kindly examined Eversmann's specimen for me) can find any character distinguishing No. 1471 from the co-types of *A. (P.) strelzowi*. In all probability No. 1471 came from the Altai and some mistake has been made with reference to its locality.

*Characters*.—Size medium; hind-foot 20 to 22 mm.; condylo-basal length up to 29.1 mm. General outward appearance as in normal *Alticola*. Fur very soft and fine in adolescent specimens, somewhat harsher in fully adult individuals. Ears large, fully haired as a rule, but in some specimens naked towards the tip externally (? pathological or seasonal). Hands and feet normal; thumb very small, bearing a minute flattened nail; palmar pads five; plantar pads six; soles densely haired posteriorly. Tail long, from about one-third to half the length of the head and body; densely clothed with long, stiff, adpressed bristles, which completely conceal the annulations and form a long and dense terminal pencil. Mammæ, 2 — 2 = 8.

Colour of upper parts ashy grey, more or less irregularly brightened by the yellowish or slightly rufous subterminal bands of the hairs, inconspicuously and to a varying extent "lined" by the longer black hairs and dusky hair-tips. In younger

individuals the colour of the upper parts is darker, richer, and warmer than in old adults, in which the dorsal colour tends to become a uniform cold, pale grey. Under parts white, irregularly

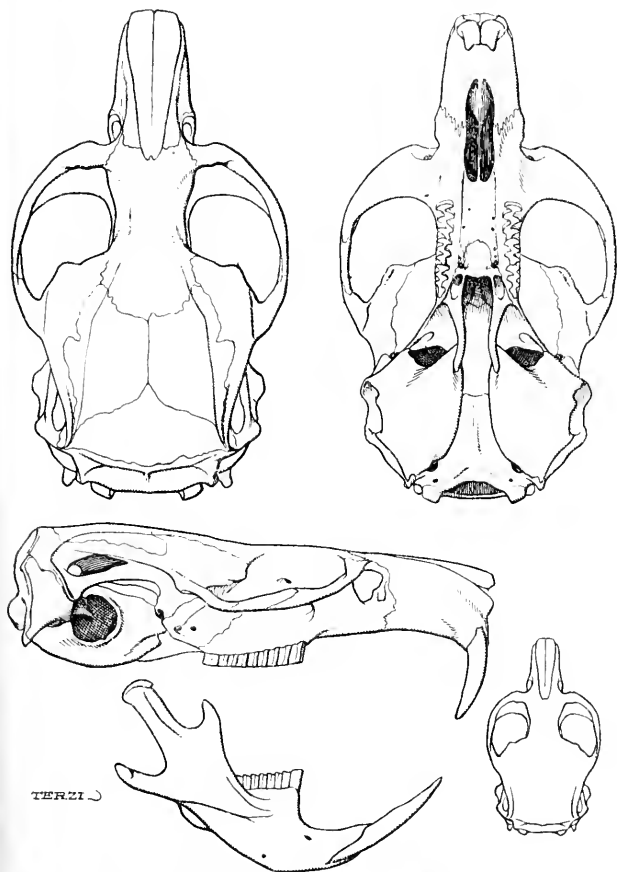


FIG. 92.—*Alticola (Platycranius) strelzowi* Kascenko.

Dorsal, ventral, and lateral views of skull; the small figure shows the skull in dorsal view, natural size.

darkened by the slaty bases of the hairs. Hands and feet white above. Tail white or cream throughout, sometimes slightly darker (cream-buff) above than below (cream-white).

Skull (Fig. 92) delicately built, broad, remarkably depressed, and presenting a very unusual appearance in profile. The dorsal contour is gently convex along the rostrum, where it is nearly parallel with the curve of the diastema, slightly concave in the interorbital region, and thence very slightly convex along the braincase to the gently shelving occiput. Owing to the depression of the upper surface, the frontals rise very little above the zygomata. Rostrum and zygomata slender and delicate. Zygomata diverging posteriorly; jugals very light. Nasals ending in front about flush with the anterior surfaces of the incisors, terminating behind very slightly in advance of the front margin of the orbits. Interorbital region unusually broad, slightly concave from before backwards as well as transversely. Temporal ridges well marked in adults, although widely separated in the interorbital region and throughout. Squamosals showing some tendency to encroach upon frontals anteriorly, with well-developed post-orbital crests, and large supratympanic fenestræ. Interparietal large and normal. Infraorbital canal essentially as in other voles, but its upper part rather wider, its inferior slit-like portion lower and broader, and its outer wall rather narrower than usual. Anterior palatal foramina large, reaching back almost to the molar region. Palate essentially as in *Alticola*; but the slender postero-lateral bridges are usually complete and the post-palatal pits and choanæ are shallower than usual. Pterygoid fossæ large but shallow, their floors scarcely dorsal to the ventral surface of the basisphenoid. Ectopterygoid plates low, forming an unusually obtuse angle with the alveolar borders of the maxillæ. Auditory bullæ simple as in *Alticola*, rather large though not greatly inflated, the parts around the eustachian tube forming a long pointed process. Mandible very slender, with long slender processes; angular process with its lower border thickened throughout for insertion of anterior portion of *masseter lateralis* muscle.

Dentition throughout light and weak. Upper incisors strongly curved, slightly opisthodont. Lower incisor displaces  $m_3$  in the normal way, but terminates in the base of the condylar process below the dental foramen. Cheek-teeth (Fig. 91, figs. 3a, 3b) persistently growing, with a little cement in the re-entrant folds. Enamel pattern as in *Alticola*, the peculiar stretched-out appearance of the teeth very noticeable in adults, less so in adolescent specimens;  $m^3$  much simplified with three salient angles on each side, the first outer triangle small and broadly confluent with the anterior loop.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—Nine specimens of this interesting vole, viz., one presented by Mr. G. H. Miller in 1908, and eight received from Prof. Sushkin in 1923, are now available. They were collected at various points on the Altai Mountains at elevations between 1000 metres and 8500 feet. Making due allowance for differences

of individual age they form a very uniform series and suffice to show that *A. (P.) strelzowi* is one of the best-marked species in Central Asia. It may, hereafter, turn out to be merely a sub-species of the imperfectly known "*Mus*" *alliarus* Pallas described below.

## 2. *Alticola (Platycranius) alliarus* Pallas.

1779. *Mus alliarus* Pallas, Nov. Spec. Quadr. Glir. Ord., p. 252.

1901. *Microtus (Platycranius?) alliarus* Kascenko, Ann. Mus. Zool. Acad. Imp. Sc. St. Petersburg, 6, p. 201.

*Type*.—Unknown.

*Type locality*.—Neighbourhood of Jenisseisk, Jenisseisk Province, Siberia.

*Range*.—Apparently from Jenisseisk eastwards to the north-eastern extremity of Lake Baikal.

Pallas states that the species had been well known for a long time to the inhabitants of the environs of Jenisseisk, Karum, and Angara, in consequence of its habit of invading their cellars, where it devoured onions and other acrid bulbs; he received his two specimens in fluid from the neighbourhood of Jenisseisk.

*Characters*.—The species is known only from Pallas's description and his figure of its skull. Both clearly apply to a member of the subgenus *Platycranius*. Apart from the difference of locality, the only important point of difference between *A. (P.) alliarus* and *A. (P.) strelzowi* seems to be that the former has a bicoloured tail ("Cauda, præter tractum supra fuscum, alba"), whereas in the latter it is essentially unicoloured. Pallas states that his animal possesses six mammæ ("Mammæ duæ pectorales, totidem abdominales et duæ inguinales"), not eight as in other species of *Alticola*. But that discrepancy is readily explained. Pallas's measurements indicate that his specimens were immature. Kascenko raises another objection pointing out that the lateral view of the skull of "*Mus alliarus*" (presumably a *Platycranius*) is no more depressed than is that of "*Mus gregalis*" (a *Stenocranium*) given on the same plate (Nov. Spec. Quadr. Glir. Ord., Tab. xxvii, figs. xvii 22\* and xvii 20\*). That is perfectly true so far as it goes. But if we compare Pallas's fig. xvii 22\* with a skull of *Platycranius* we see that the figure is a very fair representation of the skull; and on turning to fig. xvii 20\* we see that although the dorsal view (fig. xvii 20\* B) is a fair representation of a *Stenocranium*, the profile (fig. xvii 20\* A) is not. I am inclined to believe that by some mischance *Platycranius* served as the model for both the lateral views in question.

Genus : 10. **HYPERACRIUS** Miller.

1880. *Arvicola* Blanford, J.A.S. Bengal, 49, pt. 2, p. 244 (in part).  
 1881. *Alticola* Blanford, J.A.S. Bengal, 50, pt. 2, p. 99 (in part);  
 section of genus *Arvicola*.  
 1891. *Alticola* Selater, Catal. Mamm. Ind. Mus., pt. 2, p. 88 (in part);  
 subgenus of *Arvicola*.

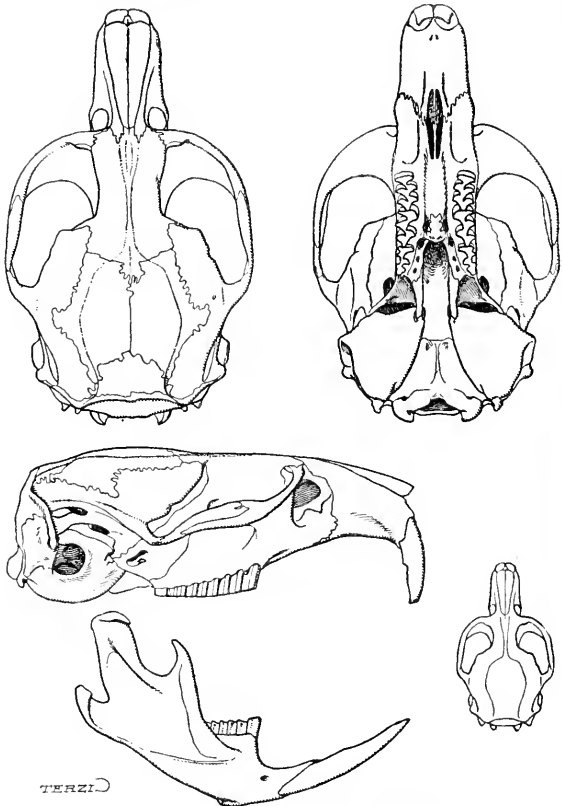


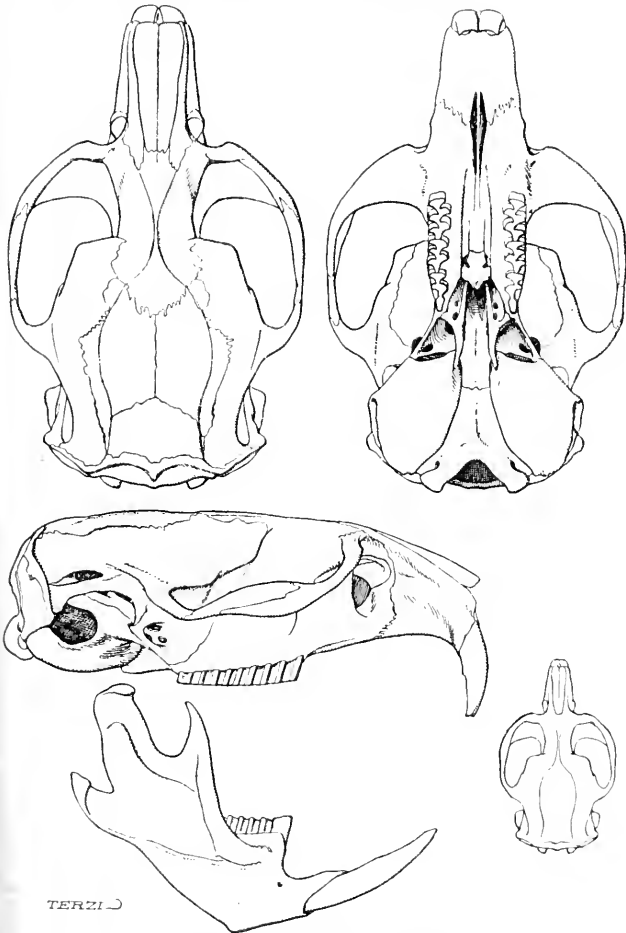
FIG. 93.—*Hyperacrius fertilis brachelix* Miller.

Dorsal, ventral, and lateral views of skull; the small figure shows the skull in dorsal view, natural size.

1891. *Microtus* Blanford, Fauna Brit. India, Mammalia, p. 431 (in part).  
 1896. *Hyperacrius* Miller, N. Amer. Fauna, No. 12, p. 54; Proc. Biol. Soc. Washington, 11, p. 141, 1897; Proc. Acad. Nat. Sci.



Philadelphia, 1899, p. 289; Wroughton, "Summary," J. Bombay N.H.S., 27, p. 61, 1920; subgenus of *Microtus*.



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FIG. 94.—*Hyperacrius wynnei* Blandford.

Dorsal, ventral, and lateral views of skull; the small figure shows the skull in dorsal view, natural size.

1899. *Alticola* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 291 (in part); Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 59 (in part); subgenus of *Microtus*.

*Genotype*.—*Arvicola fertilis* True.

*Range*.—Himalayan portions of the Punjab and Kashmir, northwards as far as Gilgit.

*Characters*.—Fur short and dense, softer and finer than in *Alticola*; in one species (*H. wynnei*) almost mole-like. Vibrissæ short and weak. Eyes very small. Ears small, simple, and suborbicular; sometimes concealed by the fur, sometimes visible above it. Hands and feet normal; with long and slender claws, those of the hand thinner and slightly longer than those of the foot. Pollex small, provided with a flattened nail. Palmar

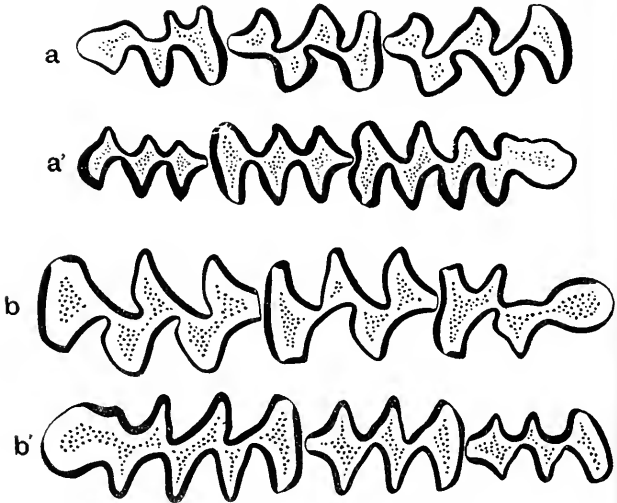


FIG. 95.—Cheek-teeth of *Hyperacrius*.

*a, a'*. *H. fertilis* True. Right upper and left lower molars.

*b, b'*. *H. wynnei* Blanford. Left upper and right lower molars.

tubercles 5; plantar tubercles 5; soles hairy between the posterior pad and the heel. Tail short, its length varying from about one-third to about one-fifth of the head and body measurement, fully clothed with hair; hairs of ventral surface of tail extending backwards noticeably beyond the true tail-tip. Mammæ, 1 — 2 = 6; pectoral mammæ represented by a single pair situated considerably behind the axillæ, at a point just behind the place where the elbow comes in contact with the body when the fore-limb is folded against the chest.

Skull highly modified. Bony palate essentially as in *Evotomys* and *Alticola*. Temporal ridges, in adult skulls, fusing to form a weak but linear sagittal crest in the interorbital region; squamo-

sals, frontals, and parietals correspondingly and progressively more or less modified with advancing age. Posteriorly the temporal ridges are also rather closely approximated in adults and the intertemporal portions of the frontals, parietals, and interparietals are correspondingly and progressively diminished. Auditory bullæ very small, somewhat flattened, thin-walled, and without any internal filling of spongy bone. Rostrum long and shallow. Anterior palatal foramina small; short and narrow. Upper incisors projecting well in advance of the nasal tips. Mandible with  $m_3$ , displaced lingually by the shaft of the lower incisor, which ascends into the condylar process, where its termination is marked by a hump on the outer surface of the bone; angular processes of mandible rather small.

Cheek-teeth light, rootless, and tall-crowned, the capsule of  $m^2$  rising up conspicuously in the floor of the sphenorbital fissure. Enamel well differentiated as in *Microtus*. Re-entrant folds without visible cement. Enamel patterns of teeth essentially as in *Alticola*, but  $m^3$  with its posterior loop shorter, broader, and more reduced than usual in the latter genus (Fig. 95).

*Remarks.*—Hitherto *Hyperacrius* has been accorded merely subgeneric rank within the genus *Microtus*; but the peculiar combination of cranial and external characters shown by all its species clearly entitles the group to be regarded as a distinct genus. As already stated in the introduction *Hyperacrius* seems to be an offshoot from some primitive species of *Alticola*; it has made considerable progress along a path of fossorial specialization parallel apparently to that pursued by *Ellobius* or its forerunners.

Four forms are at present known, and their distinguishing characters may be keyed as follows:—

- A. Size large (hind-foot about 18 mm.; condylo-basal length of skull 28–29 mm.).
- a. Fur highly modified and mole-like; colour variable, upper parts light brown or dusky. Skull less specialized than in the smaller species; interstephanic portion of frontals less reduced; zygomata more normal . . . *H. wyneei* Blandford.
- b. Fur short and dense, not specially modified; colour of upper parts yellowish-brown. Tail obscurely bicoloured. Skull imperfectly known . . . *H. aitchisoni* Miller.
- B. Size smaller. (Hind-foot not exceeding 17 mm.; condylo-basal length of skull not exceeding 25 mm.) Fur short and dense, not specially modified; colour dark reddish-brown, near sepia. Tail obscurely bicoloured. Skull more highly specialized; interstephanic portion of frontals more reduced; zygomata unusually elevated. . . *H. fertilis* True.
- a. Ear larger (meatus to tip 9–11 mm.), visible above the fur.  
*H. f. fertilis* True.
- b. Ear smaller (meatus to tip 7–9 mm.), concealed in the fur.  
*H. f. bracheliz* Miller.

1. **Hyperacrius fertilis** True.

(Synonymy under subspecies.)

*Range*.—Mountains of Kashmir at altitudes between 6000 and 13,000 feet.

*Characters*.—Size small, hind-foot 15–17 mm.; condylo-basal length to 25 mm. Fur short and dense, not specially modified.

Colour dark reddish-brown above passing insensibly into dull ochraceous below; belly irregularly darkened by slaty bases of the hairs. Tail about one-fifth of the head and body length; obscurely bicoloured, sepia above, dirty white below. Feet dusky.

Skull small, with a rather broad and much flattened brain-case, the zygomatic arches running backwards at an unusually high level in relation to its upper surface. Interstephanic portion of frontals relatively rather more reduced in adults than in *H. wyntsi*, but subject to a good deal of individual variation. Nasals often terminating in a sharp point behind, much pinched between the ascending branches of the premaxillaries. Anterior palatal foramina rather large, not greatly constricted posteriorly. Lateral bridges of palate slender; palatal shelf often with an irregular, short, but perfectly horizontal median projection; post-palatal lateral pits with well-defined, though not particularly salient inner edges, which run forwards and curve ventrally to join the dorsal surface of the palatal shelf at some little distance beyond its edge. Other characters as described under the genus.

Cheek-teeth (Fig. 95a) with the pattern and structure characteristic of the genus.

*Subspecies*.—Two forms, hitherto regarded as specifically distinct, are in this work treated as subspecies of *H. fertilis*. In the typical *H. f. fertilis* the ears are large, equalling or even overtopping the fur; in *H. f. brachelix* they are small and hidden. But the extremes are connected by a continuous series of gradations and at the most *H. brachelix* can only be regarded as subspecifically separable from *H. fertilis*.

1a. **Hyperacrius fertilis fertilis** True.

1867. *Arvicola roylei* Jerdon, Mammals of India, p. 216 (in part).  
Not of Gray.

1894. *Arvicola fertilis* True, Proc. U.S. Nat. Mus., 17, p. 10.

1896. *Microtus (Hyperacrius) fertilis* Miller, N. Amer. Fauna, No. 12, p. 54; Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 289; Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 61.

*Type*.—U.S. Nat. Mus., No.  $\frac{20147}{35510}$ ; adult female, skin and skull, collected August 30, 1891, by Dr. W. L. Abbott.

*Type locality*.—Pir Panjal Mountains, Kashmir. Altitude 8500 feet.

*Range*.—Central Kashmir, extending northwards perhaps to

Gilgit (Rattoo). Recorded from the Pir Panjal Range and the Kaj Nag Mountains, at altitudes between 7000 and 12,000 feet.

*Characters*.—Ears moderately long, about equal to the fur in length, according to Miller; overtopping it by 4 mm., according to True; judging from the dried skins before me the ears are just visible above the fur and are concolorous with the back.

The colour in the five skins of the typical series is described by Miller (Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 290) as follows: "In all, the entire dorsal surface is a fine grizzle of dull wood brown and seal brown, the result of which is a general tint not far from sepia. Such variation as occurs is due to slight differences in the balance between the component colours. On the sides and belly the seal brown disappears, and the wood brown changes to a yellowish clay-colour, varying slightly in intensity and in the amount of clouding due to the dark bases of the hairs." Feet "dusky sepia, varying considerably in depth; occasionally almost blackish."

For *external and cranial measurements*, see tables at end of volume.

### 1b. *Hyperacrius fertilis brachelix* Miller.

1899. *Microtus (Hyperacrius) brachelix* Miller, Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 290; Wroughton, "Summary," J. Bombay N.H.S., 27, 1920, p. 61.

*Type*.—U.S. Nat. Mus., No. 63445; young adult female, skin and skull, collected Nov. 15, 1895, by Dr. W. L. Abbott.

*Type locality*.—Nagmarg, Kashmir. Altitude 9000 feet.

*Range*.—Known from various localities in Kashmir, at altitudes between 6000 and 13,000 feet.

*Characters*.—Size, fur, colour, skull and teeth as in *H. f. fertilis*; ears much smaller. According to Miller the ears "are much overtopped by the surrounding fur, while in *H. fertilis* they are almost equal to the fur in length. The reduction in height is especially noticeable along the upper edge of the anterior border, which is reduced to the merest rim."

For *cranial and external measurements*, see tables at end of volume.

*Remarks*.—In all the material before me the ears seem to be concealed by the fur, whereas in those referred to *H. f. fertilis* they are more or less evident above it. The measurements recorded by the various collectors form a continuous series ranging between 7 and 10 mm. in the specimens referred to *H. f. brachelix* and between 10 and 14 mm. in those referred to *H. f. fertilis*; but no doubt many slight errors of observation have crept in. Ear measurements are, generally speaking, quite unreliable.

## 2. *Hyperacrius aitchisoni* Miller.

1897. *Microtus (Hyperacrius) aitchisoni* Miller, Proc. Biol. Soc. Washington, **11**, p. 141; Proc. Acad. Nat. Sci. Philadelphia, **1899**, p. 289; Wroughton, "Summary," J. Bombay N.H.S., **27**, 1920, p. 61.

*Type*.—B.M., No. 96.11.2.3; adult male in alcohol (skull defective), collected by Dr. J. E. T. Aitchison.

*Type locality*.—Gulmerg, Kashmir. Altitude 9000 feet.

*Range*.—Known only from the type locality.

*Characters*.—Outwardly resembling *H. fertilis*, but distinguished by its larger size (hind-foot 18 mm.) and by its apparently yellower colour.

The colour is described by Miller as follows: "Colour on back bistre slightly darkened with blackish and fading rapidly on sides into the light yellowish wood brown of belly. Tail obscurely bicoloured, dark brown above, light yellowish-brown below. Feet dusky. Whiskers scant and short, the longest reaching about to ears, mixed brown and silvery grey." Feet as usual in the genus; the claws long and slender, those of the hand slightly longer than those of the foot; thumb well developed, with a large flattened nail.

Skull reduced to fragments in the only known specimen, but obviously considerably larger than in *H. fertilis*. What is left of the frontals shows the characteristic linear crest of the inter-orbital region. Palate and teeth as in smaller members of the genus, differing only by their larger size.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—This form is undoubtedly very closely allied to *H. fertilis*. When further and better material comes to hand from Kashmir it is not unlikely that this animal will have to be regarded merely as a subspecies.

## 3. *Hyperacrius wynnei* Blanford.

1863. *Arvicola roylei* Blyth, J.A.S. Bengal, **32**, p. 89; Catal. Mus. As. Soc., p. 125, 1863. Not of Gray.
1880. *Arvicola wynnei* Blanford, J.A.S. Bengal, **49**, pt. 2, p. 244; *ibid.*, **50**, pt. 2, p. 99, 1881 [section *Alticola*].
1891. *Arvicola (Alticola) wynnei* Selater, Catal. Mamm. Ind. Mus., pt. 2, p. 90.
1891. *Microtus wynnei* Blanford, Fauna Brit. India, Mammalia, p. 431; Miller, N. Amer. Fauna, No. **12**, 1896, p. 55.
1899. *Microtus (Alticola) wynnei* Miller, Proc. Acad. Nat. Sci. Philadelphia, **1899**, p. 292; Wroughton, "Summary," J. Bombay N.H.S., **27**, 1920, p. 60.

*Co-types*.—B.M., Nos. 8.3.9.18 and 92.2.27.1.

*Lectotype*.—B.M., No. 8.3.9.18, selected by Thomas (J. Bombay N.H.S., **25**, 1918, p. 371); adult male, skin and skull (ex alcohol), collected by A. B. Wynne.

*Type locality*.—Murree, Punjab. Altitude 7000 feet.

*Range*.—Apparently restricted to the Rawal Pindi district of the Punjab and the adjoining portion of Western Kashmir. Known from the vicinity of the type locality at an altitude of about 7000 feet; and from Sardalla, Kashmir at an altitude of 8700 feet.

*Characters*.—Size large (hind-foot 18–19 mm.; condylo-basal length 28–29 mm.). Fur highly modified; moderately long, very soft and velvety, dense and mole-like. Vibrissæ short and weak. Ears small, concealed in the fur, hairy externally, naked within. Palms and soles each with five tubercles; sole hairy from heel to posterior pad and thence naked; pollex well developed, with a small, short and stout claw. Claws of digits II–IV, and particularly that of digit III, of the hand considerably longer than those of the corresponding digits of the foot. Mammæ, 1 – 2 = 6.

Two well-marked colour phases occur.

*Light colour phase*.—Upper parts yellowish-brown, varying in different individuals between “cinnamon brown” and “Prout’s brown” (Ridgway), more or less darkened by the slaty bases of the hairs; in some individuals the backs are greyish-brown rather than yellowish-brown. Under parts greyish, with a well-marked wood-brown or dirty whitish suffusion produced by the light hair-tips, more or less darkened and mottled irregularly by the slaty ground-colour. Feet and hands greyish-brown above. Tail obscurely bicoloured, dark greyish-brown above, paler grey below.

*Dark colour phase*.—Upper parts ranging between a lustrous seal-brown and a glossy blackish-brown. Under parts duller and paler, lightened by the very short whitish or yellowish tips of the ventral hairs. Hands and feet dark grey above. Tail dusky grey, its bicoloration less noticeable than in the light phase.

In both phases the dorsal colour merges insensibly on the flanks into that of the ventral surface; some specimens are decidedly grey above and more or less intermediate between the light and dark phases.

Skull large and robust; in some respects rather less modified than in the smaller species of the genus. Temporal ridges diverging posteriorly more rapidly from the interorbital crest, so that the interstephanic portion of the frontals is never so reduced as it often is in skulls of *H. fertilis*. Anterior portions of zygomatic arches descending more steeply from before backwards below the orbit. These characters indicate less powerfully developed temporal and masseter muscles and less reduced eyes than in the smaller species. Anterior palatal foramina very small, usually much narrowed posteriorly. Posterior median sloping septum of palate represented by a small median spinous process which has a dorsal and posterior inclination; lateral

palatal bridges stout; post-palatal pits deep, their inner borders sharp and salient, each passing forward and curving ventrally to join the dorsal surface of the palatal shelf near the base of the median spine (Fig. 94).

Cheek-teeth with the structure and enamel pattern (Fig. 95*b*) characteristic of the genus.

For *external and cranial measurements*, see tables at end of volume.

*Remarks.*—The relationships of this striking species have long been doubtful (cf. Miller, N. Amer. Fauna, No. 12, p. 55, 1896), but a study of the fine material collected at Murree by Mr. H. W. Wells for the Bombay Natural History Society's Mammal Survey, coupled with a re-examination of all the other material representing the related species in the British Museum, enables me now to assign it definitely to the genus *Hyperacrius*. Its relatively large size and, as regards the parts influenced by the temporal and masseter muscles, slightly less modified skull stamp the species as being fundamentally a little more primitive than are the other known species of *Hyperacrius*. But its palatal structure is slightly more advanced, foreshadowing the structure so characteristic of the higher voles; its highly modified mole-like fur, completely concealed ears, and lengthened fore-claws, are important specializations for underground life, specializations which afford a parallel to those seen in *Ellobius*. In this connection the presence of two colour phases in *H. wynnei* is of great interest; for just such a variability of colour has long been recognized as one of the most conspicuous characters of at least the best-known species of *Ellobius*, viz., *E. talpinus*. The light colour phase of *H. wynnei* is no doubt equivalent to the normal pelage of most other voles. The dark phase might perhaps be regarded as a partial melanism, but in my opinion it is susceptible of another explanation. It bears such a close resemblance to the normal dusky youthful pelage found not only in other species of *Hyperacrius*, but in the young of many (or most) other Microtine genera and it is so little like an ordinary example of melanism, that it seems reasonable to suppose that we have in this dusky pelage one of those rare instances of the life-long persistence of characters normally peculiar to infancy or adolescence. Quite possibly this very tendency to retain the dark immature coloration throughout life is to be regarded as a result of subterranean habits; deprived of the light stimulus the normal bright adult colour fails to appear in many individuals at the appropriate moment and such animals thereafter continue to wear the dusky coats of the young and probably of the ancestral forms.

According to the field notes of Major H. H. Dunn, who presented a specimen to the British Museum, this species has "mole-like habits and it is found in grass ground in the pine-forests" at an altitude of 7000 feet. Quite probably the normal habits of this species are strictly subterranean, and if so further search



in the Himalayan region will very likely show that its range is much more extensive than is at present known.

Genus: **11. DOLOMYS** Nehring.

1851. *Arvicola* H. von Meyer, Neues Jahrb. f. Min., 1851, p. 679; J. S. Petenyi's hinterlassene Werke, 1, 1864, pp. 77 and 80 (Hungarian). Not of Lacepède.
1894. *Phenacomys* Nehring, Naturwiss. Wocheschr., No. 28, 1894. Not of Merriam.
1898. *Dolomys* Nehring, Zool. Anz., 21, p. 13; Forsyth Major, P.Z.S., 1902, 1, p. 107; Méhely, Ann. Mus. Nat. Hungar., 12, 1914, p. 178.
1914. *Pliomys* Méhely, Ann. Mus. Nat. Hungar., 12, p. 195; genotype *P. episcopalis* Méhely.
1921. *Chionomys* Martino, Ann. Mag. N.H., [9], 9, p. 413. Not of Miller.
1925. *Dolomys* Hinton, Proc. Linn. Soc. London, 1924-25, p. 36.

*Genotype*.—*Dolomys milleri* Nehring.

*History*.—The remains, upon which this genus is primarily based, were discovered in 1847 by Petenyi in a bone breccia filling fissures in limestone at Beremend in Southern Hungary. The remarkable characters of these fossils escaped notice until 1879, when Nehring observed that the molar teeth were rooted, and probably belonged to an undescribed genus<sup>1</sup>; in 1894 he referred them, together with Newton's *Arvicola* (*Evotomys*) *intermedius* from the late Pliocene of Britain, to Merriam's North American genus *Phenacomys*. Two years later Miller (N. Amer. Fauna, No. 12, 1896, pp. 40 and 75) pointed out that the British fossils described by Newton are certainly not referable to *Phenacomys*, and said that "there can be little doubt that the animal represents a genus distinct from any now living." In 1898 Nehring, supported upon the firm ground provided by Miller's study of the living Microtine genera and subgenera, described his genus *Dolomys*, which he based upon one of the fossil species occurring at Beremend (*D. milleri*). In this genus he included also the British fossils; but these latter were in 1902 referred by Forsyth Major to a new genus, *Mimomys*. In 1914 Méhely gave a detailed account of those Hungarian fossil voles in which the cheek-teeth are provided by roots. A full review of Méhely's work is given in this monograph under the "History" of *Mimomys*. Of the three new genera established by Méhely one (*Pliomys*) must in my opinion be merged, at all events for the present, in the synonymy of *Dolomys*; while another (*Apistomys*), described below, is scarcely entitled to distinct generic rank.

In 1921 Martino described a vole which he found living upon

<sup>1</sup> NEHRING, Jahrb. d. k.k. geolog. Reichsanstalt in Wien, 1879, p. 492.

the mountains around Cetinje, Montenegro; this animal, undoubtedly new to science, was regarded by its discoverer as a Snow Vole and received from him the name *Microtus (Chionomys) bogdanovi*. The type of this species (a young specimen) and an adult collected later at the same place were acquired by the British Museum. On examining this material I was surprised to find that the adult specimen had rooted molars and represented a new genus so far as living voles are concerned; but on closer study I have been unable to discover any character in the palate, jaws and teeth which will serve to distinguish Martino's vole from the Pliocene *Dolomys*. We therefore seem to have before us one of those rare cases in which a recent mammalian genus has been first detected by the palæontologist.

*Range*.—Fossil remains of the genus have so far been found only in Hungary, where they occur in the Upper Pliocene of Beremend and Csarnóta and in the Lower Pleistocene of Püspökfürdő. As a recent animal the genus is known only from Montenegro.

*Characters*.—*Dolomys* is characterized chiefly by its normal palate; rooted molars in which no cement is present in the re-entrant folds; the *Evotomys*-like general form of the cheek-teeth; and particularly by the presence of five substantially closed triangles in  $m_1$ .

Palate normal, nearly as in *Arvicola*, its posterior median sloping septum short and broad.

Mandible with the alveolus of the lower incisor passing from the lingual to the labial side of the ramus beneath the posterior root of  $m_2$  and terminating behind slightly below or at about the level of the dental foramen.

Cheek-teeth provided with roots in adult stages of growth;  $m^1$  with three roots, of which the anterior two sometimes coalesce, other molars with two roots each. No cement in the re-entrant folds. Inner and outer re-entrant folds approximately equal in depth and perfectly alternating. General form of the teeth, particularly that of  $m_1$ , recalling that of *Evotomys*, *Alticola*, etc. Enamel pattern of  $m^1$  and  $m^2$  normal;  $m^3$  nearly as in *Arvicola* and *Mimomys intermedius*, with three well-developed salient angles on each side, and with two or three substantially closed triangles; first outer infold of  $m^3$  subject to reduction by insulation in one species (*D. episcopalis*), the tooth then assuming a form much like that seen in the  $m^3$  of *Alticola* and *Hyperacrius*;  $m_1$  with five substantially closed triangles, in addition to the posterior and anterior loops, and with four outer and five inner salient angles;  $m_2$  and  $m_3$  normal, the outer angles of the latter tooth more or less well developed.

The foregoing description is based entirely upon the fragmentary fossils from the Pliocene and Pleistocene of Hungary for which the genus was established. The discovery of *Dolomys* among living mammals has brought, of course, many other

characters of generic importance to our notice; and these are dealt with below in the account of *D. bogdanovi*.

*Remarks.*—*Dolomys* is distinguished from *Mimomys* chiefly by the presence of five closed triangles, instead of three only, in its  $m_1$ ; and from *Apistomys* chiefly by its narrower palate and by the *Evotomys*-like general form of its molars. Its relationships with other genera are discussed above at p. 45.

Three species are at present known, viz., *D. milleri* Nehring, a large form, with primitive dentition, occurring in the Upper Pliocene of Hungary; *D. episcopalis* M  hely, a small species, with some dental specializations, found in the Lower Pleistocene of Hungary; and *D. bogdanovi*, a large species, apparently closely related to *D. milleri*, living in Montenegro.

### 1. †*Dolomys milleri* Nehring.

1898. *Dolomys milleri* Nehring, Zool. Anz., 21. p. 13, figs. 1-3 (in part; the original description embodies some characters described from Hungarian specimens of *Mimomys pliocenicus*, see M  hely, 1914, p. 182).

1914. *Dolomys milleri* M  hely, Ann. Mus. Nat. Hungar., 12, p. 181.

*Lectotype.*—Neither Nehring nor M  hely indicates which of the specimens before him should be taken as the type; I therefore select the imperfect left mandibular ramus of which the cheek-teeth are figured by Nehring (*op. cit.*, figs. 2 and 3) as lectotype. A better figure of the teeth of this specimen is given by M  hely (*op. cit.*, Taf. ii, fig. 8). The specimen belongs to the Natural History Museum of Vienna and was collected in June 1847 by J. S. Petenyi.

*Type locality and horizon.*—Upper Pliocene bone breccia filling fissures in limestone at Beremend, near Mohacz, Southern Hungary.

*Range in time and space.*—Known only from the Upper Pliocene of Hungary. Most of the specimens hitherto determined were obtained at Beremend; but M  hely figures the teeth of two mandibular rami from the Upper Pliocene of Csarn  ta, Hungary, which were collected by Dr. T. Kormos and are now in the collection of the Hungarian Geological Survey.

*Characters.*—Size large, the length of the mandibular tooth-row in adults ranging between 8.5 and 9 mm. Alveolus of lower incisor extending posteriorly to level of lower border of dental foramen.

Cheek-teeth rooted; their infolds without cement. Enamel pattern of  $m^1$ ,  $m^2$ ,  $m^2$  and  $m_3$  normal;  $m_3$  with outer salient angles almost as well developed relatively as in  $m_2$ ;  $m^3$  with three salient angles on each side and a bulge on the outer side behind representing a vestige of a fourth outer angle, its dental spaces substantially closed;  $m_1$  with a posterior loop, five closed triangles and an anterior loop composed of the fourth outer and the fifth and sixth inner salient angles, the last-named angle

being often obsolete. In young specimens the salient angles are acute, but in later stages of wear they are rounded and the crown view of the teeth acquires a general appearance strikingly like that seen in *Evotomys* and some other genera. The anterior loop of  $m_1$  in specimens in which the sixth inner angle is obsolete closely resembles that of *Microtus* (*Chionomys*) *nivalis* or *Evotomys glareolus*.

Molar roots:  $m^1$  with three roots, a large anterior, a smaller posterior and a very slender root supporting the second inner angle;  $m^2$  with two roots, an anterior and a posterior, the former being the stouter;  $m^3$  with two recurved roots of which the posterior is the stouter and shows a strong lateral compression;  $m_1$ ,  $m_2$  and  $m_3$  each with two roots, the anterior root being the stouter in  $m_1$ , the posterior the stouter in  $m_2$  and  $m_3$ .

Palate nearly as in *Arvicola* with a broad, flat median crest; short, well-defined and complete lateral bridges; shallow lateral grooves; and short and broad posterior median sloping septum.

*Measurements* (cited from Méhely).— $m^1$ – $m^3$  (adult) measured on grinding surface, 8.1 mm.;  $m_1$ – $m_3$  (adult) 8.5–8.6 (alveolar measurement, 9 mm.). Individual teeth:  $m^1$ , 3;  $m^2$ , 2.4;  $m^3$ , 2.7–3.3;  $m_1$ , 4.4–2 (juv. 3 mm.);  $m_2$ , 2.4–2.5 (juv. 1.7 mm.);  $m_3$ , 2.

*Remarks*.—This remarkable species is known to me only from the admirable descriptions and figures published by Nehring and Méhely.

## 2. †*Dolomys episcopalis* Méhely.

1911. *Evotomys glareolus* Kormos, Földtani Közlöny, **41**, p. 740. Not of Schreber.

1914. *Pliomys episcopalis* Méhely, Ann. Mus. Nat. Hungar., **12**, p. 198.

*Lectotype*.—Since Méhely has not indicated which of the specimens described by him should be taken as the type, I now formally select the subject of his Taf. v, fig. 10, as the lectotype. The specimen referred to is an old right mandibular ramus collected by Dr. Kormos and Dr. Ehik, and now in the collection of the Hungarian Geological Survey (Kön. Ung. Geolog. Reichsanstalt).

*Type horizon and locality*.—Lower Pleistocene ("erste interglaciale Periode") of the Somlyó-Berg, near Püspökfürdő, Bihar, Hungary.

*Range in time and space*.—At present known only from the type locality and horizon.

*Characters*.—Distinguished from *D. milleri* by its smaller size and more reduced  $m^3$ .

Palate normal, but with the lateral bridges short or incomplete; median sloping septum short and broad, though perhaps somewhat longer than in *Mimomys intermedius*, etc. Alveolus of lower incisor extending posteriorly to the level of the upper

border of the dental foramen or even slightly higher. Cheek-teeth essentially like those of *D. milleri*; but third root of  $m^1$  sometimes tending to fuse with the anterior root, and  $m^3$  of a somewhat more reduced type. The latter tooth presents three outer and three inner salient angles as usual in the group; but the second outer angle is relatively small, as in some species of *Pitymys*, and the first outer fold separating this structure from the anterior loop is shallow, its inner portion, judging from a specimen figured by Méhely (*op. cit.*, Taf. iv, fig. 10), being reduced by insulation. The vestigial third outer infold, represented by the concave posterior wall of the third outer angle, is still shallower than in *D. milleri*. As the result of these differences only the second triangle (second inner angle) is substantially closed in *D. episcopalis*; whereas in *D. milleri* there are four substantially closed dentinal spaces behind the anterior loop. In the  $m_1$  the anterior loop is smaller and slightly more reduced than in *D. milleri*, a sixth inner angle being apparently never present, at all events in adult stages of wear. General form of this tooth much like that of *Evotomys*.

*Measurements* (according to Méhely).—Length of tooth-rows,  $m^1$ – $m^3$  measured at grinding surface, 5.5 mm.;  $m_1$ – $m_3$ , 5.2–6. Individual teeth:  $m^1$ , 2–2.1;  $m^2$ , 1.6–1.8;  $m^3$ , 1.6;  $m_1$ , ad. 2.8, juv. 2.4–2.6;  $m_2$ , ad. 1.6, juv. 1.5;  $m_3$ , ad. 1.5, juv. 1.3–1.4.

*Remarks*.—Prof. Méhely places this species in a special genus *Pliomys*, but although it is quite sharply differentiated from *D. milleri* by its smaller size and more reduced  $m^3$  the characters are of specific and not of generic value. The peculiarities of the  $m^3$  in *D. episcopalis* are exactly those which characterize the corresponding tooth of several widely different genera such as *Alticola*, *Hyperacrius* and some species of *Pitymys*.

### 3. *Dolomys bogdanovi* Martino.

1921. *Microtus* (*Chionomys*) *bogdanovi* Martino, Ann. Mag. N.H., [9], 9, p. 413.

1925. *Dolomys bogdanovi* Hinton, Proc. Linn. Soc. London, 1924–25, p. 36 (October); Abstr. Proc. Linn. Soc. London, p. 2, April 23, 1925.

*Type*.—B.M., No. 22.7.5.1; young male, skin and skull, collected December 1, 1921, by E. and V. Martino.

*Type locality*.—Cetinje, Montenegro. Altitude 680 metres.

*Range*.—Known only from the type locality.

*Characters*.—Size large, hind-foot 25 mm.; condylo-basal length 32.7 mm. Tail long, about three-fourths the length of the head and body. Ears large, suborbicular, and densely haired. Thumb very small, bearing a minute flattened nail; claws of other digits short and sharp, about equal in length on hands and feet. Palms and soles naked; soles becoming hairy towards the heels. Palmar pads 5; plantar pads 6; all pads, but especially the posterior plantar tubercle, very large.

Fur soft, dense, and moderately long; hairs of back, in a specimen collected in May, about 12 mm. in length. General colour above greyish-brown, below greyish-white, the dorsal and ventral colours merging insensibly on flanks. Hair bases slaty everywhere, irregularly and considerably darkening the under surface. Tail clothed with short stiff hairs, which do not completely conceal the scaly annulations; provided with a short, stiff and thin pencil, 5-6 mm. in length; bicoloured, dark brown above, white on sides, below, and (in the single adult specimen examined) at the tip. Feet white.

Young pelage.—The young male, upon which the species was based, differs from the adult described above in its greyer or bluer general colour.

Skull (Fig. 96) large, strongly built, long and narrow; gently convex above from before backwards, the highest point in the mid-parietal region. Occiput vertical. Rostrum rather long and of moderate breadth. Nasals normal, ending flush with incisors in front, and, with the premaxillaries, about opposite the middle of the superior maxillary root of the zygoma behind. Temporal ridges fusing anteriorly in old age to form a weak but linear sagittal crest in the interorbital region; moderately approximated posteriorly and compressing the rather large interparietal. Interorbital region considerably constricted. Postorbital squamosal crests well developed; anterior squamosal encroachment well marked in adult, and the interstephanic portion of the frontals conspicuously narrowed. Upper border of jugal boldly convex. Infraorbital canal and its outer wall normal; no superior preorbital zygomatic notch. Alveolar portion of maxilla shallow, the molar capsules not rising up conspicuously in the floor of the orbit, nor obstructing the sphenorbital fissure. Anterior palatal foramina moderately large. Palate slightly abnormal behind; the posterior median sloping septum very broad, flat, and ill defined; postero-lateral pits very shallow. Pterygoid fossæ of normal depth; ectopterygoid plates moderately developed. Mesopterygoid fossa rather wide and shallow, reaching forwards to middle of  $m^3$ . Presphenoid and basisphenoid not strikingly compressed. Auditory bullæ large, conspicuously inflated, with very thin and papery walls; middle ear without any trace of spongy bone; mastoid portion slightly inflated; tegmen tympani articulating by squamous contact with alisphenoid. Stapedial artery enclosed in a bony tube as it approaches stapes; but apparently naked during its passage through the stapes.

Mandible normal, with long, slender coronoid and angular processes; horizontal ramus rather slender, not so deep as in most voles towards the symphysis. Alveolus of lower incisor terminates at the posterior base of the condylar process immediately below the dental foramen; it passes from the lingual to the labial side of the jaw below  $m_3$  without disturbing this

tooth to any marked extent, the jaw in this respect resembling that of *Evotomys*.

*Teeth*.—Upper incisors moderately broad, slightly recurved,

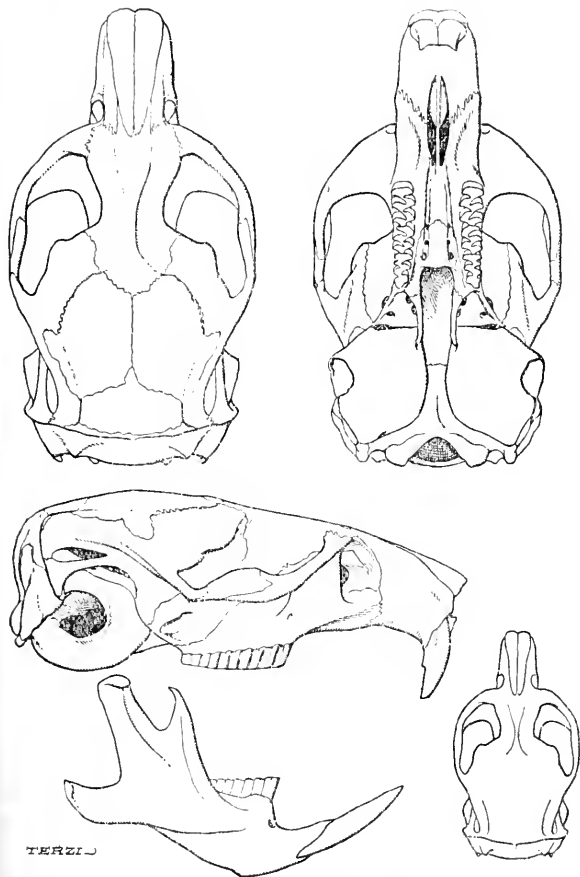


FIG. 96.—*Dolomys boglanovi* Martino.

Dorsal, ventral, and lateral views of adult skull; the small figure shows the skull in dorsal view, natural size.

with a very faint trace of a groove on the external part of the anterior face. Wearing surface of each tooth hollowed out postero-internally. Lower incisors rather slender, deeper than broad.

Cheek-teeth (Figs. 97, 98) rooted, each tooth, in adults, provided with two roots, one anterior, the other posterior; their re-entrant folds containing cement. Enamel thicker on convex walls of inner salient angles of upper molars; but elsewhere about equal on convex and concave walls. Salient angles alternating, the dentinal spaces rather tightly closed in all teeth, except  $m_3^3$ . Enamel pattern (Fig. 98) of  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  normal;  $m_3$  with its first outer infold deep enough to close the first pair of triangles substantially, its second outer infold shallow, the anterior pair of triangles broadly confluent and the third outer angle somewhat reduced;  $m^3$  with four outer and

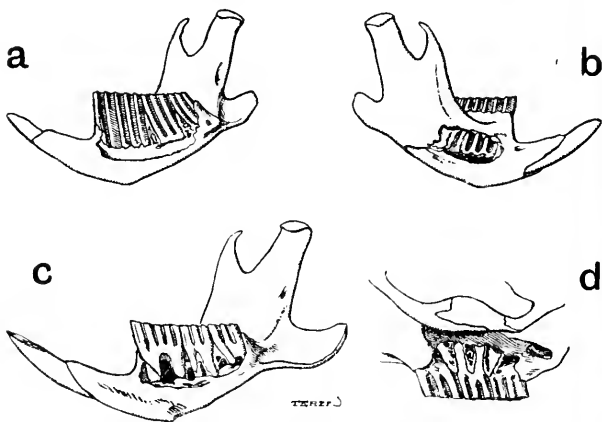


FIG. 97.—*Dolomys bogdanovi* Martino.

- a. Inner, b. outer view of right mandibular ramus of type; dissected to show the closed cement spaces of the molars.  
 c. Right mandibular ramus of adult; dissected to show molar roots.  
 d. Left maxilla of adult skull; dissected to show molar roots.

three inner salient angles, its first outer infold shallow as in *Alticola*, etc., leaving the first triangle confluent with the anterior loop; second and third triangles substantially closed; fourth and fifth triangles (third inner and fourth outer salient angles) widely confluent with each other and forming the short posterior loop;  $m_1$  with a posterior loop, five rather tightly closed triangles, and a short anterior loop, formed chiefly by the large fourth outer and fifth inner salient angles, the general shape of the anterior loop being somewhat nivaloid.

In the young type specimen the upper incisors show rather more distinct traces of grooves. The upper molars (Fig. 98a) present the usual youthful features, but no additional complications are shown by  $m^3$ . Similar remarks apply to  $m_2$  and



$m_3$ ; but  $m_1$  (Fig. 98a') shows some interesting complications of the anterior loop. Tubercles representing a fifth outer and a sixth inner angle are present; and between them is an antero-medial tubercle. These, with the little valleys separating them, are ephemeral structures confined to the upper strata of the tooth and doomed to disappear long before wear touches that part of the tooth now emerging from the alveolus. In this specimen the cement spaces on the inner sides of the lower molars are closed below; while on the outer side of  $m_1$  the beginning of the large anterior fang is plainly seen (Fig. 97b).

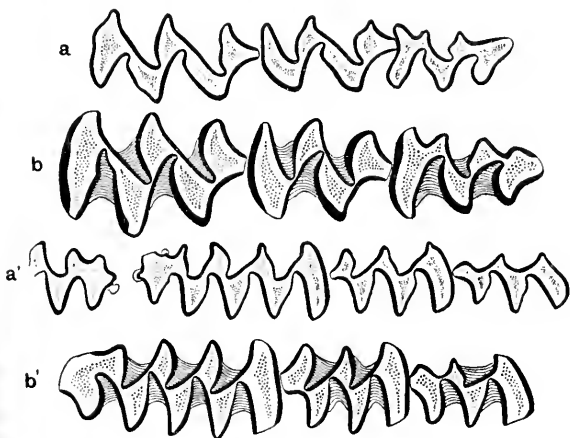


FIG. 98.—Cheek-teeth of *Dolomys bogdanovi* Martino.

Left upper (a. b.) and right lower (a'. b'.) molars.

- a. and a'. Molars of type specimen (immature); the anterior loop of  $m_1$  shows ephemeral complications, and part of the left  $m_1$  is figured for comparison with the right  $m_1$ , the teeth being in slightly different stages of wear on the two sides of the jaw.
- b. and b'. Molars of adult specimen (B.M., No. 23.11.1.8).

*Measurements* (taken in the flesh by the collector) of the type and of an adult male (in parentheses).—Head and body, 99 (130) mm.; tail, without hair, 74 (101); hind-foot, 25 (25.4); ear, 15 (18.5).

For *skull measurements*, see table at end of volume.

*Remarks*.—The outward appearance and the more superficial characters of the dentition and skull, particularly in the young specimen from which this species was first described, somewhat resemble those of the Snow Voles, and Dr. Martino was quite naturally misled into describing this remarkable animal as a new species of *Chionomys*. The possession of rooted molars,

the structure of  $m^3$ , the structure of the auditory bullæ, and the characters of those parts of the skull immediately under the influence of the temporal muscles indicate, of course, that it is very widely removed from *Chionomys*. These and many of the other characters described above show that this vole cannot be referred to any genus hitherto known among living forms. On the other hand, in dentition, palate, and jaw structure it agrees so closely with *Dolomys*, known previously only from fragmentary fossil remains obtained from the late Pliocene and Pleistocene deposits of Hungary, that I am compelled to refer it to that genus.

In palate and tooth structure it makes a very near approach to *D. milleri*, the older of the two Hungarian fossil species; the only important difference is that the teeth of the recent species possess cement, whereas those of the fossil lack it. The development of cement in the molars of voles is a progressive character; its presence in one species and absence in another, is not a difference of generic importance.

†Genus: **12. APISTOMYS** Méhely.

1913. *Evotomys* Ehik, Földt. Közl., 43, p. 7. Not of Coues.

1914. *Apistomys* Méhely, Ann. Mus. Nat. Hungar., 12, p. 203.

*Genotype*.—*Apistomys coronensis* Méhely.

*Range in time and space*.—Known only from the Pleistocene ("Zweite interglaciale Periode") of Hungary.

*Characters*.—Differing from *Dolomys* chiefly by its broader palate and the peculiar form of the  $m_1$ ; the differences scarcely of generic value.

Palate essentially as in *Dolomys* and *Mimomys*, but strikingly broad, its least width opposite  $m^1$  considerably greater than the antero-posterior length of that tooth; the posterior-medial sloping septum very short and broad.

Alveolus of incisor crosses from the lingual to the labial side of the mandibular ramus below the posterior root of  $m_2$  according to Méhely (though his figure, *op. cit.*, Taf. vi, fig. 7, scarcely bears this statement out).

Cheek-teeth in adults furnished with two roots each; the anterior root of  $m^1$  with two points and obviously a compound of the anterior root proper and of the third or central root found as an independent structure in *Dolomys* and some species of *Mimomys*. Surfaces of fangs channelled by vertical grooves, which continue the furrows formed by the cement spaces beyond the limits of the crowns of the teeth. No cement present in the re-entrant folds. Enamel pattern of  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  as in normal voles; outer salient angles of  $m_3$  reduced in size;  $m^3$  with three salient angles on each side, nearly as in *D. episcopalpis*,

the first outer infold shallow, leaving the anterior loop and first triangle confluent with each other, the second outer fold deep, substantially closing the second or inner triangle, the third and fourth triangles broadly confluent with each other and with the short and broad posterior loop;  $m_1$  with a posterior loop, five substantially closed triangles, and an anterior loop formed by a little modified fourth outer angle opening anteriorly into the loop proper, which consists of a widely confluent and opposed fifth pair of salient angles. This tooth differs from that of *Dolomys* in that its fourth outer angle retains its primitive transverse direction instead of being turned backwards, while the fourth outer infold is quite clearly developed although rather shallow transversely. These peculiarities impart to the  $m_1$  of *Apistomys* an appearance greatly resembling that which it has in such typical voles as *Microtus arvalis*, and very different from that seen in *Chionomys*, *Evotomys*, *Alticola*, *Dolomys* and many other genera in which the anterior loop of  $m_1$  is "helmet-shaped" in consequence of the backward or more longitudinal direction of the fourth outer angle.

*Remarks.*—As is evident from this description the differences which separate *Apistomys* from *Dolomys* are scarcely of generic importance. The broad palate and especially the peculiar *arvalis*-like  $m_1$  are, however, striking features in a member of the group to which *Dolomys* and *Mimomys* belong; they indicate that the possessor of such features was evolving in a different direction from those pursued by the two other genera mentioned. In these circumstances, Méhely having already established the genus, *Apistomys* may for the present be treated as distinct from *Dolomys*.

The only species known is *A. coronensis*.

1. † ***Apistomys coronensis*** Méhely.

1913. *Evotomys glareolus* Ehik, Földt. Közl., 43, p. 7. Not of Schreber.

1914. *Apistomys coronensis* Méhely, Ann. Mus. Nat. Hungar., 12, p. 203.

*Lectotype.*—Since Méhely does not indicate a type for this species, I now formally select the subject of his Taf. vi, figs. 6 and 7, as the lectotype. This is an imperfect left mandibular ramus (belonging to an old individual) with all the teeth in place, collected by Dr. J. Ehik and now in the collection of the Hungarian Geological Survey.

*Type horizon and locality.*—Pleistocene ("Zweite interglaciale Periode") of the Gesprengsberg, near Brasso (Kronstadt), Hungary.

*Range in time and space.*—Known only from the type horizon and locality.

*Characters.*—Size as in larger members of the *Microtus arvalis*-

*agrestis* groups. Other characters sufficiently described under the genus.

*Measurements* (according to Méhely).—Length of the upper and lower tooth-rows ( $m^1$ – $m^3$ ) measured on the grinding surface, 6.3 mm. Individual teeth:  $m^1$ , 2.5;  $m^2$ , 2.1;  $m^3$ , 1.7;  $m_1$ , 2.9;  $m_2$ , 1.8;  $m_3$ , 1.6.

†Genus: **13. MIMOMYS** Forsyth Major.

1846. *Arvicola* Owen, Brit. Foss. Mamm., p. 205 (remains from Pliocene of Norfolk and Suffolk indicating a species intermediate in size between “*A. amphibius*” and “*A. arvalis*”); Blackmore and Alston, P.Z.S., 1874, p. 462 (in part).
1872. *Arvicola* Forsyth Major, Atti Soc. Ital. Sci. Nat., 15, p. 389 (jaws with rooted molars from the Upper Pliocene lignite of Lefte, Lombardy).
1882. *Arvicola* (*Evotomys*) Newton, Vert. Forest Bed, p. 83 (British Pliocene forms with rooted molars referred to subgenus *Evotomys*).
1894. *Phenacomys* Nehring, Naturwiss. Wochenschr., 1894, No. 28, (forms with rooted molars from Beremend, Hungary, together with those from the British and Italian Pliocene, referred to *Phenacomys* Merriam). Not of Merriam; see Miller, N. Amer. Fauna, No. 12, 1896, p. 75.
1898. *Dolomys* Nehring, Zool. Anz., 1898, p. 13 (in part). Genus based upon one of the species occurring at Beremend, Hungary (*D. milleri*), and supposed to be congeneric with the British and Italian forms.
1902. *Mimomys* Forsyth Major, P.Z.S., 1902, 1, p. 102; genus for all those voles “with rooted molars, which are clearly different from *Evotomys*, *Phenacomys* and *Dolomys*.” Recognized three species from the Pliocene of Britain and Italy.
1902. *Microtus* Hinton and White, Proc. Geol. Assoc., 17, p. 414; referred a rooted molar from Early Pleistocene (High Terrace) of the Thames Valley to “*Microtus intermedius* Newton.”
1908. *Microtus* (*Mimomys*) Newton, Bull. Soc. Belge de Géol. Mém., 21, p. 592; Rütten, Die diluviale Säugethiere der Niederlande, 1908–10, p. 88; remains from Holland and Belgium referred to subgenus *Mimomys*.
1910. *Mimomys* Hinton, Proc. Geol. Assoc., 21, p. 491 (genus); Méhely, Ann. Mus. Nat. Hungar., 12, 1914, p. 185.
1914. *Microtomys* Méhely, Ann. Mus. Nat. Hungar., 12, p. 209.

*Genotype*.—*Mimomys pliocenicus* Forsyth Major; formally selected by Méhely (Ann. Mus. Nat. Hungar., 12, 1914, p. 185).

*History*.—The essential details relating to the history of this important genus are given in the notes intercalated in the synonymy above. For many years after the first discovery of its remains in the British Pliocene, species of the genus, on account of the great superficial likeness of their teeth to those of the Water Vole, were referred to *Arvicola amphibius*. In 1872 Forsyth Major found that the cheek-teeth of some speci-

mens from the Italian Pliocene were rooted and not developed from persistent pulps as in the Water Vole. Ten years later, and quite independently, Newton made a similar discovery with respect to the British species, and he accordingly referred all the remains before him to a new species, *Arvicola intermedius*, which he placed in the subgenus *Evotomys*. In 1894 Nehring, studying somewhat similar material from the Pliocene of Hungary, realized that voles of this kind were quite different from *Evotomys*, and so he referred them to *Phenacomys*, a remarkable N. American genus described a little earlier by Merriam. Miller pointed out shortly afterwards that the reference to *Phenacomys* was erroneous. Thereupon Nehring described his genus *Dolomys*, basing it upon one of the Hungarian species before him and referring to it the remains previously described from the Pliocene of Britain and Italy. In 1902 Forsyth Major found that the British and Italian forms were not congeneric with the Hungarian *Dolomys milleri*, and he established his genus *Mimomys* for their reception. In the same year White and the present writer found that the genus had lingered in Britain until the early Pleistocene (High Terrace of the Thames), and we referred the remains from that horizon to "*Microtus intermedius*" Newton, a well-known Forest Bed species. In 1910 I accorded *Mimomys* full generic rank, and briefly diagnosed four new species from British deposits. Lastly in 1914 M ehely published a complete and beautifully illustrated account of the Hungarian fossils. He showed that the deposits of that country contained in addition to *Dolomys milleri* the remains of several other species with rooted molars. Two of these he regarded as congeneric with *Mimomys*; but on others he based three new genera, viz., *Pliomys*, *Apistomys*, and *Microtomys*, of which the last-named, for reasons given below, is regarded by me as a synonym of *Mimomys*.

Having regard to its bearing upon the systematics of the present genus it is, perhaps, most convenient to intercalate the following note upon M ehely's work at this place, although the matters dealt with are partly those which I have endeavoured to expound in the introduction to this Monograph.

M ehely divides the Microtin e into three super-genera, viz., *Lemmi*, *Microti*, and *Fibrin e*; he includes in the last named all living and extinct genera with rooted molars. To my mind this is rather an ill-conceived classification, because the "*Fibrin e*" are merely relatively primitive types which *may* belong either to *Microti* or *Lemmi*. It so happens that all known "*Fibrin e*" link themselves with *Microti* and not with *Lemmi*; but that *Lemmi* also have had ancestors provided with rooted molars is a very safe inference to be drawn from present knowledge. In any case the "*Fibrin e*" cannot be regarded as forming a division equal in rank to those of the *Lemmi* and the *Microti*.

M ehely further subdivides the "*Fibrin e*" into two sections :—

*Acrorhiza*, in which the posterior root of  $m_2$  lies partly on the inner and partly on the outer side of the incisor.

*Pleurorhiza*, in which the posterior root of  $m_2$  is wholly labial to the incisor.

To *Acrorhiza* Méhely ascribes the genera *Dolomys*, *Mimomys* (as he restricts it), and his genera "*Pliomys*" and *Apistomys*. In *Pleurorhiza* he includes "*Fiber*" (= *Ondatra*), *Phenacomys*, *Evotomys*, and his genus "*Microtomys*." The *Acrorhiza* comprise the most ancient and generalized forms; the *Pleurorhiza* the more modern and progressive types. According to Méhely the *Pleurorhiza* must have evolved from the *Acrorhiza* by a change in the kind and manner of mastication; the postero-internal angle of  $m_2$  must have gradually ceased to have a functional importance, and therefore the part of the root lying immediately below it atrophied and eventually disappeared. He says that the older form of mastication was a grinding ("*mahlende*") process, and that this was replaced by a percussive ("*stossende*") action. Since grinding serves for the detrition of harder vegetable substances, and percussion for the treatment of a softer diet, Méhely infers that the *Acrorhiza* lived under dry steppe-like conditions; whenever a damper "forest-period" followed, softer vegetation came in vogue and "percussive" voles were evolved. In the most primitive forms,  $m^2$  and  $m^3$  had three roots each; later on, the number was reduced to two roots to each tooth. Méhely thinks that the purpose of the third root was to attach the tooth as firmly as possible and that its presence, therefore, is evidence of the harder and tougher food of the most ancient forms as compared with that of their, in this respect, degenerate descendants.

In my opinion this classification together with the ingenious theories and most of the new genera to which it has given origin are all based upon a series of misconceptions. I can confirm Méhely in his observation that the posterior root of  $m_2$  in *M. pliocenicus* rests straddle-wise upon the dorsal surface of the lower incisor, whereas in *M. intermedius* the molar root in question passes wholly to the labial side of the incisor. This difference, however, is due solely to the circumstance that whereas *M. pliocenicus* remained a relatively brachyodont animal, *M. intermedius*, like all other modernized "*Fibrinæ*," has made comparatively great strides towards hypsodonty. The lower molars by deepening their crowns have had their bases brought into closer relations with the shaft of the incisor, which found its way through the entire horizontal ramus of *Microti* at a very early stage in the history of the group, at a time long before either the crowns or the roots of the molars had penetrated the ramus to such deep levels; a structure so well established and so important as this perforating incisor shaft would not give way before the gradual advance of the growing bases of the cheek-teeth and the

latter have therefore had to mould and adjust themselves to the presence of the incisor. In all modern voles the bases of  $m_1$  and  $m_2$  pass to the labial side, and that of  $m_3$  passes to the lingual side of the incisor; this difference in the courses of the deep portions of the three cheek-teeth is occasioned by the spiral twisting of the incisor as it passes from before backwards. *M. pliocenicus* represents the penultimate stage of the process of adjustment; both roots of  $m_1$ , the anterior root of  $m_2$ , and both the roots of  $m_3$  are already fully adjusted to the presence of the incisor; the posterior root of  $m_2$  alone remains partly dorsal to the incisor shaft.

Méhely's notion of the course of evolution followed by the Microtine dentition is beyond question a complete inversion. Persistently growing molars of prismatic form, invested by well-differentiated enamel sheets, are characteristic of many other rodents besides voles and lemmings; in all cases they have been evolved gradually from brachyodont tubercular teeth as the rodent groups possessing them have become addicted to a harder and coarser vegetable diet. In such rodents the molar dentition has ceased to be a grinding or bruising apparatus; it has become a more or less powerful shearing and slicing machine. With the deepening of the teeth, their roots become shorter and develop later and later in the history of the individual; finally they are not formed at all. The teeth are implanted in the jaws by their crowns, which acquire peculiar curvatures; by this curvature and their continual growth the teeth are kept tightly "keyed" together by contact with each other near the wearing surface; in addition, cement is developed in the most highly specialized forms and, partly filling the re-entrant folds of the teeth, gives attachment to a special series of ligaments which bind the teeth to the alveolar walls. Having regard to the work done by the machine it may be said that such a mode of implantation affords an incomparably firmer union of the teeth with the jaws than any that could be secured by means of fangs alone.

*Range.*—The genus is abundantly represented in the later Pliocene deposits of S.E. England, and is known from deposits of similar age in Holland, Belgium, Italy and Hungary. It is also known from the early Pleistocene of England and Hungary.

*Characters.*—Cheek-teeth developing roots in the adults in earlier species or in old age in the later species; each tooth with two roots, except  $m^1$  and  $m^2$ , which in the earlier forms possess three. Cement usually present in the re-entrant folds, but in some species lacking. Enamel usually differentiated into thick and thin tracts, the thicker portions forming the convex sides of the salient angles instead of their concave sides as in most living voles. Enamel pattern very similar to that of *Arvicola* in general appearance;  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  of normal pattern;  $m^3$  rather simple, nearly as in *Arvicola*, usually with

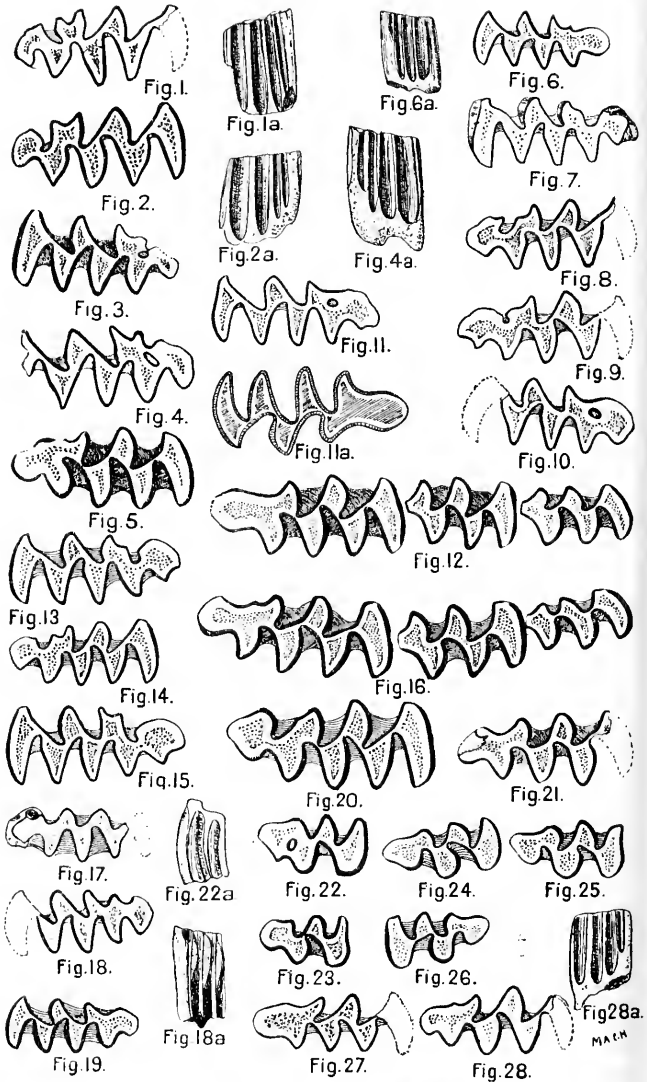


FIG. 99.—Cheek-teeth of *Mimomys*.  
 (For explanation see opposite page.)



## EXPLANATION OF FIG. 99.

N.C. = Norwich Crag. U.F.B. = Upper Freshwater Bed.

- 1, 1a. *Mimomys pliocænicus* Forsyth Major. Right  $m_1$  young, crown and outer views; cement spaces closing, third outer fold intact. N.C. (Norwich Mus., No. 971a, Fitch Coll.).
- 2, 2a. *M. pliocænicus*. Right  $m_1$  young, crown and outer views; cement spaces closed, third outer fold intact. U.F.B., Ostend (but probably derived from an older deposit, the base of the tooth being somewhat rolled and its mineral condition as in Norwich Crag fossils) (Norwich Mus., No. 2708a, Gurney Coll.).
3. *M. pliocænicus*. Left  $m_1$  adult, crown view; for outer and inner views see Pl. XIII, figs. 1, 1a. Roots moderately long, inner portion of third outer fold just insulated. N.C., Yarn Hill (A. S. Kennard).
- 4, 4a. *M. pliocænicus*. Left  $m_1$  adult, crown and outer views; with short roots, inner portion of third outer fold completely insulated. N.C., Thorpe (Norwich Mus., No. 971d (a), Fitch Coll.).
5. *M. pliocænicus*. Right  $m_1$  old, crown view; roots very long, "prism-fold," third outer fold and enamel islet worn away. N.C., Yarn Hill (A. S. Kennard).
- 6, 6a. *M. reidi* Hinton. Left  $m_1$  adult (type of species), crown and outer views. Weybourne Crag, Trimmingham (Mus. Pract. Geol., No. C.R. 836).
7. *M. intermedius* Newton. Left  $m_1$  very young, crown view; pulp cavities open, anterior coronal tubercles present, "prism-fold" and third outer valley intact. U.F.B., West Runton (Savin Coll., No. 9.7.30.3).
8. *M. intermedius*. Right  $m_1$  very young, crown view (outer view, Pl. XIII, fig. 5). U.F.B., West Runton (Savin Coll., No. 9.7.24.1.)
9. *M. intermedius*. Right  $m_1$  young, crown view (outer view, Pl. XIII, fig. 6); inner portion of third outer fold nearly insulated. U.F.B., West Runton (Savin Coll., No. 9.7.30.1).
10. *M. intermedius*. Left  $m_1$  young, crown view (outer view, Pl. XIII, fig. 4); inner portion of third outer valley insulated. U.F.B., West Runton (Savin Coll., No. 9.5.4.1).
- 11, 11a. *M. intermedius*. Left  $m_1$  young, crown and basal views; pulp cavities open, third outer fold insulated. U.F.B., West Runton (Savin Coll., No. 9.7.30.2).
12. *M. intermedius*. Right  $m_1$ ,  $m_2$  and  $m_3$  adult, crown views (type of species). U.F.B., West Runton (Mus. Pract. Geol.).
13. *M. savini* Hinton. Left  $m_1$  very young, crown view (outer view, Pl. XIII, fig. 9). U.F.B., West Runton (Savin Coll., No. 9.4.23.1).
14. *M. savini*. Right  $m_1$  young crown view. U.F.B., West Runton (Mus. Pract. Geol., No. 959J).
15. *M. savini*. Left  $m_1$  young, crown view (outer view, Pl. XIII, fig. 7). U.F.B., West Runton (Savin Coll., No. 9.4.24.1).
16. *M. savini*. Right  $m_1$ ,  $m_2$  and  $m_3$  adult, crown view. U.F.B., West Runton (Savin Coll., No. 820.2).
17. *M. majori* Hinton. Right  $m_1$  very young, crown view (outer view, Pl. XV, fig. 1); fourth outer valley represented by an ephemeral islet and persistent external vestige. U.F.B., West Runton (G. White Coll.).
- 18, 18a. *M. newtoni* Forsyth Major. Left  $m_1$  imperfect, young, crown and outer views. Upper Pliocene, Tegelen-sur-Meuse (B.M. presented by Mr. and Mrs. Clement Reid).
19. *M. newtoni*. Left  $m_1$  adult, crown view. "Clay-gravel," East Runton (Mus. Pract. Geol., No. C.R. 979.A).

20. *M. majori*. Right  $m_1$  adult, crown view. U.F.B., West Runton (*Savin Coll.*, No. 824.2).
21. *M. cantianus* Hinton. Right  $m_1$  adult, imperfect, type of species, crown view (outer and inner views, Pl. XIII, figs. 11, 11a). High Terrace of the Thames, near Greenhithe, Kent (*G. White Coll.*).
- 22, 22a. *M. pliocenicus*. Right  $m^3$  adult, crown and inner views. Weybourne Crag, East Runton (*A. S. Kennard*).
23. *M. newtoni*. Right  $m^3$  adult, crown view. Upper Pliocene, Tegelen-sur-Meuse (*B.M.*, presented by Mr. and Mrs. Clement Reid).
- 24-26. *M. intermedius*. Right and two left  $m^3$ , adult, crown views. U.F.B., West Runton (*Mus. Pract. Geol.*, Nos. 906A, B, and C).
27. *M. newtoni*. Right  $m_1$  imperfect, adult, crown view. "Clay-gravel," East Runton (*Mus. Pract. Geol.*, No. 979B).
28. *Mimomys* sp. Right  $m_1$  imperfect, crown view; with two short roots and no trace of enamel islet. N.C., Thorpe (*Norwich Mus.*, No. 971h (1), *Fitch Coll.*).

three salient angles on each side, its second inner infold usually persistent, but in one species (*M. pliocenicus*) subject to reduction by insulation;  $m_1$  with three closed triangles following the posterior loop as in *Arvicola*, and an anterior loop of complex structure. In some species the third outer infold of this tooth persists throughout the crown (*newtoni* group); in others this fold is reduced by the insulation of its internal part. In the earlier or more primitive species the enamel islet, which results from the reduction of this outer fold, persists as a conspicuous feature of the grinding surface until an advanced stage of wear has been reached; but in later or more progressive forms the islet is an ephemeral feature which vanishes long before the molar roots begin to develop. Third outer angle of  $m_1$  in some species cleft by a peculiar fold called the "prism-fold,"<sup>1</sup> which may or may not persist throughout the crown.

In the earlier, or more brachyodont, species the lower incisor passes from the lingual to the labial side of the jaw beneath the posterior root of  $m_2$ ; but in later, or more hypsodont, species the incisor crosses between  $m_2$  and  $m_3$ , so that  $m_2$  like  $m_1$  is wholly labial to the incisor shaft.

Skull imperfectly known. Temporal ridges in some species, at all events, widely separated in the interorbital region. Masseteric plate (outer wall of infraorbital canal) essentially as in modern voles. Palate of normal Arvicoline type with postero-lateral bridges and pits, and with the postero-median sloping septum clearly defined although short and broad. Mandible essentially as in most other voles; the lower incisor ascending the condyloid process to a point often well above the dental foramen; the termination of the alveolus of the incisor often producing a well-marked hump on the outer surface of the jaw.

*Relationships*.—The relationships of *Mimomys* have been fully discussed above. It has no doubt the same ancestry as

<sup>1</sup> For the significance of this structure see p. 111.

*Dolomys* and *Apistomys*, and from it, in turn, the modern genera *Arvicola* and *Phaiomys* seem to be descended.

*Species*.—Eight species are at present recognized, but no doubt others will have to be defined when more satisfactory material is obtained. Of the eight, seven are known from British deposits. Recent work, done with the advantage of much more extensive material, confirms Forsyth Major's conclusions as to the distribution in time of the chief British species. From the Norwich Crag only the older forms, *M. pliocænicus* and its allies and perhaps *M. newtoni* are known; whereas in the Upper Fresh-water Bed at West Runton we find only the newer species *M. intermedius*, *M. savini* and *M. majori*. But in the East Runton deposit ("shelly crag") of intermediate age both the older and the newer species occur together. One species, *M. cantianus*, probably a descendant of *M. majori*, occurs in the early Pleistocene High Terrace Drift of the Thames.

As already indicated, the species fall into two groups; in one, in this respect the more primitive, comprising *M. newtoni*, *M. majori* and *M. cantianus*, the third outer infold of the  $m_1$  is persistent; but in the other, comprising *M. pliocænicus*, *M. reidi*, *M. savini*, *M. intermedius* and *M. pusillus* this infold is reduced by insulation, and in the later members of the group is almost completely obliterated in all but the very youngest stages of wear.

In each group the molar roots are developed earlier in the older species than in the more modern ones, and the vanishing elements of the crown become in successive geological horizons more and more ephemeral. Thus the general trend of dental progress seen within this genus, as elsewhere in the subfamily, is towards the persistent growth (complete hypsodonty) of the molars and the simplification of their crown structure.

#### 1. † *Mimomys pliocænicus* Forsyth Major.

1872. *Arvicola* sp. Forsyth Major, Atti Soc. Ital. Sci. Nat., 15, p. 389.  
 1874. *Arvicola amphibius* Blakmore and Alston. P.Z.S., 1874, p. 462, fig. 1a (in part); Tuecime, Mem. d. Pontificia Accad. d. Nuovi Lincei, 9, 1897, p. 35.  
 1882. *Arvicola (Evotomys) intermedius* Newton, Vert. Forest Bed, p. 83, pl. xiii, fig. 12 (in part).  
 1889. *Arvicola pliocænicus* Forsyth Major, in Weithofer, Jahrb. d. k.k. geolog. Reichsanstalt, 39, p. 86.  
 1902. *Mimomys pliocænicus* Forsyth Major, P.Z.S., 1902, 1, p. 103, fig. 8 (text-fig. 13); Hinton, Proc. Geol. Assoc., 21, 1910, p. 491; Méhely, Ann. Mus. Nat. Hungar., 12, 1914, p. 186.  
 1907. *Microtus (Mimomys) pliocænicus* Newton. Bull. Soc. Belge Géol., 21, Mém., p. 592; Rütten, Die diluviale Säugethiere der Niederländ, 1910, p. 88.

*Type*.—Florence Museum. Part of a left mandibular ramus, with the incisor,  $m_1$  and  $m_2$  in place; figured by Forsyth Major, P.Z.S., 1902, 1, p. 103, figs. 8 and 9 (text-fig. 13).

*Type locality and horizon.*—Upper Pliocene lacustrine deposits of the Val d'Arno.

*Range in time and space.*—This species occurs in the Upper Pliocene of Britain, Holland, Belgium, Italy and Hungary.

In Britain it is known from the Norwich Crag in Norfolk and Suffolk, from "clay-pebbles" in a "clay-gravel" at East Runton, Norfolk (see p. 376), and from a "shelly crag" (Lower Cromerian or Weybourne Crag) at East Runton.

In the Norwich Crag it occurs alone, or perhaps in association with *M. newtoni*; in the "shelly crag" at East Runton it is associated with *M. savini*, *M. intermedius* and *M. majori*.

In Holland teeth of *Mimomys* were obtained from a boring at Gorkum; these were referred by Harting (Ver. Comm. Geol. Kaart van Nederland, 1853, p. 103) to "*Hypudæus terrestris*." Rütten (Die diluviale Säugethiere der Niederland, 1910, p. 88) has described and figured three of these teeth, correctly referring them to the present genus. Of these a fragment of maxilla with the left  $m^3$ , obtained from a depth of 165.5 metres, is in my opinion undoubtedly referable to the present species, the tooth showing the characteristic islet developed in connection with the reduction of its second inner valley. A left  $m_1$  and a right  $m^1$  from a higher level (127.3–129.9 metres) may also belong to this species or rather to a later development of the same stock; these two specimens Rütten compares with *M. intermedius*, but from the general form of the  $m_1$  I think its affinities are with *M. pliocænicus*. Further study of this specimen and a good figure of its external surface are necessary before it can be satisfactorily determined. A fourth specimen from the same level is referred by Rütten "mit ziemlicher Sicherheit" to *Arvicola amphibius*; but such a determination is, in my opinion, open to the gravest suspicion.

In Belgium the species is known from the Upper Pliocene clay of Tegelen-sur-Meuse, from which deposit a very characteristic left  $m_1$  has been described and beautifully figured by Newton (Bull. Soc. Belge Géol., 21, 1907, p. 592).

In Italy, in addition to the jaw from the Upper Pliocene lacustrine deposits of the Val d'Arno upon which Forsyth Major based the present species, two jaws have been obtained and described by Tuccimei (Mem. Pont. Accad. Nuovi Lincei, 9, 1897, p. 35) from the Upper Pliocene lacustrine marl of Bocchignano in Sabino. From the figures and description these specimens would appear to be referable to *M. pliocænicus* or a near ally. Tuccimei has, however, completely misunderstood the characters of the dentition. He states correctly that the molars of *Arvicola* are rootless; shows the rooted character of the fossil teeth most clearly in his figures; describes how the cement spaces die out below; and then says there is no doubt that these remains are to be referred to *Arvicola amphibius*. The characteristic enamel "islet" is present in the  $m_1$  of the younger jaw, and this

Tuccimei regards as a character of advanced wear, which would have appeared a little later on in the somewhat older specimen—but from the  $m_1$  of the latter the "islet" has in reality vanished for ever. Molar teeth resembling those of *Arvicola* in pattern and size but provided with roots were recorded by Forsyth Major from the lignite of Lefte, in Lombardy, in 1872 (Atti Soc. Ital. Sci. Nat., 15, p. 389); whether these should be referred to *M. pliocenicus* or to some other species of *Mimomys* is unknown.

Lastly from Hungary Méhely has described and figured from the late Pliocene deposits of Beremend, Csarnóta, and Berg Nagy-Harsány the most perfect remains of *M. pliocenicus* yet discovered.

*Characters*.—Size medium; tooth-row measuring 7–8 mm. in length. Skull practically unknown. Palate as figured by Méhely (Ann. Mus. Nat. Hungar., 12, Taf. iii, fig. 2) not essentially different from that of *Arvicola*,<sup>1</sup> but probably with an unusually short and broad posterior median sloping septum; maxillo-palatine suture extending forwards to a point opposite the postero-internal salient angle of  $m^1$ ; anterior palatine foramina terminating posteriorly a little in advance of the tooth-rows. Outer wall of the infraorbital canal ("masseteric plate") substantially as in other Microtines.

Mandible with moderately large angular and coronoid processes; the lower incisor crosses from the lingual to the labial side of the jaw beneath the posterior root of  $m_2$ , displacing  $m_3$  lingually, and ascends the condylar process to a point above the level of the dental foramen; the termination of the alveolus of the incisor is marked by a strong protuberance upon the outer side of the bone below the condyle; condylar process somewhat inflected above the just-mentioned protuberance (see Méhely, *op. cit.*, Taf. iii, fig. 5).

*Cheek-teeth* with perfectly alternating triangles, and re-entrant folds containing cement. Characterized especially by the early development of the roots, and by the reduction of the third outer fold of  $m_1$  and of the second inner fold of  $m^3$ . In each case the reduction of the fold takes place by the insulation of its deeper and inner portion, and in adult stages of wear the insulated portion of the fold is represented upon the worn surface of the tooth by a long persistent enamel islet. In this species the formation of the tooth-fangs commences before the reduction of the two molar folds just named becomes apparent at the wearing surfaces of the teeth.

*Upper cheek-teeth*.— $m^1$  and  $m^2$  (Fig. 100, 15–18) with three roots each in adult stages of growth; the third root compara-

<sup>1</sup> The only palate of this species known to me is that described and figured by Méhely; he says of it that it is "nach dem *Evotomys*—Typus gebaut, steht aber zu *Dolomys* nahe." The posterior edge, as shown in the figure cited, seems to be slightly mutilated and rather thick; it appears to me that there is room for a very short, broad, median sloping septum which has been broken away.

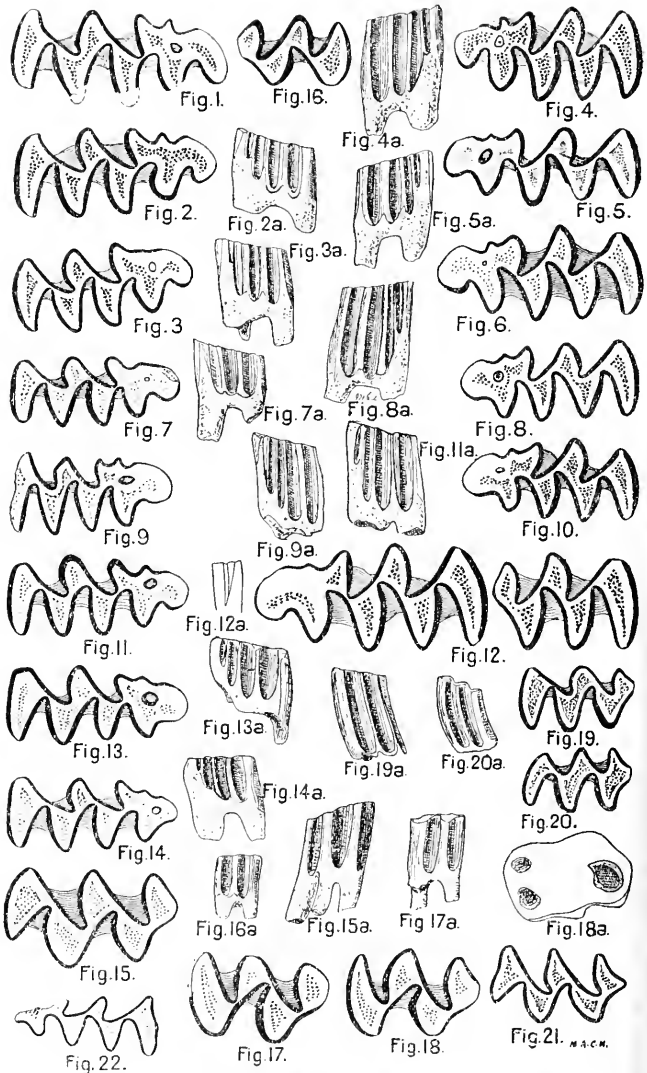


FIG. 100.—Cheek-teeth of *Mimomys pliocœnicus* Forsyth Major.  
(For explanation see opposite page.)

## EXPLANATION OF FIG. 100.

N.C. = Norwich Crag.

1. *Mimomys pliocænicus* Forsyth Major.  $m_1$  of a fragmentary left ramus of large size ( $m_1$ - $m_3$  must have measured nearly 9 mm.); adult, bases of cement spaces at alveolar level. N.C., Thorpe (*Norwich Mus.*, No. 551,\* *Fitch Coll.*).
- 2, 2a. *M. pliocænicus*. Left  $m_1$  crown and outer views. N.C., Thorpe (*Norwich Mus.*, No. 971b (2), *Fitch Coll.*).
- 3, 3a. *M. pliocænicus*. Left  $m_1$ , crown and outer views. N.C., Thorpe (*Norwich Mus.*, No. 971b (5), *Fitch Coll.*).
- 4, 4a. *M. pliocænicus*. Right  $m_1$ , crown and outer views. N.C., Thorpe (*Norwich Mus.*, No. 971d (b), *Fitch Coll.*).
- 5, 5a. *M. pliocænicus*. Right  $m_1$ , crown and outer views. N.C., Thorpe (*Norwich Mus.*, No. 971b (4), *Fitch Coll.*).
6. *M. pliocænicus*. Right  $m_1$ . N.C. ("Lower Bed"), Bramerton (*Norwich Mus.*, No. 747, *Reeve Coll.*).
- 7, 7a. *M. pliocænicus*. Left  $m_1$ , crown and outer views. N.C. (*Norwich Mus.*, No. 971g, *Fitch Coll.*).
- 8, 8a. *M. pliocænicus*? Right  $m_1$ ; infolds with little or no cement, fifth inner angle obsolete. N.C. (*Norwich Mus.*, No. 971b (1), *Fitch Coll.*).
- 9, 9a. *M. pliocænicus*? Left  $m_1$ , similar to the specimen represented in Fig. 8. N.C., Bramerton (*A. S. Kennard*).
10. *M. pliocænicus*? Right  $m_1$  of a fragmentary jaw, smaller than subject of Fig. 1 ( $m_1$ - $m_3$  must have measured about 7.4 mm.). N.C., Thorpe (*Norwich Mus.*, No. 551, *Fitch Coll.*).
- 11, 11a. *M. pliocænicus*. Left  $m_1$ , crown and external views. "Shelly-crag," East Runton (*B.M.*, No. M.6967, *Savin Coll.*).
- 12, 12a. *M. pliocænicus*. Crown views of  $m_1$  and  $m_2$  of a right mandibular ramus, with the anterior part of the external view of  $m_1$  (12a). N.C. ("Upper Bed"), Bramerton (*Norwich Mus.*, No. 524, *Reeve Coll.*).
- 13, 13a. *M. pliocænicus*? Left  $m_1$  (cf. Figs. 8 and 9). N.C. (*B.M.*).
- 14, 14a. *M. pliocænicus*? Left  $m_1$ . N.C. ("Lower Bed"), Bramerton (*Norwich Mus.*, No. 747, *Reeve Coll.*).
- 15, 15a. *M. pliocænicus*. Left  $m^1$ , crown and inner views. N.C. ("Lower Bed"), Bramerton (*Norwich Mus.*, No. 747, *Reeve Coll.*).
- 16, 16a. *M. pliocænicus*. Right  $m^2$ , crown and outer views. N.C., Thorpe (*Norwich Mus.*, No. 971c, *Fitch Coll.*).
- 17, 17a. *M. pliocænicus*. Left  $m^2$ ; crown and inner views. N.C., Thorpe (*Norwich Mus.*, No. 971f, *Fitch Coll.*).
- 18, 18a. *M. pliocænicus*. Left  $m^2$ , crown and basal views. N.C., Thorpe (*Norwich Mus.*, No. 971f,\* *Fitch Coll.*).
- 19, 19a, 20, 20a. *M. pliocænicus*. Left  $m_2$  and left  $m_3$ . N.C., Thorpe (*Norwich Mus.*, No. 971c, *Fitch Coll.*).
21. *Mimomys* sp. Left  $m^1$ . N.C., Thorpe (*Norwich Mus.*, No. 971c, *Fitch Coll.*).
22. *Mimomys* sp. Right  $m_1$ . N.C., Thorpe (*Norwich Mus.*, No. 971, *Fitch Coll.*).

tively slender, supporting the first closed triangle (second inner prism) in  $m^1$ , and the inner part of the anterior loop in  $m^2$ . Enamel pattern of these two teeth normal.  $m^3$  with two roots. Young specimens of this tooth (Méhely, *op. cit.*, Taf. iii, fig. 3) show an anterior loop, followed by four alternating triangles, of which the last two are more or less confluent with each other; on each side of the tooth there are three well-developed salient angles, separated by two deeply re-entrant folds. In older stages, as the tooth wears down, the central portion of the postero-internal re-entrant fold is seen to lose its connection with the periphery of the tooth in the deeper levels of the crown, and is converted into an enamel islet, which long persists as a conspicuous and highly characteristic feature of the worn surface of the adult tooth. In such teeth there are three outer but only two inner salient angles, and correspondingly two outer but only one inner re-entrant fold. But on the inner side of the crown, opposite the enamel islet, a long persistent though shallow vertical groove remains as the peripheral vestige of the reduced second inner fold (Fig. 99, 22, 22a). Disregarding the islet and the external vestige of the second inner fold (which are vanishing elements), the adult  $m^3$  of *M. pliocænicus* is an extraordinarily simple tooth showing that this species in spite of its many very primitive characters was highly and perhaps precociously specialized in this one direction.

*Lower cheek-teeth* (Figs. 99, 100).—All three are provided when adult with two roots each.  $m_1$  has its crown composed of a posterior loop, followed by three substantially closed triangles, and completed by an anterior loop of complex structure. This anterior loop is composed of three chief elements, viz., the fourth and fifth triangles (forming the third outer and fourth inner salient angles respectively), and a small anterior loop proper, which is produced internally to form the fifth inner salient angle. The third outer angle (or fourth triangle) is partially cleft from its worn surface to the base of the crown by a vertical furrow called by me the "prism-fold"; each lip of the prism-fold forms a small salient angle. In the type, from the Val d'Arno, the prism-fold is narrow and deep, but in specimens from England and Hungary it is usually wider and shallower. As a rule the prism-fold does not contain cement; but in one tooth a little was observed in this situation (Fig. 100, 4). In young examples (including such as are commencing to develop their roots, Fig. 99, 1, 2), there is a deep re-entrant fold—the third outer valley—immediately in front of the third outer angle; this fold is partly filled with cement. In the deeper parts of the crown, exposed at the surface in later stages of wear, this fold (like the second inner fold of  $m^3$ ) is reduced; its internal portion is cut off from the periphery of the tooth and converted into an enamel islet filled with cement; its outer portion persists as a wide shallow vertical groove channelling the outer surface



of the tooth immediately in front of the prism-fold. The enamel islet persists as a feature of the worn surface until a very advanced stage of wear has been reached (Fig. 100, 7); but the groove or external vestige of the third outer valley dies out at a variable distance above the level of the base of the prism-fold (Fig. 100, 2a-14a).<sup>1</sup> Sometimes a faint sulcus is impressed upon the outer surface of the fang, and this, when present, appears to represent a downward continuation of the external vestige in question (Pl. XIII, fig. 1).

As regards enamel pattern  $m_2$  and  $m_3$  (Fig. 100, 12, 19, 20) do not differ essentially from the corresponding teeth of *Arvicola*. The outer salient angles of  $m_3$  are quite well developed. The outer re-entrant folds, in both teeth, may substantially shut off the outer from the inner triangles; but one or both folds may be shallow, so as to leave a more or less wide confluency between the triangles of the corresponding pair or pairs (Fig. 100, 20).

*Remarks.*—The early development of the molar roots, the presence of three roots each in  $m^1$  and  $m^2$ , the great complexity of the crown in the young  $m_1$ , and the long persistence of the insulated portion of the third outer fold of  $m_1$ , are characters which stamp *M. pliocenicus* as being a very primitive member of the genus to which it belongs. In one respect, viz., in the reduction of the second inner fold of  $m^2$ , it is, however, highly specialized; this specialization, as a step in the wrong direction, prevents us from regarding the species as the ancestor of the later members of the same group. In confirmation of this view we may cite the fact that at East Runton *M. pliocenicus* occurs in association with the later forms in question (*M. savini* and *M. intermedius*).

## 2. †*Mimomys reidi* Hinton.

1882. *Arvicola (Evotomys) intermedius* Newton, Vert. Forest Bed, p. 85, pl. xiii, fig. 8 (in part).  
 1910. *Mimomys reidi* Hinton, Proc. Geol. Assoc., 21, p. 491.  
 1915. *Mimomys petenyii* Méhely, Ann. Mus. Nat. Hungar., 12, p. 191, Taf. iv, figs. 5-8.

*Type.*—Mus. Practical Geology, No. C.R. 836; a detached left  $m_1$ , collected by Clement Reid, F.R.S.

*Type horizon and locality.*—Weybourne Crag, Upper Pliocene; Trimingham, Norfolk.

*Range in time and space.*—In England known only from the Weybourne Crag of Trimingham. Remains of the same or a very

<sup>1</sup> Mr. J. B. Johnson has lent me a left mandibular ramus which he found in the Norwich Crag at Bramerton. This belonged to an old individual and has the incisor,  $m_1$  and  $m_2$  in place; the molar roots are visible above the alveolar margin and the enamel islet has been worn away from  $m_1$ . The specimen is of interest, as it shows upon its outer surface insertion marks for the *masseter medialis* muscle similar to those occurring in *M. intermedius* and in *Arvicola*.

closely allied species have been described, under the name *M. petenyii*, from the Upper Pliocene of Beremend, Hungary, by Prof. Méhely.

*Characters*.—Size small, about as in *M. newtoni*. Cheek-teeth with well-differentiated enamel; a little cement present in the re-entrant folds. Lower cheek-teeth with the outer re-entrant folds rather shallow, leaving noticeable confluencies between the outer and inner triangles; triangles distinctly alternating in  $m_1$ . In  $m_1$  (Fig. 99, 6, *6a*) the third outer angle has a well-developed prism-fold, of which the anterior costa is a prominent feature; external vestige of the third outer valley distinct, but dying out upon the side of the crown considerably above the level of the base of the prism-fold; inner portion of the third outer valley reduced, the reduction probably being effected in the normal manner by the conversion of this part of the fold into an enamel islet. Supposing it to exist at some stage of wear, this islet is a much more ephemeral structure than it is in *M. pliocænicus*; for no trace of it remains in the type specimen, which belonged to a young adult, for it has the beginnings of two large roots. In *M. pliocænicus* of equal age insulation of the fold would have scarcely yet been complete. Fifth inner angle obsolete.

In the Hungarian remains upon which Prof. Méhely has based his *M. petenyii*,  $m_1$  is very similar to the tooth just described, and Méhely himself cites Newton's figure of my type in the synonymy of his species. The only difference appears to be that whereas the English specimen has a little cement in the re-entrant folds, the Hungarian teeth lack it. Further material may indeed show more important differences; but for the present *M. petenyii* must be regarded as a synonym of *M. reidi*.

The Hungarian specimens show that in the mandible the course of the lower incisor is similar to that described above in *M. pliocænicus*, and that the posterior root of  $m_2$  stands in a similar relation to the shaft of the incisor. The palate closely resembles that of the Hungarian specimen of *M. pliocænicus*;  $m^1$  has three roots as in the latter species, although the middle root is a little more slender relatively; but both  $m^2$  and  $m^3$  have only two roots apiece.

*Remarks*.—The tooth upon which *M. reidi* is based presents a remarkable combination of characters; in it, confluency of the dentinal spaces—a primitive character in voles—is coupled with a highly specialized or reduced form of anterior loop and small size. Although averse from describing species from single teeth, I was not able to resist the temptation in this case, and the opinion formed in 1907, when I first studied the type and only known English specimen, has since been confirmed by the discoveries made in Hungary by Prof. Méhely.

3. † *Mimomys savini* Hinton.

1902. *Mimomys intermedius* Forsyth Major, P.Z.S., 1902, 1, p. 106, text-fig. 15, figs. 22, 22a, and 22b (in part).

1910. *Mimomys savini* Hinton, Proc. Geol. Assoc., 21, p. 491.

*Type*.—B.M., No. M. 6986b (Savin Collection). A detached right  $m_1$ ; collected by Mr. A. C. Savin; figured by Forsyth Major (P.Z.S., 1902, 1, p. 106, text-fig. 15, figs. 22, 22a, and 22b).

*Type horizon and locality*.—Upper Freshwater Bed (Cromerian Series), at West Runton, Norfolk.

*Range in time and space*.—*M. savini* first appears, so far as is known, in the "shelly sand" at East Runton, Norfolk, a deposit which may be part of the Weybourne Crag. In the British Museum there are from this deposit at East Runton three detached examples of the  $m_1$  (all of the left side), and a fragmentary right ramus with this tooth in place (B.M., Nos. M. 6967, 1, 5, and 16, and M. 6965a); these do not differ in any way from those found in the later deposit at West Runton, where the species occurs in all three divisions of the Upper Freshwater Bed; it is abundant in the lower sandy stratum, which has been so profitably worked by Mr. Savin and is common in the middle peaty division; I have a single specimen, a right  $m_1$  from the overlying "Monkey Gravel." The species is not known to occur in any foreign deposit.

*Characters*.—Size medium; length of lower cheek-tooth row 7–8 mm. In the mandible the incisor crosses from the lingual to the labial side of the jaw between  $m_2$  and  $m_3$ , and the posterior root of  $m_2$  is wholly labial to the incisor. Molars more hypsodont than in the earlier species, developing roots at a comparatively late period of life; with well-differentiated enamel; the re-entrant folds partly filled with cement.  $m_1$  with a persistent prism-fold developed in connection with the third outer angle; its third outer valley, intact in the youngest stages of wear, but reduced in later stages, as in *M. pliocenicus*, by the conversion of its inner portion into an enamel islet. The reduction, however, takes place at a much earlier moment (*i.e.*, at a far higher level of the crown) than in *M. pliocenicus*, and the resulting enamel islet is a much more ephemeral feature of the wearing surface than in the latter species, being formed and worn completely away before the molar roots have commenced to develop; an external vestige of the third outer valley usually persists throughout the crown (Fig. 101, 1a, 2a, and Pl. XIII, figs. 7, 8, 10). The remaining lower cheek-teeth,  $m_2$  and  $m_3$ , the upper cheek-teeth and skull fragments are not distinguishable at present from those of the associated species *M. intermedius* and *M. majori*.

Several very young examples of the  $m_1$  (Fig. 99, 13–15) from the Upper Freshwater Bed at West Runton afford material for the investigation of the earlier stages of wear

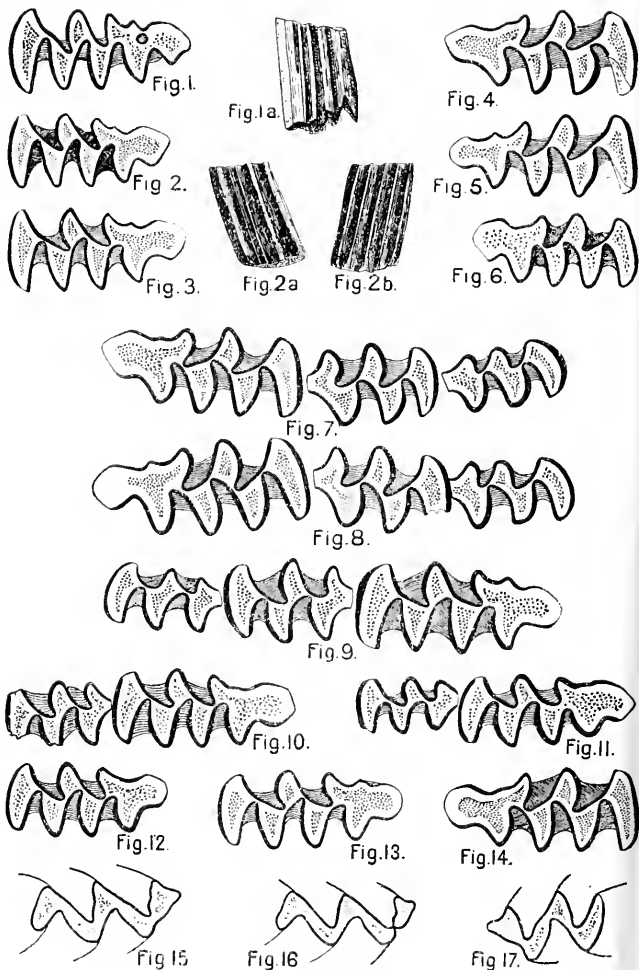


FIG. 101.—Cheek-teeth of *Mimomys savini* Hinton.  
(For explanation see opposite page.)

## EXPLANATION OF FIG. 101.

All the specimens figured are from the Upper Freshwater Bed at West Runton, and with the exception of the subjects of figs. 15, 16 and 17 all are referred to *Mimomys savini* Hinton.

- 1, 1a. Left  $m_1$ , young with enamel islet; crown and outer views (*B.M.*, No. 6968, *Savin Coll.*).
- 2, 2a, 2b. Left  $m_1$ , young adult, cement spaces closing; crown, outer, and inner views.
3. Left  $m_1$ , young adult, cement spaces closed; outer view, Pl. XIII, fig. 8 (*Mus. Pract. Geol.*, No. C.R. 959I).
4. Right  $m_1$ .
5. Right  $m_1$ , adult; outer view Pl. XIII, fig. 2 (*Mus. Pract. Geol.*, No. 959H).
6. Right  $m_1$  (*G. White*).
- 7, 8, and 9. Molars of three mandibular rami, adult; two right, one left (*Savin Coll.*, Nos. 821.2 (Peat), 820.1 and 821.1).
- 10, 11. Left  $m_1$  and  $m_2$  of two adult jaws (*Mus. Pract. Geol.*, Nos. C.R. 950 and XVII 5.2.15).
12. Left  $m_1$ , cement spaces closed, prism-fold very faint at grinding surface, stronger lower down (*Mus. Pract. Geol.*, No. 959F).
13. Left  $m_1$ , adult; outer view, Pl. XIII, fig. 3 (*Savin Coll.*).
14. Right  $m_1$ , adult; outer view, Pl. XIII, fig. 10 (*Savin Coll.*).
- 15, 16. *Mimomys* sp. Left  $m^1$ , two specimens slightly worn.
17. *Mimomys* sp. Right  $m^2$ , slightly worn.

in this species. In these young stages, the third outer angle is cleft externally by a prism-fold just as in *M. pliocænicus*; in front of the prism-fold is a deep re-entrant third outer valley, partly filled with cement. On the inner side of the tooth anteriorly there is a prominent fifth inner angle. So far as prism-fold, third outer valley, and fifth inner angle are concerned, these teeth are comparable with the second stage of wear in *M. pliocænicus* (cf. Fig. 99, 2); but whereas in the latter the cement spaces are closed below (Fig. 99, 2a), so that the initial operation in the development of the roots has already been performed, in these young teeth of *M. savini* the pulps are still active and growth would have to continue for some considerable time before closure of the cement spaces at the base of the crown could happen (Pl. XIII, figs. 7, 9). It is clearly apparent from these facts that the earlier stages in the development of the crown pattern have been accelerated in *M. savini* as compared with the more ancient *M. pliocænicus*.

The next stage of wear is shown by a left  $m_1$  (*B.M.*, No. 6968, *Savin Coll.*, West Runton; Fig. 101, 1, 1a) in which there is no sign of rooting, the pulp cavities and cement spaces being still widely open below. In this tooth, which has the persistent prism-fold characteristic of the species, the third outer valley is already reduced, its inner part being represented by an enamel islet and its outer portion by a groove which, in this specimen, extends from the present summit half-way to the base of the tooth. In pattern therefore the tooth is similar to a middle-aged  $m_1$  of *M. pliocænicus* (cf. Fig. 99, 4). In front of the external vestige

of the third outer valley there is another narrower, fainter, but long persistent groove, which I interpret as the last feeble vestige of a much more reduced fourth outer valley (see p. 379).

In slightly older specimens than the one just described we meet with the typical adult pattern of *M. savini*. Such examples (Fig. 101, 2) show that the enamel islet is worn out and disappears before the closure of the cement spaces is effected below; such a pattern is developed in *M. pliocenicus* only in the latest stages of wear when the individual is on the threshold of senility (cf. Fig. 100, 2). Still older examples of the  $m_1$  of *M. savini* (Pl. XIII, figs. 8, 10), with closed cement spaces, prove that the prism-fold is always persistent, and that the external vestige of the third outer valley is usually persistent throughout the crown in this species. The only change of pattern which takes place rather regularly in the closing stages of wear is that the fifth inner angle tends to become obsolete in old age (Fig. 101, 9).

Typically in *M. savini* the prism-fold is narrow and the external vestige of the third outer valley wide; in the crown view, the emargination formed by the latter structure usually makes a nearer approach to the middle line of the tooth than does that formed by the prism-fold. As in *M. pliocenicus* the relative antero-posterior widths of the two structures in question may vary considerably; in some specimens (Fig. 101, 13) the prism-fold becomes very wide at the expense of the valley vestige, and I have seen a few teeth in which the latter disappears before reaching the general base of the crown (Fig. 101, 1a). Occasionally the anterior costa of the prism-fold is but feebly developed, and in such cases it is sometimes difficult to distinguish jaws of this species from those of *M. intermedius* (Figs. 101, 12).

#### 4. † *Mimomys intermedius* Newton.

1881. *Arvicola (Erotomys) intermedius* Newton, Geol. Mag., [2], 8, p. 258; Vert. Forest Bed, 1882, p. 83, pl. xiii, figs. 3, 3a, and 3b (in part).  
 1890. *Microtus intermedius* Woodward and Sherborn, Catal. Brit. Foss. Vert., p. 366 (in part).  
 1902. *Mimomys intermedius* Forsyth Major, P.Z.S., 1902, 1, pp. 103-105 (in part).  
 1910. *Mimomys intermedius* Hinton, Proc. Geol. Assoc., 21, p. 491.  
 1914. *Microtomys intermedius* Méhely, Ann. Mus. Nat. Hungar., 12, p. 211.

*Type*.—Museum Practical Geology; an adult right mandibular ramus with all the teeth in place, collected by Clement Reid, F.R.S. Figured by Newton, Vert. Forest. Bed, 1882, Pl. xiii, figs. 3, 3a and 3b, and in the present work (Fig. 99, 12).

*Type horizon and locality*.—Upper Freshwater Bed, Cromerian, Late Pliocene; West Runton, Norfolk.

*Range in time and space*.—In Britain remains of *M. intermedius*

occur rarely in the "shelly sand" (? Weybourne Crag) at East Runton; but they are among the most abundant fossils of all three parts ("Lower Sandy," "Middle Peat," and upper "Monkey-Gravel") of the Upper Freshwater Bed at West Runton. On the continent, remains certainly referable to this species have been found only in the Upper Pliocene or earliest Pleistocene deposits of Hungary, at Beremend and at Nagy-Harsány.

*Characters*.—Size medium; jaws about as large as in the smaller species of *Arvicola* (e.g., *A. scherman*); lower tooth-row in adults from 7-8.5 mm. Distinguished from *M. savini* by the form of  $m_1$ , in which, in adults, the third outer angle is not complicated by a prism-fold.

Skull known only from fragments; temporal ridges well marked in adults but remaining widely separated in the interorbital region; outer wall of the infraorbital canal not essentially different from that of modern voles, the maxillary zygomatic process extending as far back, the jugal no further forwards than in *Arvicola*; ascending branches of premaxillaries extending slightly further backwards than the nasals; frontals perfectly coalesced in adults and sending a small process forwards between the posterior ends of the nasals. Palate (Pl. XIV, fig. 1) essentially as in *Arvicola*, quite unlike that of *Evotomys*; in its fore-part, lateral grooves and median spear-shaped ridge more or less prominently sculptured; point of spear-shaped ridge jutting in between the anterior palatine foramina from behind; the foramina extending backwards to a point somewhat in advance of the front edges of the tooth-rows; postero-lateral bridges complete and massive; post-palatal lateral pits deep; the intervening, or posterior median sloping septum, short, wide, and sometimes grooved; interpterygoid fossa square or slightly rounded anteriorly, very slightly indenting the palatal shelf in the middle line; maxillo-palatine suture extending forwards to a point nearly opposite the middle of  $m^2$ . In the figured specimen a longitudinal median fissure seems to suggest that occasionally, at all events, the median palatal suture persisted in adults.

Mandible in general appearance much like that of a small species of *Arvicola*; angular and coronoid processes well developed; lower incisor crossing from lingual to labial side of jaw between  $m_2$  and  $m_3$  (the former tooth wholly labial, the latter wholly lingual to the shaft of the incisor) and ascending the condylar process to a point about level with the dental foramen. Muscular impressions on outer surface sharply defined and indicating that the two divisions of the masseter medialis muscle agreed with those of *Arvicola* as regards their arrangement and insertion (Pl. XIV, fig. 2).

*Cheek-teeth*.—Enamel well differentiated; re-entrant folds partly filled with cement; teeth provided with roots in old age

as follows:  $m^1$  with two distinct roots, viz., a large anterior and a smaller posterior fang. An examination of about 100 specimens, all from West Runton and all with more or less well-grown roots, showed clearly that the anterior fang in this species is a compound structure consisting of the anterior fang proper and a coalesced, though still clearly recognizable, representative of the intermediate root which supports the second inner prism in this species as in *M. pliocenicus*; in the latter species, as described above, this intermediate fang is distinct from, and not fused with, the front root. Both  $m^2$  and  $m^3$  have normally two roots each in *M. intermedius*; among a very large number of examples of the  $m^2$  from West Runton, old enough to show more or less well-developed roots, I found that the anterior root varied, being sometimes considerably and sometimes only a little larger than the posterior fang. Two specimens (a left  $m^2$  from the lower sandy division of the Upper Freshwater Bed, and a left  $m^2$  from the overlying peaty stratum at West Runton, are remarkable for showing a third quite distinct but very small root, which supports the second inner prism; this exceptional third root is not the homologue of that normally occurring in the  $m^2$  of *M. pliocenicus*, for in that species the third root supports the inner part of the anterior loop (Fig. 100, 18a). In the lower jaw each tooth develops two roots, an anterior and a posterior.

In *enamel pattern* the adult cheek-teeth of *M. intermedius* are almost exactly like those of most species of *Arvicola*. In the upper jaw  $m^1$  and  $m^2$  agree with those of *Arvicola* and other normal voles, although when little worn or unworn (Fig. 101, 15-17) they show ephemeral complications which are of great interest because of their bearing upon some of the problems connected with the evolution of the Microtine dentition, a matter discussed above (p. 102). Although subject to a good deal of variation in small points, all the very numerous examples of the  $m^3$  from West Runton examined by me agree in one important respect; in this tooth the second inner fold persists as a normal fold throughout the crown instead of being subject to reduction by insulation as in *M. pliocenicus* (Fig. 99, 24-26). This character alone suffices to prove that *M. intermedius*, and its allies in the Upper Freshwater Bed, are not the descendants of *M. pliocenicus*, but must have arisen from some unknown species no doubt related to it but differing in the less reduced form of the  $m^3$ .

It must be understood that the foregoing description of the skull and the maxillary dentition is based upon the remains of all three species (*M. intermedius*, *M. savini*, and *M. majori*) found associated in the Upper Freshwater Bed at West Runton. With the fragmentary though abundant material at present available no means of distinguishing between these species other than by the characters afforded by the  $m_1$  have as yet been discovered.

In adult stages of wear the lower cheek-teeth agree closely



with those of *Arvicola* in pattern (Fig. 102);  $m_1$  has a posterior loop, followed by three substantially closed triangles, and is completed by an anterior loop of complex structure; there are three outer and five inner salient angles, two outer and four inner re-entrant folds; the third outer salient angle is simple and not complicated (in adults) by a prism-fold; the first outer infold may be rather shallow leaving the first pair of triangles more or less confluent with each other;  $m_2$  and  $m_3$  are of the normal Microtine form; the first outer fold in  $m_3$  is sometimes shallow, leaving the first and second triangles partly confluent; the third outer salient angle is always well developed in  $m_3$ .

It is interesting to trace the steps by which the adult simplified pattern of  $m_1$  is developed gradually from the tubercular cap of the unworn tooth. Although several hundreds of specimens of this tooth have been carefully examined, not one has been found to show the tooth in a quite unworn condition; such a specimen would be of the greatest interest. The earliest stage available is afforded by a young left  $m_1$  in Mr. Savin's private collection from West Runton. In this tooth (Fig. 99, 7) the dentinal spaces are all widely confluent with each other; the pulp cavities and the cement spaces are widely open below, and the tooth would obviously have to grow for a long time before closure of the cement spaces could begin. At its present surface the third outer angle bears a weak "prism-fold" (the anterior costa of this fold being hardly indicated), which dies out rapidly when traced downwards upon the outer side of the crown. In front of it is a wide and deep (transversely) third outer valley containing cement; this also dies out below. Other elements of the region corresponding to the adult anterior loop are a large fifth inner angle, a small fourth outer angle and a small sixth inner angle; the two last-named structures are at present unworn tubercles, separated from each other externally by a shallow oblique sulcus representing a reduced fourth outer valley; another shallow sulcus, the fifth inner valley, separates the tubercular sixth inner angle from the large fifth inner angle. All these unusual features would vanish quickly with further wear, and, as the open pulp cavities below show, this tooth, in adult life, would have become precisely like any other normal example of the  $m_1$  of *M. intermedius*. A right  $m_1$  (Fig. 99, 8), also in Mr. Savin's collection, is slightly more worn; the weak prism-fold and intact third outer valley are still to be seen; the tubercles representing the fourth outer and sixth inner angles have been worn away and those structures are now blended in the anterior loop. In the left  $m_1$  described above all trace of a fourth outer valley would have been lost had it suffered as much detrition as the present tooth has done; but in this there is in front of the third outer valley upon the outer side of the crown a persistent vertical groove, which on the grinding surface appears as a small curl in the enamel of the outer border of the anterior loop; this groove is probably to be regarded as a weak vestige of

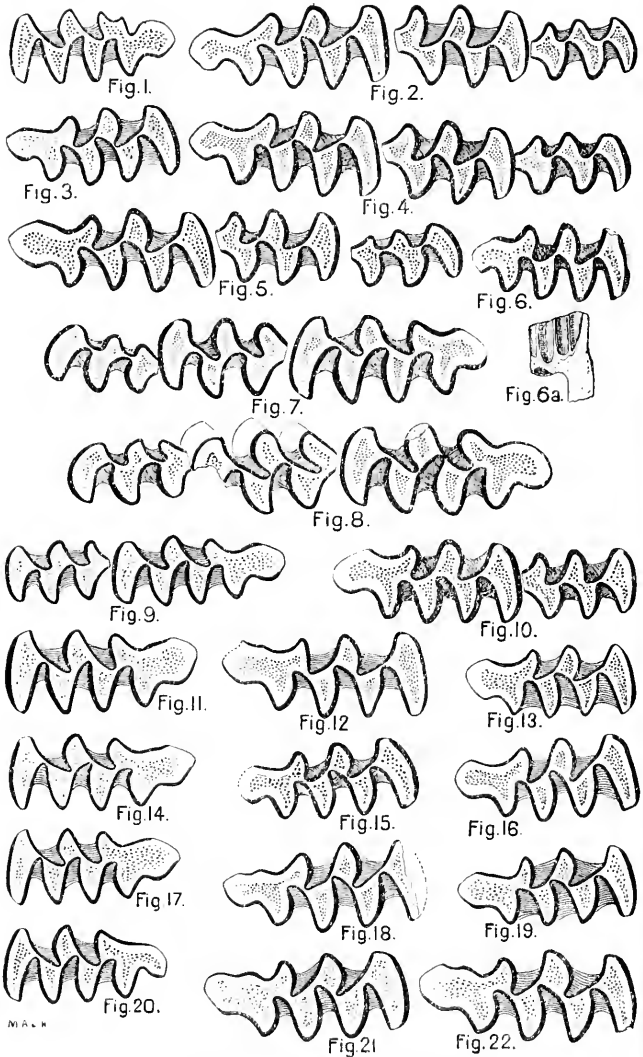


FIG. 102.—Cheek-teeth of *Minomys intermedius* Newton.

(For explanation see opposite page.)

## EXPLANATION OF FIG. 102.

All the specimens figured are from the Upper Freshwater Bed at West Runtton, and with the exception of the subjects of figs. 18, 21 and 22 all are referred to *Mimomys intermedius* Newton.

1. Left  $m_1$ , very young, with prism-fold and third outer valley intact (*Mus. Pract. Geol.*, No. 959*G*).
2. Molars of an adult right mandibular ramus (*Savin Coll.*, No. 827.1).
3. Right  $m_1$ , with well-developed roots (*Mus. Pract. Geol.*, No. 959*E*).
- 4, 5. Molars of two adult right mandibular rami (*Savin Coll.*, Nos. 825.2 and 826.1).
- 6, 6a. Right  $m_1$ , old (*Mus. Pract. Geol.*, No. C.R. 959*L*).
- 7, 8. Molars of two adult left mandibular rami (*Savin Coll.*, Nos. 829 and 828.1).
9. Left  $m_1$  and  $m_2$ , adult (*G. White*).
10. Right  $m_1$  and  $m_2$ , adult (*G. White*).
11. Left  $m_1$ , adult (*Mus. Pract. Geol.*, No. C.R. 959).
12. Right  $m_1$ , adult (*Savin Coll.*, No. 825.1).
13. Right  $m_1$ , adult; "Monkey-gravel," West Runtton.
14. Left  $m_1$ , adult (*Mus. Pract. Geol.*, No. C.R. 959*C*).
15. Right  $m_1$ , old, with long roots.
16. Right  $m_1$ , adult (*Mus. Pract. Geol.*, No. C.R. 959*D*).
17. Left  $m_1$ , cement spaces just closed (*Mus. Pract. Geol.*, No. C.R. 959*D*).
18. *M. majori*? Right  $m_1$ , adult, with vestige of fourth outer valley (*G. White*).
19. Right  $m_1$ , cement spaces just closed (*Mus. Pract. Geol.*, No. C.R. 959*B*).
20. Left  $m_1$ , adult (*G. White*).
21. *M. majori*? Right  $m_1$ , adult (*Savin Coll.*, No. 828.2).
22. *M. majori*? Right  $m_1$ , adult (*Savin Coll.*, No. 645.6).

the fourth outer valley (cf. p. 379); it is a feature which, although frequently absent, is seen in many adult teeth of *M. intermedius*. Another right  $m_1$  in Mr. Savin's collection (Fig. 99, 9) is imperfect but important. Judging from its general appearance it probably belonged to a slightly younger animal than did the tooth just described; but notwithstanding this it shows a slightly more advanced stage in the reduction of the primitive crown, and it thus affords an illustration of that variability which is so characteristic of vanishing structures. In it the prism-fold is large but weak, and the inner part of the third outer valley is now undergoing insulation. A left  $m_1$  (Fig. 99, 10) and a similar specimen figured by Forsyth Major (P.Z.S., 1902, 1, p. 103, text-fig. 13, fig. 1) carry the story a stage further, since in these the prism-fold is no longer distinct, and all that remains of the third outer valley is an ephemeral enamel islet. The open pulp cavities of all the teeth described above show the pattern of adult *M. intermedius*. Lastly, a specimen (Fig. 99.11.11a) is figured for the purpose of showing that as in *M. savini* the vanishing elements, although essentially not different from those found in the older species *M. pliocenicus*, have now become so ephemeral that the adult or reduced pattern is brought to the grinding surface of the tooth by the wear of the crown before the cement spaces become closed

below, and therefore before the growth of the crown can be said to be completed.

5. † **Mimomys pusillus** Méhely.

1914. *Microtomys pusillus* Méhely, Ann. Mus. Nat. Hungar., 12, p. 214.

*Lectotype*.—No type being indicated in the original description I now select the young left mandibular ramus, of which the cheek-teeth are figured by Méhely in his Taf. vii, fig. 8, as the lectotype of this species.

*Type horizon and locality*.—Bone breccia of the Somlyó-Berg, Püspökfürdő, Hungary; Late Pliocene ("erste interglaziale Periode" of Méhely).

*Range in time and space*.—Known only from the type horizon and locality.

*Characters*.—Closely resembling *M. intermedius* in the enamel pattern of its molars, but distinguished by its more reduced  $m^3$  and its smaller size, which does not exceed that of *Microtus arvalis*.

Skull known only from a palatal fragment, figured by Méhely (*op. cit.*, Taf. vii, fig. 1). In this the posterior-lateral bridges are situated a little further forwards than in *M. intermedius*, and the posterior median sloping septum is distinctly longer and rather narrower. The maxillo-palatine suture extends forwards to a point opposite the fore-part of  $m^2$  instead of ending opposite the middle of that tooth, and there is no trace of a median suture.

*Cheek-teeth*.—Re-entrant folds partly filled with cement;  $m^1$  and  $m^2$  of normal pattern;  $m^1$  with two roots, of which the anterior is the larger and consists of two completely fused though clearly recognizable elements;  $m^3$  with three outer and three inner salient angles, the third inner angle much less developed than in *M. intermedius*; outer infolds shallower than in the latter species, the first triangle more or less confluent with the anterior loop as in *Alticola*, etc., though substantially shut off behind from the posterior triangles, which are more or less broadly confluent with each other and with the posterior loop. In adult stages of wear typical examples of the  $m_1$  are exactly like adult specimens of the  $m_1$  of *M. intermedius* in form. In young stages the third outer salient angle usually bears a well-marked prism-fold; in front of this, in one example figured by Méhely (Taf. vii, fig. 13), there is an ephemeral enamel islet, showing that the third outer valley is reduced by insulation of its inner portion exactly as in *M. intermedius*. The "prism-fold" usually disappears completely before the tooth shows any sign of rooting; as Méhely's fig. 12 indicates it occasionally persists in specimens with well-developed roots, but it always dies out at some distance above the base of the crown, instead of being perfectly persistent as in

*M. savini*;  $m_2$  and  $m_3$  are of normal form, although the inner and outer triangles of the former tooth are more nearly opposed and less alternating than is usual in any of the species occurring at West Runton.

*Measurements* (according to Méhely).—Upper tooth-row 5.3–5.7 mm. ( $m^1$  2.1–2.3;  $m^2$  1.7–1.8;  $m^3$  1.5–1.6). Lower tooth-row 5.3–5.6 juv., 5.5–6.1 ad. ( $m_1$  2.5–2.8;  $m_2$  1.5–1.8;  $m_3$  1.3–1.5).

In two lower jaws from the same deposit the teeth are larger ( $m_1$  measuring 3 and 3.1,  $m_2$  1.9 and 2 mm.) although precisely like those of *M. pusillus* in form.

*Remarks*.—This species, known only to me by Méhely's description and admirable figures, seems to be most closely related to *M. intermedius* and *M. savini* of the "Upper Freshwater Bed" (Cromerian). In my opinion its palatal structure, more reduced  $m^3$ , and smaller size indicate a greater degree of specialization than that attained by any of the species so far discovered in the British Forest-Bed series.

In the synonymy of *M. pusillus* Méhely cites with doubt the tooth figured by Newton (Vert. Forest-Bed, Pl. xiii, fig. 8), who erroneously stated it to be from West Runton, although it came from the Weybourne Crag of Trimmingham. Méhely, however, suspects it to be referable to his *M. petenyii*, an opinion which I have confirmed above (see under *M. reidi*). Méhely also refers the subject of Forsyth Major's fig. 22 to *M. pusillus*, but a study of that specimen, and much other material from West Runton, shows it to belong to another species, *M. savini*.

#### 6. † *Mimomys newtoni* Forsyth Major.

1902. *Mimomys newtoni* Forsyth Major, P.Z.S., 1902, 1, p. 103, text-fig. 13, fig. 7; text-fig. 14, fig. 10; Hinton, Proc. Geol. Assoc., 21, 1910, p. 491.

1910. *Microtus (Mimomys) intermedius* Newton, Bull. Soc. Belge Géol., Proc. Verb., 24, p. 232.

1914. *Microtomys newtoni* Méhely, Ann. Mus. Nat. Hungar., 12, p. 223.

*Type*.—B.M., No. M. 6967a; Savin Collection; a left  $m_1$ , with the cement spaces closed below.

*Type horizon and locality*.—Cromerian (Forest Bed or Weybourne Crag) of East Runton, Norfolk.

*Range in time and space*.—Late Pliocene. In Britain known from Norfolk, where its remains have been found in deposits ranging in age between the Norwich Crag and the Lower Freshwater Bed (Cromerian). In Belgium it has been found in the Late Pliocene of Tegelen-sur-Meuse; in Hungary in deposits of similar age at Beremend and Nagy-Harsány.

*Characters*.—Size small, about as in *Microtus arvalis*; length of lower molar series about 5.5 mm., not exceeding 6 mm. Cheek-teeth provided with two roots each in adults; re-entrant folds partly filled with cement. Enamel pattern of  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  normal;  $m^3$  with three outer and three inner salient angles, its

second inner valley persisting as in *M. intermedius*, not reduced by insulation of its internal portion as in *M. pliocenicus*; posterior salient angle on each side small.  $m_1$  in adults with three substantially closed triangles, four outer and five inner salient angles; its third outer valley not reduced by the insulation of its internal portion, but persisting as in *M. majori*; a vestigial fourth outer valley often present; third outer salient angle without a "prism-fold"; fourth outer and fifth inner salient angles becoming obsolete in later stages of wear. Lower incisor wholly lingual to the roots of  $m_2$ .

The foregoing diagnosis may be supplemented usefully by the following notes on the scanty remains by which the species is at present represented in collections. Although Forsyth Major (*op. cit.*, p. 105) records the species as occurring in the Norwich Crag, I have been unable to find any remains from that deposit definitely assignable to *M. newtoni* in the British Museum, the Museum of Practical Geology, Norwich Museum, or any other collection to which I have had access.<sup>1</sup> The only British remains known to me were obtained at East Runton, Norfolk, where, however, they occur apparently in two quite distinct deposits. Those in the British Museum, including the type of the species, were collected by Mr. Savin from a bed of "shelly crag 30 yards from the cliff to the north of the gangway" at East Runton; this deposit is usually correlated with the Weybourne Crag. In the Museum of Practical Geology is a small collection of vole remains obtained by the late Mr. Clement Reid, F.R.S., from a bed of "clay-gravel" at East Runton. Mr. Reid described<sup>2</sup> this bed as a laminated clay, belonging to the middle or estuarine division of the Forest Bed series, containing numerous "pebbles" of clay derived from the greatly denuded "Lower Freshwater Bed," and it is from some of these "clay pebbles" that the vole remains in question were collected. With the exception of two fragmentary teeth ( $m_1$ ) of *M. pliocenicus*, which appear to have been derived from a still older deposit than that represented by the "clay pebbles," all the specimens in this small series are referable to *M. newtoni*.

Three of the teeth from East Runton are represented in Figs 99. and 103. In a young right  $m_1$  (Fig. 103), with the pulp-cavities still open below, the outer re-entrant folds are all shallow transversely, so that the dentinal spaces are confluent with each other; but these folds, particularly the third one, become deeper in lower levels of the crown, so that in adult stages of wear the triangles would be substantially (or rather tightly) closed as in the adult tooth here figured (Fig. 99, 19). In

<sup>1</sup> Since this was written Mr. J. B. Johnson has collected some vole remains from the Norwich Crag at Bramerton; among his specimens is a much worn right  $m_1$  of small size which may be referred to *M. newtoni*.

<sup>2</sup> REID, "Geology of the country round Cromer." Mem. Geol. Surv. 1882, pp. 27-28 and Pliocene Deposits of Britain, 1890, p. 157.

the young tooth there is a small fourth outer angle and in front of it a rather wide and shallow fourth outer valley. On the side of the crown this valley becomes rapidly narrower and shallower as it descends, until it is represented by a mere groove, which may or may not persist in the adult tooth. In the type (Forsyth Major, *op. cit.*, figs. 7 and 10a) this groove is represented by a scar impressed upon a surface of bare dentine. Forsyth Major has figured a right  $m_1$  (*op. cit.*, figs. 23 and 16); which he doubtfully refers to *M. newtoni*; I have no doubt that this specimen should be referred to this species, and would remark that the scale drawn beneath Forsyth Major's figure is too long.

Méhely has figured (*op. cit.*, Taf. viii) two jaws from the Hungarian Pliocene, one (Fig. 1) from Nagy-Harsány, the other (Figs. 2 and 3) from Beremend. In these specimens the enamel pattern of the  $m_1$  agrees closely with the English examples of *M. newtoni*. The only difference is that no cement is shown in

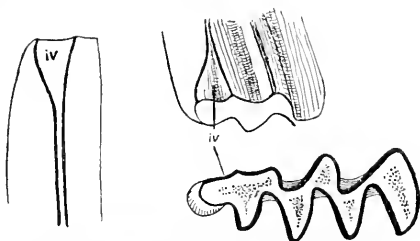


FIG. 103.—*Mimomys newtoni* Forsyth Major.

Right  $m_1$  young; crown and lateral views; "Clay-gravel," East Runton.

the infolds; but this circumstance is explained by Méhely (p. 221), who says that cement was originally present, but, unaware of its importance when he began his researches, he removed it when cleaning the figured specimens.

Newton has described two very important specimens from the Upper Pliocene brickearth of Tegelen-sur-Meuse, which have since been presented to the British Museum by Mr. and Mrs. Clement Reid. These were referred by Newton to *M. intermedius*, but after a careful study of the matter I have no doubt that they should be referred to the present species. One of these teeth is a very young left  $m_1$ , lacking the posterior loop, which has been broken off, and having the cement spaces and pulp-cavities open below (Fig. 99, 18, 18a). In this the third outer angle has no "prism-fold," while the third outer valley is filled with cement and is perfectly persistent. In front of the small fourth outer angle is a fourth outer valley; with a little more wear the inner part of this valley would be converted into a quite ephemeral enamel "islet"; below the point of insulation a faint shallow vertical groove,

impressed upon a surface of bare dentine, remains as an external vestige of the fourth outer valley. The fifth inner angle is prominent at the present grinding surface, but it would become nearly obsolete with prolonged wear. The base of the crown shows that in the adult the three triangles, widely confluent in the present stage of wear, would be almost tightly closed and that the adult pattern of this tooth would be much as in the teeth of *M. newtoni* described above. The small size of the specimen also tends to confirm my opinion.

The second important tooth from Tegelen is a right  $m^3$ , the only example of the  $m^3$  of this species known to me. Having regard to its small size, and to the character of the  $m_1$  found with it, I think it can be safely referred to *M. newtoni*. This specimen (Fig. 99, 23) has two roots; its postero-internal valley is persistent, as in *M. intermedius* and the other species occurring in the Upper Freshwater Bed at West Runton; on the other hand, the third inner and third outer angles are much more reduced than in the West Runton forms.

Of the other cheek-teeth, I have seen examples from East Runton and also a left  $m^2$  from Tegelen, mentioned by Newton. In addition to these, two examples of the  $m_2$  are figured by Méhely. These teeth offer no character of importance beyond what is mentioned in the diagnosis above.

#### 7. † *Mimomys majori* Hinton.

1902. *Mimomys intermedius*? Forsyth Major, P.Z.S., 1902, 1, p. 106, text-fig. 15, fig. 26, text-fig. 14, fig. 13

1910. *Mimomys majori* Hinton, Proc. Geol. Assoc., 21, p. 491.

*Type*.—B.M., No. M. 6968e; Savin Collection; an adult right  $m_1$  figured by Forsyth Major (*loc. cit. supra*).

*Type horizon and locality*.—Upper Freshwater Bed (Cromerian) at West Runton, Norfolk.

*Range in time and space*.—Remains of this species have been found in the "shelly-sand" or crag of East Runton (Weybourne Crag or Lower Cromerian). They occur abundantly in the lower sandy portion of the Upper Freshwater Bed at West Runton and are found also in the overlying peaty portion of the same deposit. From the "Monkey Gravel," or stratum above the peat at West Runton, the form in which the "prism-fold" of  $m_1$  is obsolete is known.

*Characters*.—Size and general character of the cheek-teeth as in *M. intermedius* and *M. savini*; but  $m_1$  retains the third outer valley as a deep re-entrant fold, which persists throughout life instead of being reduced by insulation and more or less completely obliterated in early youth. "Prism-fold" of  $m_1$  variable, strongly developed and long persistent in some specimens, weak and relatively ephemeral in others; occasionally absent altogether even in the youngest stages of wear.



Almost all stages of growth are represented in the long series of examples of the  $m_1$  now before me. As in other species the young teeth are of especial importance, for they throw light upon the significance of certain characters which, though minute, are very commonly present in the adult  $m_1$  of this and other species. In this connection, and also in order to show what range of variation is seen in the  $m_1$  of this species, attention is called in the following notes to the more interesting specimens so far examined.

In a slightly worn  $m_1$ , from the "peat" at West Runton

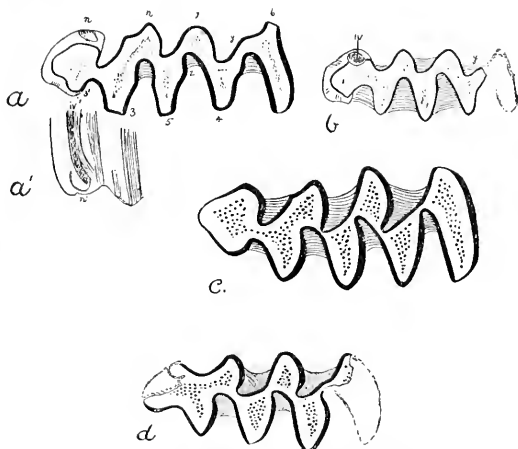


FIG. 104.—Crown views of  $m_1$  of *Mimomys majori* Hinton and *M. cantianus* Hinton.

- a. *M. majori*. Right  $m_1$  very young; a' anterior part of outer surface.  
 b. *M. majori*. Right  $m_1$  very young.  
 c. *M. majori*. Right  $m_1$  adult.  
 a, b, and c, all from the Upper Freshwater Bed of West Runton.  
 d. *M. cantianus*. Right  $m_1$  adult (type of species); High Terrace of the Thames, near Greenhithe, Kent.

(Fig. 104a), the grinding surface displays the usual juvenile confluency of the dentinal spaces and several of the ephemeral peculiarities in the form of the posterior loop and salient angles discussed above at pp. 110-115. The "prism-fold" is extremely weak; but the third outer valley is represented by a deep and perfectly persistent re-entrant fold. On the outer side of the tooth, just in front of this fold and at the level of the present grinding surface, there is a minute tubercle ( $n'$ ) and immediately below this tubercle there begins a shallow but well-defined and quite persistent vertical groove ( $iv'$ ) which, as the next

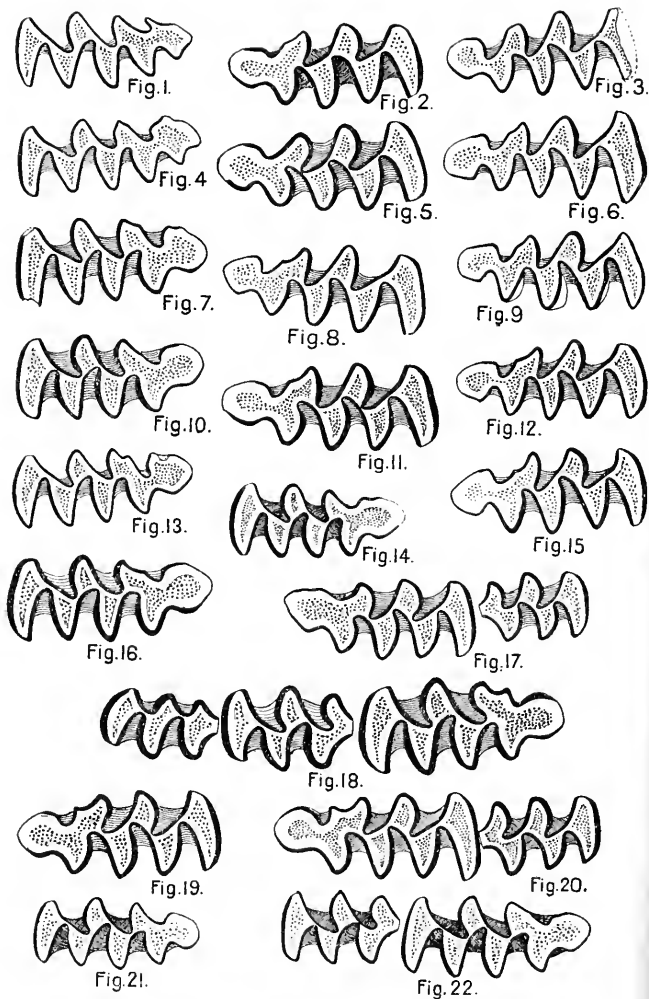


FIG. 105.—Cheek-teeth of *Mimomys majori* Hinton.

(For explanation see opposite page, and for lateral views see Pl. XV.)

## EXPLANATION OF FIG. 105.

All the specimens figured are from the Upper Freshwater Bed at West Runton, and all are referred to *Mimomys majori* Hinton.

1. Left  $m_1$  young; outer view, Pl. XV, fig. 12; basal pattern like fig. 14 below.
2. Right  $m_1$  adult; Peat.
3. Right  $m_1$  cement spaces closing; outer view, Pl. XV, fig. 6 (*Savin Coll., No. 9.5.19.2*).
4. Left  $m_1$  young, cement spaces not yet closed; basal pattern like fig. 5; outer view, Pl. XV, fig. 9 (*Savin Coll., No. 9.4.28.1*).
5. Right  $m_1$  adult (*Savin Coll., No. 824.1*).
6. Right  $m_1$  young; outer view, Pl. XV, fig. 3 (*Savin Coll., No. 9.4.28.2*).
7. Left  $m_1$  adult; outer view, Pl. XV, fig. 2 (*Savin Coll., No. 9.5.18.1*).
8. Right  $m_1$ , cement spaces closing; outer view, Pl. XV, fig. 4 (*Savin Coll., No. 9.4.30.1*).
9. Right  $m_1$  young; outer view, Pl. XV, fig. 11 (*Savin Coll., No. 9.5.21.1*).
10. Left  $m_1$  young adult (*Savin Coll., No. 823.1*).
11. Right  $m_1$  adult; outer view, Pl. XV, fig. 7 (*Savin Coll., No. 9.4.22.2*).
12. Right  $m_1$  cement spaces closing; outer view, Pl. XV, fig. 10 (*Savin Coll., No. 9.4.22.1*).
13. Left  $m_1$  young, pulp cavities open, basal pattern like fig. 14 below; outer view, Pl. XV, fig. 8 (*Savin Coll., No. 9.5.19.1*).
14. Left  $m_1$  adult, short roots; "Monkey Gravel," West Runton (*G. White*).
15. Right  $m_1$  young; outer view, Pl. XV, fig. 5 (*Savin Coll., No. 9.4.30.2*).
16. Left  $m_1$  adult (*Savin Coll., No. 822.2*).
17. Right  $m_1$  and  $m_2$  adult (*Mus. Pract. Geol., No. C.R. 950C*).
18. Molars of a left mandibular ramus (*B.M., No. M. 6966r, Savin Coll.*).
19. Right  $m_1$  adult (*Savin Coll., No. 822.1*).
20. Right  $m_1$  and  $m_2$  adult (*Savin Coll., No. 823.2*).
21. Left  $m_1$  adult; Peat (*G. White*).
22. Left  $m_1$  and  $m_2$  (*G. White*).

specimen proves, is to be regarded as the external vestige of a fourth outer valley.

Another and probably slightly younger  $m_1$  from the West Runton peat (Fig. 104*b* and Pl. XV, fig. 1) differs from the tooth just described in lacking any trace of the "prism-fold." In this stage of wear the third outer valley is not deeper transversely than are the first and second outer folds behind it; the base of the tooth shows that although the two latter folds would become deeper in adult stages of wear there would be no change in the depth of the third fold. The tubercular cap of the anterior loop is not yet quite worn off, and a minute and ephemeral "fourth outer prism" can be seen. In front of this there is a conspicuous enamel ring or "islet" (iv) placed obliquely on the outer edge of the anterior loop. The lower or outer margin of this islet is formed by a convex swelling answering to the minute tubercle seen in the young tooth described above; a little below the point where this tubercle subsides a shallow well-defined vertical groove, exactly like that seen in the first specimen, commences and persists throughout the lower levels of the tooth (Pl. XV, fig. 1). The "islet" undoubtedly represents

the internal part of a highly reduced fourth outer valley, and the vertical groove commencing below it is in my opinion to be interpreted as the external vestige of this valley; the islet and groove are fully comparable with, though much smaller than, the corresponding structures that result from the reduction of the third outer valley in *M. pliocænicus* and such later species as *M. savini* and *M. intermedius*.

*Variation in the adult  $m_1$ .*—The name *M. majori* is here used for all those Cromerian forms in which the third outer valley of the  $m_1$  is not reduced by insulation of its internal portion. In the type specimen (Forsyth Major, *op. cit.*, fig. 26) this fold is deep, the fourth outer prism is rather large, the fifth inner angle is obsolete, and the three triangles following the posterior loop are substantially closed. There is no "prism-fold" and no trace of an external vestige of a fourth outer valley. The specimen has two large roots, which are interesting inasmuch as they afford evidence of the method by which rooted molars in Microtinæ become transformed into persistently growing or rootless ones. The cement spaces on the inner side of the tooth (*op. cit.*, fig. 13b) are not completely closed below by a lip of enamel as in *M. pliocænicus*, but are weakly continued on the bare dentine of the roots as faint vertical grooves, and this downward continuation of the grooves is the first step towards a downward extension of the enamel over the surface of each fang.

Fig. 105 shows the principal variations which occur in the Upper Freshwater Bed at West Runton. In these teeth variation is seen in the development and persistence of the "prism-fold," in the size of the fourth outer and fifth inner salient angles, and in the presence or absence of an external vestige of the fourth outer valley.

Two forms call for a little notice. In one, represented by the second young specimen described above (Fig. 104b), by a right ramus from the lower sandy division of the Upper Freshwater Bed (M.P.G., No. C.R. 950c; fig. 105, 17), by a left  $m_1$  from the "Monkey Gravel" (Fig. 105, 14), and by other specimens from the intervening "peat" at West Runton, the  $m_1$  is characterized by the rather shallow third outer valley, the absence of a "prism-fold," the presence of a persistent external vestige of the fourth outer valley, and by the length of the anterior loop.

The second variety is of considerable interest, the  $m_1$  being characterized by the presence of a large persistent "prism-fold" of which the anterior costa is frequently strongly developed (Fig. 105, 18-20). The third outer valley is quite deep and persistent, although the great development of the "prism-fold" makes it at first sight appear small. The fourth outer salient angle is much reduced, and there may or may not be an external vestige of the fourth outer valley. The fifth inner angle is nearly obsolete. Teeth of this form have hitherto only been found in the lower sandy part of the Upper Freshwater Bed at West Runton. This

variety stands in an exactly similar relationship to typical *M. majori* as does *M. savini* to *M. intermedius*.

In the Savin Collection (B.M.) there are several specimens of the  $m_1$ , from the shelly sand or crag of East Runton, which having the third outer valley unreduced and persistent may be referred to this species. In these teeth the "prism-fold" is either very faintly developed or obsolete.

*Remarks.*—It is not improbable that the remains now referred to *M. majori* represent more than one species. The unparalleled richness of the Microtine fauna of the Upper Freshwater Bed and the fragmentary condition of most of the specimens find a probable explanation in what is known of the history of the Cromerian deposits. These seem to have been laid down in the fluctuating estuary of a large river, which apparently included representatives of the Rhine and Thames as well as of other streams flowing into the area that is now the southern portion of the North Sea. The estuarine deposits of that ancient river thus contain in all probability the sweepings of a very large part of Western and Central Europe. It is therefore not necessary to suppose that all the Cromerian species inhabited Britain at one and the same moment; some of them, perhaps the majority, may never have lived here at all. It is to the future discovery of inland deposits of Cromerian age, deposits free from contamination by streams of continental origin, that we must look for information as to what species actually constituted the late Pliocene Microtine fauna of Britain, and for data that will enable us to appreciate the real systematic status of the forms now recognized.

#### 8. † *Mimomys cantianus* Hinton.

1902. *Microtus intermedius* Hinton and White, Proc. Geol. Assoc., **17**, p. 414.

1910. *Mimomys cantianus* Hinton, Proc. Geol. Assoc., **21**, p. 491; Duckworth, "Prehistoric Man," Cambridge Manuals Science and Lit., p. 88, 1912.

*Type.*—A right  $m_1$ ; collected by Mr. Gilbert White (Figs. 99, 21; 104b; and Pl. XIII, figs. 11, 11a).

*Type horizon and locality.*—Early Pleistocene; High Terrace Drift of the Thames, Ingress Vale, near Greenhithe, Kent.

*Range in time and space.*—Known only from the type horizon and locality.

*Characters.*—Imperfectly known, the species being represented by only a few detached teeth. Cheek-teeth developing roots very late in life—later apparently than in the species found in the Upper Freshwater Bed at West Runton. Re-entrant folds partly filled with cement; enamel differentiated as in other species of *Mimomys*, thicker on convex, thinner on concave borders of salient angles;  $m_1$  with three outer and four inner salient angles, and with

a reduced pair of salient angles (fourth outer and fifth inner) forming the fore-part of the anterior loop; general form of the tooth rather like that of *M. newtoni* or some forms of *M. majori* in late stages of wear, the third outer fold rather deep and not apparently reduced by insulation;  $m^3$  with a persistent second inner valley and in general form agreeing closely with those from West Runton.

Although the patterns of the few cheek-teeth which have been obtained from the High Terrace Drift are such as characterize adult rather than youngish stages of wear, little progress has been made with the development of their roots. In the two mandibular teeth ( $m_1$ ) the cement spaces are only just beginning to close below; in the two maxillary teeth before me ( $m^1$  and  $m^3$ ) they remain entirely open. This circumstance and the character of the  $m_1$  would appear to indicate that the High Terrace species is most nearly related to *M. majori* and *M. newtoni*, differing from the latter in its larger size, and from both the species mentioned by the more tardy development of the roots to its molars.

*Remarks.*—The few teeth upon which this species is based were all obtained from a small pit, in the High Terrace gravel of the Thames, which was opened many years ago at Ingress Vale, near Greenhithe, Kent. These scanty remains are of great importance, since they prove that the genus lingered on in southern England until a comparatively late moment. Until recently the majority of British geologists have accepted and maintained the view that the High Terrace of the Thames is a "Post-Glacial" deposit, in the sense that it was formed after the culmination of the glacial period in south-eastern England. The argument upon which this view is based was formulated before anything of the palæontology of the High Terrace was known, and before a reasonable and coherent theory of the evolution of the English river system had been developed. The High Terrace fauna proves, however, in the clearest possible way that there was no break in the continuity of the terrestrial life of the region between Upper Pliocene and High Terrace times. Numerous Pliocene relicts survived in south-eastern England in the High Terrace period, that is to say to a date later than that of their disappearance elsewhere. Among the mammals so surviving may be mentioned, in addition to *M. cantianus*, *Trogotherium cuvieri*, *Sus* sp. n., *Hippopotamus*, *Elephas antiquus*, and *Rhinoceros leptorhinus* Cuv. (= *R. megarhinus* de Christol); among the Mollusca *Neritina grateloupiana*, a Miocene species. Nor is this all. A monkey, *Macaca*, has been determined in the uppermost part of the Cromerian Upper Freshwater Bed (a stratum known in consequence as the "Monkey Gravel"), and this genus has been found, associated with *Hippopotamus*, *Elephas antiquus* and *Rhinoceros leptorhinus* Cuv., in the early Middle Terrace deposit at Grays Thurrock, Essex, *i.e.*, in a deposit

considerably newer than the High Terrace. These mammalia are such that we cannot imagine them to have survived the rigours of glaciation in this region; and had they ever been driven out of this country in consequence of climatic changes, or from any other cause, they would never have returned to it in High Terrace or early Middle Terrace times.<sup>1</sup>

Genus: **14. ARVICOLA** Lacepède.

1799. *Arvicola* Lacepède, Tab. des Mammifères, p. 10.
1836. *Hemiotomys* de Sélvs-Longchamps, Essai monographique sur les Campagnols des environs de Liège, p. 7 (in part; "section" based upon "*Arvicola fulvus*" [= *Microtus arvalis*] and "*Arvicola amphibius*" [= *A. terrestris*]).
1857. *Paludicola* Blasius, Säugethiere Deutschlands, p. 333 (in part); subgenus of "*Arvicola*" [= *Microtus*] based upon "*Arvicola amphibius*" [= *A. scherman*], "*Arvicola*" [= *Microtus*] *nivalis*, and "*Arvicola*" [= *Microtus*] *ratticeps*. Preoccupied by *Paludicola* Wagner, 1830 (Amphibia).
1867. *Ochetomys* Fitzinger, Sitzungsber. Math.-Naturwiss. A. k. Akad. Wissensch., Wien, 56, p. 47; based primarily upon the water rats of Europe.
1867. *Praticola* Fatio, Les Campagnols du Bassin du Léman, p. 36 (in part); subgenus based upon *Arvicola* "*amphibius*" [= *A. scherman*], [*Microtus*] *nivalis*, and [*M.*] *arvalis*, [*M.*] *ratticeps* and [*M.*] "*campestris*" [= *M. arvalis*]. Preoccupied by *Praticola* Swainson, 1837 (Aves).
1883. *Arvicola* Lataste, Le Naturaliste, 2, p. 349 (subgenus of *Microtus*); Miller, N. Amer. Fauna, No. 12, 1896, p. 66.
1908. *Arvicola* Miller, Ann. Mag. N.H., [8], 1, p. 195 (genus); Trouessart Faune Mamm. d'Europe, 1910, p. 193; Miller, Catal. Mamm. W. Europe, 1912, p. 723.

*Genotype*.—*Mus amphibius* Linnæus.

*Range*.—Widely distributed in the Palæarctic Region, ranging from the Mediterranean coast of Europe, Asia Minor, Palestine and the northern base of the Himalayas, northwards to the Arctic coasts of Europe and Asia, and from Great Britain eastwards to the Amur River at least.

*Characters*.—General form nearly as in *Microtus*, but size always large (in recent species hind-foot 22–35 mm.; condylo-basal length 32–44 mm.); tail about half the length of head and body or more; flank glands present in adult males and sometimes in both sexes; plantar tubercles more or less reduced.

Skull strongly built, the anterior portions of the temporal muscles powerfully developed, producing in the adults of all living species, and of fossil species from early Middle Terrace times onwards, well-marked post-orbital squamosal crests and a more or less salient linear median interorbital crest. Pterygoid fossæ

<sup>1</sup> See HINTON, Rivers and Lakes, 1924, pp. 49–81. Proc. Yorkshire Geol. Soc. (forthcoming number); and Proc. Geol. Assoc., 21, 1910, p. 499.

usually extensive and deep. Palate normal, nearly as in *Microtus*. Auditory bullæ moderately large, without spongy tissue within, but with the postero-external part of the wall of each bulla more or less thickened and strengthened by cancellous bone; stapedia artery more or less completely enclosed in a bony tube in adults.

Mandible normal, the angular processes sometimes greatly reduced. Incisors more or less protruding; the lower incisor passes to the labial side of the jaw between  $m_2$  and  $m_3$ , displacing the latter tooth lingually, and ascends the condylar process, where its termination above the dental foramen is marked by a more or less conspicuous hump on the outer surface of the bone.

Cheek-teeth robust, hypsodont, rootless and persistently growing; their alveolar capsules protruding into the floors of the orbit and braincase modifying their surroundings (*e.g.*, pre-sphenoid reduced to a slender rod of bone) and causing the mandible to be unusually stout. Cement present in the infolds or valleys of the teeth. Enamel usually differentiated into thick and thin portions; in earlier species the differentiation is as in *Mimomys*, thick enamel bounding the convex sides, thinner enamel the concave sides of the salient angles; in later species the differentiation is converse. Pattern of  $m^1$ ,  $m^2$ ,  $m_2$  and  $m_3$  not essentially different from that of normal *Microtus*;  $m^3$  simplified with only three salient angles on each side, the anterior loop followed by two or three substantially closed triangles, the posterior loop short and simple;  $m_1$  consisting of a posterior loop, three closed triangles, and an anterior loop of complex structure, with three or four outer salient angles and four or five inner salient angles.

When quite unworn the cheek-teeth have tubercular caps and show various ephemeral complications, which are described above at pp. 107-110.

### 1. † *Arvicola bactonensis* sp. n.

1846. *Arvicola amphibia* Owen, Brit. Foss. Mamm., p. 205 (in part).  
 1882. *Arvicola amphibioides*? Newton, Vert. Forest Bed, p. 87 (in part).  
 1885. *Arvicola amphibioides* Lydekker, Cat. Foss. Mamm. B.M., pt. 1, p. 230 (in part).  
 1890. *Microtus amphibioides*? Woodward and Sherborn, Cat. Brit. Foss. Vert., p. 365.

*Type*.—B.M., No. 17634, Geol. Dept. (Green Collection). An imperfect skull, both mandibular rami, and the greater part of the skeleton of an adult.

*Type horizon and locality*.—A lacustrine or freshwater deposit at Ostend, near Bacton, Norfolk, of Late Cromerian Age.

*Range*.—Known only from the type horizon and locality.

*Characters*.—Size probably a little larger than in *Mimomys intermedius*, smaller than in *A. amphibioides* or *A. terrestris*; dental



measurements as in *M. intermedius*, but skeleton more robust. Cheek-teeth exactly like those of *M. intermedius* in enamel pattern, and in the details of the process by which the adult pattern of  $m_1$  is developed from its unworn tubercular cap; but persistently growing as in the genus *Arvicola*, not developing roots when adult or in old age as in *Mimomys*.

*Description of type skeleton.*—The skull is represented by the maxillo-palatine region with all the cheek-teeth in place; in addition there are crushed fragments of other parts, but these are too imperfect for study. The palatal structure, form of the maxillary root of the zygoma, and position of the anterior end of the jugal arc, as in *Mimomys intermedius*, essentially as in *Arvicola*. The maxillo-palatine suture is a little more forwardly placed than in *M. intermedius*, being in line with the front of  $m^2$  instead of opposite the middle of that tooth; in this the fossil agrees with recent *Arvicola*. Both rami of the mandible are present and of the usual form; each unfortunately is injured behind, although all the cheek-teeth are in place. Several other palatal fragments and lower jaws from Bacton are available; so far as they are preserved they agree with those parts of the type skeleton, but do not give any further information. The frontal region of the skull is unknown, so that we cannot say whether the temporal ridges met in the middle line above to produce a median interorbital crest as in *Arvicola*, or remained low down and widely separated as in *Mimomys*. In size the skull and jaws agree exactly with those of *M. intermedius*.

So far as pattern, structure, and size are concerned there is nothing to distinguish the teeth of the Bacton fossil from those of *M. intermedius*. The enamel is differentiated as in *Mimomys*, being thicker on the convex, thinner on the concave sides of the salient angles. In  $m^3$  the dentinal spaces are similarly rather confluent and the second inner fold is persistent;  $m_1$  agrees exactly in form with that of *M. intermedius*; similar characters are shown by a great many detached teeth from Bacton in the Green Collection. Part of a young left  $m_1$  shows that the adult pattern of this tooth is developed from the unworn tubercular cap in precisely the same way as in *M. intermedius*, for the inner part of the reduced third outer fold is represented by the last trace of an ephemeral enamel "islet." In recent species of *Arvicola* also,  $m_1$  is frequently quite similar in form to the adult  $m_1$  of *M. intermedius*; but in these recent species the adult pattern is developed differently, the inner part of the third outer fold never being reduced by insulation. The only reason for separating the Bacton animal from *M. intermedius* that can be found in the dentition is that in no specimen, although many adult teeth from the deposit are before me, can the slightest sign of failure of the dentinal pulps or of closure of the cement spaces be seen. The cheek-teeth thus seem to have acquired the power of persistent growth and we must conclude

therefore that the West Runton species *M. intermedius* had, by the date of the deposition of the Bacton beds, taken an important step forwards and had developed into a species of *Arvicola* for which the name *A. bactonensis* may be used.

*Skeleton*.—In the type the cervical vertebræ are missing and those of the thoracic and sacral regions are represented merely by fragments. Eleven caudal vertebræ are preserved in sequence; they are much lighter than in recent *Arvicola* and form a series 48 mm. long.

The fore-limbs are represented by the distal end of the right scapula, with which is still articulated the entire right humerus; and by the greater part of the left humerus, together with some carpal and metacarpal bones. Of the hind limbs both innominate bones (each damaged behind), both femora (of which the right is perfect), both tibiæ, the right calcaneum, the left astragalus, and some other bones of the feet are preserved. The proximal epiphyseal sutures of the humerus and tibia, and the distal suture of the femur are still visible, although the bones are otherwise full grown; in the existing *A. amphibius*, however, the sutures in question appear never to close fully, and both *A. bactonensis* and the still older *Mimomys intermedius* probably resembled the living Water Vole in this respect (cf. Pls. III and IV).

The limb bones of *A. bactonensis* are much smaller and lighter than those of *A. amphibius*, although they are a little larger and stouter than those of *M. intermedius*. The humerus differs from that of *A. amphibius* in its weaker deltoid crest, relatively smaller external tuberosity, so that the smaller head lies more directly upon the top of the bone, less developed supinator ridge and narrower trochlea; in all these features it agrees with the humerus of *M. intermedius*. The ulna appears to be relatively a little stouter and straighter than in *A. amphibius*. The *os innominatum* has, anteriorly at all events, much the same form as in the Water Vole; in the ilium the *linea iliaca* and *crista glutea* have similar courses, but are less clearly defined than in the Water Vole, the tract between these ridges being merely flattened instead of concave. In the femur the lesser trochanter is less developed and the head relatively smaller; but in other respects the bone is quite like that of *A. amphibius*. The tibia is also much like that of the latter species; but it is relatively much shorter, being no longer than the femur, and the groove for the tendon of the *tibialis posticus* muscle is shallower and not distinctly separated from that for the *flexor longus digitorum*. The fibula is fused with the tibia below at about the same point as in *A. amphibius*; its upper free portion, notwithstanding the much smaller size of the fossil bones, is absolutely stouter. The calcaneum and astragalus are distinguished by their small size, the latter bone in addition being relatively narrower than in the Water Vole. The following comparative measurements bring out some interesting differences:—

	<i>Mimomys</i>	<i>Arvicola</i>	
		<i>bactonensis.</i>	<i>amphibius.</i>
1. Zygomatic breadth.		18±	23·2
2. Width of palate across front ends of $m^{1-1}$ .		6·2	8·2
3. Maxillary cheek-teeth (alveolar).		7·5	9·6
4. Length of mandible.		18·5±	26
5. Mandibular molars (alveolar).	7-8·5	7·5	9·8
6. Length of humerus.	19±	19·8	24·3
7. „ femur.	21-22	24·5	28·1
8. Least width of femoral shaft.	2-2·3	2·5	3·6
9. Length of tibia.		24·7	33·5
10. „ calcaneum.		4·8	7·5
11. „ astragalus.		3·0	4·7
12. Breadth of astragalus (posterior)		1·5	2·7
13. Length of metatarsal IV.		9·6	12·9

*Remarks.*—Some remarks upon the meaning of this species and the age of the deposit in which its remains occur are given after the description of *A. greenii* below. But in this place I think something should be said about the Green Collection. The Rev. C. Green was an enthusiastic collector who exercised a most mischievous ingenuity in “restoring” his fossils. He often restored the palate of a vole with the teeth of three or four individuals; built up a “skull” or so with fish bones and other odds and ends from the Bacton deposit; and arranged “skeletons” of rodents made up of the bones of mammals, amphibia and fishes upon slabs of clay or plaster, apparently with a desire to imitate the gypsum blocks of Cuvier, which were then attracting so much attention. When the matrix is plaster, the character of the “restoration” is at once apparent; but when it is clay the “skeletons” are apt to deceive. One very choice vole skeleton embedded in clay looks quite genuine until closely examined; its skull is then seen to consist of fragmentary lower jaws most cleverly worked in, and the other parts are equally fraudulent. These restorations for the most part bear late numbers in Green’s Catalogue.

The specimen I have described above is labelled “Skeleton of an Extinct Species of Rat Freshwater Ost-end, Bacton, No. 23,” and after a very close examination I have come to the conclusion that this is genuine and trustworthy. The bones are embedded in a slab of clay and lie nearly in their natural positions. None is duplicated, and no other genera or species are represented on the slab; I do not think Green can have made more than a slight adjustment. The early catalogue number suggests that it was the discovery of this specimen that awakened Green’s interest in “synthetic palæontology,” and it probably served as a pattern for many of his later studies.

## 2. † *Arvicola greenii* sp. n.

The synonymy given under *A. bactonensis* applies equally to this species.

*Type*.—B.M., No. 15984a; Geol. Dept. (Green Collection); a detached right  $m_1$ .

*Type horizon and locality*.—Freshwater deposit at Ostend, near Bacton, Norfolk; Late Cromerian.

*Characters*.—Cheek-teeth persistently growing like those of *A. bactonensis*; distinguished from the latter species, so far as is known, only by the form of  $m_1$ , which resembles that of *Mimomys majori* in having a persistent third outer fold, whereas in *A. bactonensis* and in *M. intermedius* the third outer fold of  $m_1$  is, in adult stages of wear, reduced by insulation.

In the type specimen (Fig. 106, 1) the third outer fold is deep, narrow, and quite persistent; the third outer salient angle bears a faint trace of the "prism-fold"; the anterior loop is short with rather prominent fourth outer and much reduced fifth inner angles; the three triangles in front of the posterior loop are almost tightly closed; the enamel is rather thick, but tends to be differentiated in the normal way of *Mimomys*. This tooth is unquestionably adult; yet no trace of a coming closure of the cement spaces can be seen below.

A left  $m_1$  (No. 17627e) from the same deposit shows one of the earliest stages of wear. In this specimen some of the peculiarities of form seen in the posterior loop and prisms of young Microtine molars are still present, while the dentinal spaces are all confluent with each other; the third outer valley is a persistent fold, and there is no trace of a "prism-fold." The outer border of the anterior loop shows irregularities which mark the remnants of ephemeral complications. A minute islet obliquely placed on the outer edge is the last trace of a fourth outer valley. The fifth inner angle is still prominent, but with further wear would tend to become obsolete.

Other examples from Bacton show many of the variations of form which are found in the  $m_1$  of *M. majori* in the West Runton deposit. Conspicuous among these are those with a well-marked "prism-fold" associated with a persistent third outer valley (Fig. 106, 2). Some of these specimens further show the groove which, from the West Runton evidence, we know to be the last vestige of the fourth outer valley. The retention of such features and the peculiar differentiation of the enamel (thick portions on convex, thin on concave sides of the salient angles) show clearly that this species like *A. bactonensis* is to be regarded as representing a later phase in the evolution of *Mimomys*. Although many of the Bacton teeth are beyond doubt adult, and some of them probably aged, I have not been able to find any trace of closing cement spaces among them.

*Remarks*.—*A. bactonensis* and *A. greenii* may, in my opinion, be fairly considered to be the direct descendants of *Mimomys intermedius* and *M. majori*, the two most divergent of the three species of *Mimomys* occurring in the Upper Freshwater Bed at West Runton. Of a descendant of *M. savini*, the West Runton

species in which the third outer fold is reduced by insulation while the "prism-fold" persists, no trace has been found at Bacton. Not improbably *M. savini* died out without issue before the Bacton beds were deposited.

The mammalia recorded from the Cromerian Beds at Bacton are "*Ursus spelæus*," *Canis* sp., *Rhinoceros etruscus*, *Cervus fitchii*, *C. sedgwickii*, *Trogontherium cuvieri*, *Sciurus*, *Talpa*, *Sorex savini*, *S. runtonensis*, "*Myogale*," and *Balænoptera*, in addition to the voles. This is clearly a Cromerian assemblage, but whether all came from one horizon or not is uncertain. In any case, it does not matter very much so far as we are concerned, because some of the remains here referred to *A. bactonensis* and *A. greenii* came from the "gravel-pan" which usually forms the base of these freshwater deposits of the Norfolk coast. I suspect that, like the "Bone-Bed" at the base of the Craggs, the "gravel-pan" is of different ages in different localities; but be that as it may, I think, from the character of the voles that there can be no question that the Bacton (or rather Ostend) deposit is later than is the Upper Freshwater Bed at West Runton.

Bosco<sup>1</sup> has described, under the name "*Arvicola pliocenicus*" Major, some teeth of a vole, from the Upper Pliocene of the Val d'Arno, characterized as follows:—"Animale di dimensioni intermedie fra quelle dell' *Arvicola amphibius* e dell' *A. nivalis*; con denti molari senza radici e prismi spigoli salienti arrotondati ed il primo molare inferiore con cinque prismi dal lato interno e quattro dal lato esterno." It is evident from what he says of Tuccimei's account of the fossils from Bocchignano, etc., that Bosco is fully acquainted with the characters of rooted teeth, and therefore there is no reason to doubt his accuracy when he describes these Val d'Arno teeth as rootless. If we suppose these rootless molars to be young teeth of *Mimomys*, then their crown patterns should show some of the ephemeral complications characteristic of the young  $m_1$  in all known species of *Mimomys*. The crown views given by Bosco, although not very well drawn, appear to me to be good enough to show that the teeth are in an adult stage of wear and that all ephemeral complications have disappeared. It is to be hoped that these specimens will be again examined and carefully figured; for it seems likely that they will supply an Italian parallel to the Bacton forms.

### 3. † *Arvicola præceptor* sp. n.

1890. *Arvicola amphibius* Newton, Geol. Mag., [3], 7, p. 453; and in Whitaker, Geology of London, 1, 1889, p. 336 (in part).

1890. *Microtus amphibius* Woodward and Sherborn, Cat. Brit. Foss. Vert., p. 365 (in part).

1901. *Microtus amphibius* Hinton and Kennard, Essex Nat., 11, p. 348.

1910. *Arvicola* sp., Hinton, Proc. Geol. Assoc., 21, p. 492.

<sup>1</sup> Bosco, I Roditori Pliocenici del Val d'Arno superiore. *Palæontographia Italica*, 5, p. 93, Tav. xii (ii), fig. 15, 1899.

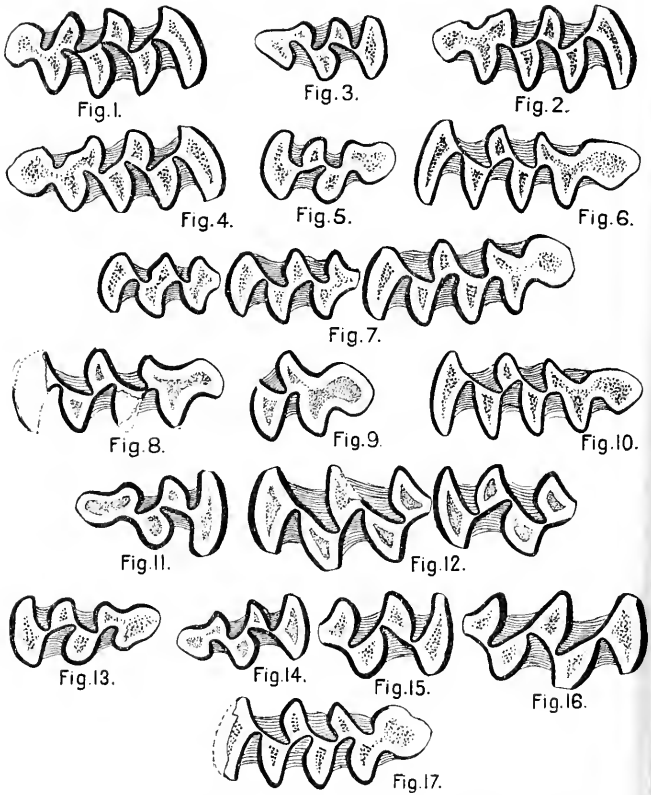


FIG. 106.—Cheek-teeth of early Pleistocene species of *Arvicola*  
(crown views).

(For explanation see opposite page.)

## EXPLANATION OF FIG. 106.

*Arvicola greenii* Hinton.

Freshwater Deposit, Ostend, near Bacton, Norfolk.

1. Right  $m_1$  (type of species; *B.M. Geol. Dept., No. 15984a, Green Coll.*).
2. Right  $m_1$  (*B.M. Geol. Dept., No. 17627a, Green Coll.*).

*Arvicola praeceptor* Hinton.

Pleistocene; early Middle Terrace.

3. Right  $m^3$ ; Grays Thurrock, Essex.
4. Right  $m_1$ ; Grays Thurrock.
5. Left  $m^3$ ; Grays Thurrock.
6. Left  $m_1$ ; Grays Thurrock.
7. Left  $m_1$  and  $m_2$  (type of species) and a detached left  $m_3$ ; Grays Thurrock.
- 8 and 9. Left  $m_1$ , two mutilated specimens; Barrington, Cambridgeshire.
10. Left  $m_1$ ; Grays Thurrock.
11. Right  $m^3$ ; Barrington.
12. Left  $m^1$  and  $m^2$ ; Barrington.
13. Left  $m^3$ ; Grays Thurrock.
14. Right  $m^3$ ; Barrington.
15. Right  $m^2$ ; Grays Thurrock.
16. Right  $m^1$ ; Grays Thurrock.
17. Left  $m^1$ ; Grays Thurrock.

*Type*.—Part of a left mandibular ramus, with the incisor,  $m_1$  and  $m_2$  in place.

*Type horizon and locality*.—Early Middle Terrace deposits of the Thames, at Grays Thurrock, Essex.

*Range*.—Known from the Middle Terrace of the Thames at Grays and Ilford, Essex, and from a deposit of similar age at Barrington, Cambridgeshire.

*Characters*.—Size slightly larger than *A. greenii* from the Cromerian of Bacton. Cheek-teeth persistently growing as in *Arvicola*, but with the enamel in adult specimens differentiated as in *Mimomys*, thick on the convex, thinner on the concave sides of the salient angles. Enamel pattern (Fig. 106, 3-17):  $m^1$ ,  $m^2$ ,  $m_2$ , and  $m_3$  normal;  $m^3$  with the second inner infold persistent, never reduced by insulation, though sometimes shallow, with three salient angles on each side, the third inner angle sometimes tending to become obsolete, and with two substantially closed triangles following the anterior loop;  $m_1$  with a persistent, though sometimes shallow, third outer fold which is never reduced by insulation of its internal portion, with the third outer salient angle often complicated by a more or less well-developed and long persistent "prism-fold," with three substantially closed triangles following the posterior loop, and with four outer and five inner salient angles, of which the anterior angle on either side may be weakly developed or obsolete. Skull (as indicated by a specimen from Barrington) with the temporal ridges fused into a median crest in the hinder part of the interorbital region. Mandible, so far as is known, normal.

*Remarks*.—This species is represented by a left mandibular

ramus, containing the incisor,  $m_1$  and  $m_2$ , five detached examples of the  $m_1$  and four detached specimens of  $m^3$ , together with many other teeth and fragmentary limb bones collected by Mr. Kennard and the writer long ago at Grays; by a series of remains including seven examples of the  $m_1$  and four of the  $m^3$ , collected at Grays by Mr. G. White; by a small series, including specimens of the  $m_1$  and  $m^3$  together with the frontal bones of an old adult and other fragments of the skull, from the brickearth at Barrington, Cambridgeshire, collected by Mr. Kennard and the writer.

The characters of the molars show very clearly that this Middle Terrace *Arvicola* is a direct descendant of the Late Pliocene *Mimomys*, a genus known to have lingered to the times represented by the High Terrace of the Thames. The Middle Terrace *Arvicola* is further shown by the peculiarities of its  $m_1$  (persistence of the third outer valley and frequent persistence of the "prism-fold") to be closely related to, possibly identical with, *A. greenii*, the species occurring in the Late Cromerian beds near Bacton, Norfolk, and like *A. greenii* it is to be regarded as a direct descendant of *M. majori* of the Cromerian beds at West Runton. As previously explained the High Terrace *Mimomys* appears to be a survivor of the same stock. It is noteworthy and suggestive that although three species of *Mimomys* occur at West Runton, descendants of only two of them are found at Bacton, and in the Middle Terrace one alone has been found. It is further suggestive that the primitive stock thus shown to have survived to Middle Terrace times is precisely the one which agrees with modern *Arvicola* in the method by which the third outer fold of the  $m_1$  is reduced. The Barrington frontlet is important, showing firstly that we have old adult material before us, so that there is good evidence for the rootlessness of the teeth, and secondly that *A. preceptor* had made a great advance from the condition of the Late Pliocene *Mimomys*, and perhaps also from that of *A. greenii*, by acquiring temporal muscles which were as powerfully developed anteriorly as they are in modern species of *Arvicola*.

#### 4. †*Arvicola mosbachensis* Schmidtgen.

1910. *Hypudæus amphibius* von Reichenau, Notizblatt d. Vereins f. Erdkunde, Darmstadt, [4], 31, p. 122.  
 1911. *Microtus mosbachensis* Schmidtgen, Notizblatt d. Vereins f. Erdkunde, Darmstadt, [4], 32, p. 186.

*Co-types*.—Fragmentary jaws and teeth in the Museums of Mainz, Frankfurt-am-Main, and Wiesbaden.

*Type horizon and locality*.—Mosbach Sands, Mosbach; Lower Pleistocene.

*Characters*.—Size small; cheek-tooth row 6–7 mm. measured on grinding surface. Enamel pattern essentially as in *Arvicola* or later species of *Mimomys*; dentinal spaces narrowly confluent. Cheek-teeth apparently persistently growing.



*Remarks.*—There can be no doubt that Schmidtgen is justified in separating this form from recent *Arvicola*. It is evidently closely related to the species described above from the earlier Pleistocene deposits of Britain; but the precise status of these forms cannot be determined with existing materials.

### 5. *Arvicola amphibius* Linnæus.

(Synonymy under subspecies.)

*Range.*—Great Britain. In a fossil state known only from Holocene deposits.

*Characters.*—Size large; hind-foot usually 30-34 mm., but occasionally larger, ranging up to 38 mm.; condylo-basal length in adults ranging between 40 and 44.6 mm. General form robust. Rhinarium small, only the integument covering the ends of the nasal cartilages naked, divided by a groove continuous with the lip-cleft below. Eyes small, placed midway between muzzle and ears. Ears well developed, though almost hidden in the fur, clothed within and without by rather long hair; provided with a well-developed naked meatal valve or antitragus, which when the ear is closed fits the lower border of a similar but more highly placed valvular ingrowth ("tragus") from the anterior or inner margin of the ear. Hands large and broad, not specially modified, but hair along the external margin somewhat lengthened and stiffened to form an incipient swimming fringe; each with five digits, the thumb being very small; the third digit is the longest, slightly exceeding the fourth, which is slightly longer than the second; the fifth digit is much shorter, only about half the length of the fourth; all with the exception of the thumb, which bears a small laterally compressed nail, armed with short, sharp, slender and slightly curved claws. Palms naked, with five large pads; the skin between the pads finely wrinkled or granular and forming scaly annulations upon the lower surfaces of the digits. Feet large, with incipient swimming fringes (most noticeable in old individuals), upon both the inner and the outer margins; with five digits related to each other substantially as in the hands, the first or hallux being, however, less reduced than is the thumb; all including the hallux armed with claws, like those of the fingers, but longer and stouter. Soles naked, like the palms, but the region between the heel and pads sometimes (particularly in young individuals) pubescent. Plantar tubercles variable, apparently undergoing reduction; five usually present, the postero-external pad being usually suppressed; in some specimens the postero-external pad is clearly developed though small; in others a small supplementary pad is developed to the outer side of that lying at the base of the fifth toe; in one specimen the pads are not differentiated, but are represented merely by a tumid mass of flesh. Tail long, from one-half to two-thirds of the length of the head and body; clothed with

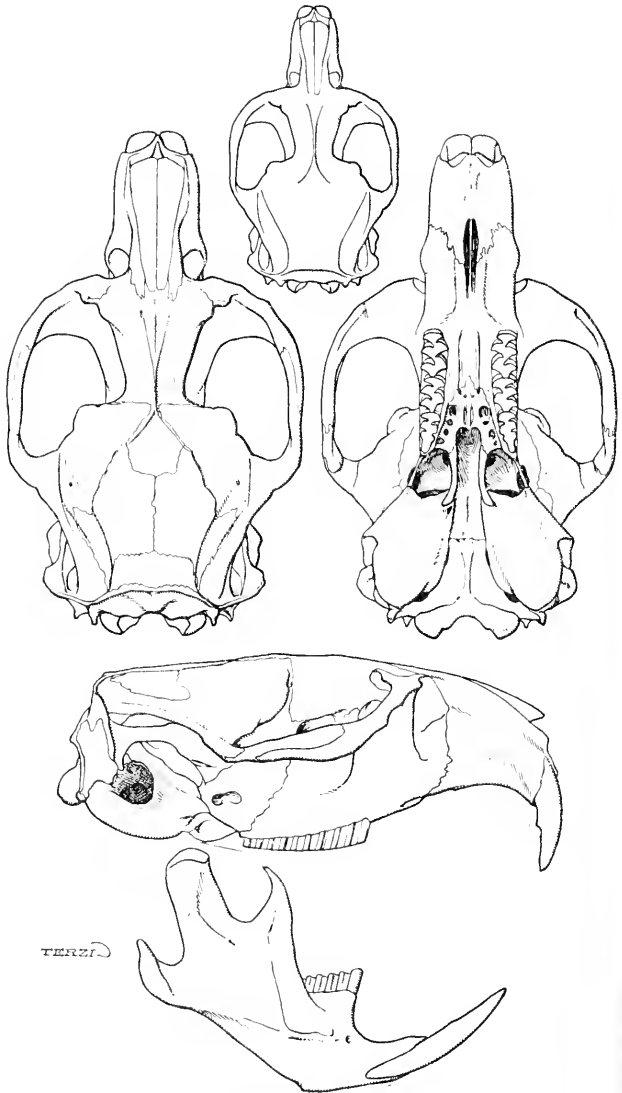


FIG. 107.—*Arvicola amphibius* Linnaeus.

Dorsal, lateral, and ventral views of skull; the small figure shows the skull in dorsal view, natural size.

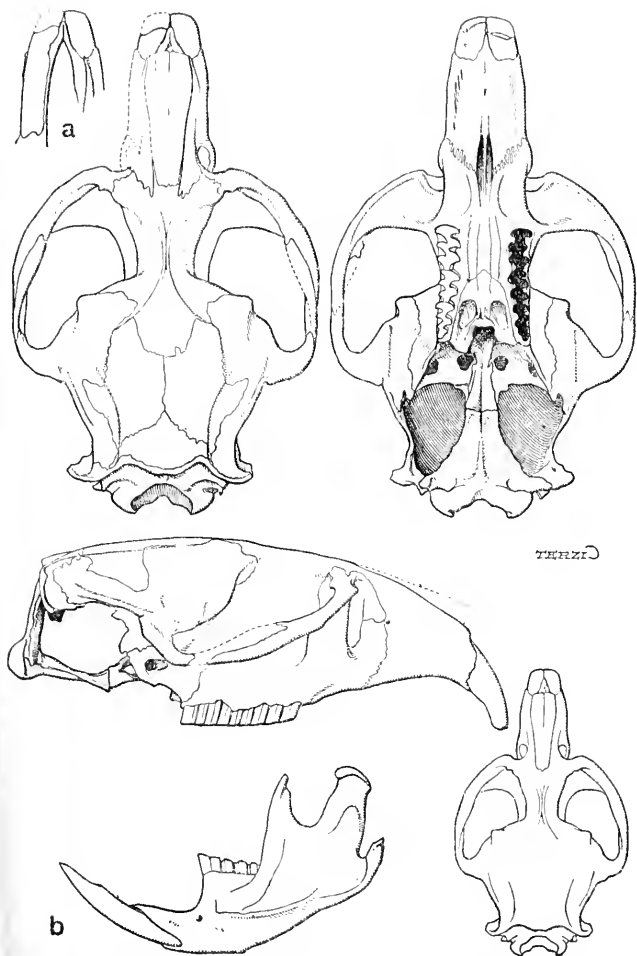


FIG. 108.—*Arvicola abbotti* Hinton. Late Pleistocene, Ightham Fissure. Dorsal, ventral, and lateral views of type skull; the small figure shows the skull in dorsal view, natural size. Dorsal view slightly restored; the small figure *a*. shows the actual condition of the fossil. *b*. Left mandible of a second individual.

rather long hairs (4-5 mm.) which do not completely conceal the annulations; the hair (particularly in old specimens) longer and denser upon its under than upon its upper surface. Flank glands are present in both sexes, oval in shape (measuring  $17 \times 12$  mm.), and each with its long axis parallel to that of the body; surface of gland slightly raised, closely and irregularly wrinkled and pitted so as to produce a honeycombed appearance; from the cavities of the pits hairs, resembling those of the ordinary pelage, arise; these hairs become scarcer towards the centre of the gland. Mammae,  $2 - 2 = 8$ .

Fur close, dense and long; the under fur thick and woolly. Colour of upper parts normally dark brown, ranging from "broccoli brown" to "mars brown" or darker, darkest along the spine, palest on the face and sides, but without noticeable contrasts; sides usually lined with black, the cheeks and ears usually tinged with ochraceous buff or light raw umber. Under surface varying between ochraceous-buff and slate grey, the latter tint produced by the dark bases of the hairs. Feet ranging from "hair brown" to "ecru drab," sometimes blackish. Tail blackish; its under surface sprinkled with greyish hairs.

Two irregular moults (spring and autumn) occur; the summer coat is shorter and often redder, owing to the absence or scarcity of long hairs with dark tips. In the young the juvenal coat is black; the post-juvenal coat resembles the summer adult pelage.

Skull (Figs. 1-8, 107) large and massive, strongly ridged and angular when fully adult, but not essentially different from that of *Microtus*. Rostrum long and stout, distinctly broader than interorbital region in adults. Zygomatic arches strong, widely spreading, their greatest width behind over squamosal roots. Upper incisors moderately protruding, their front faces entirely visible in the dorsal view beyond the tips of the nasals. Nasals short and rather narrow, their greatest width always noticeably less than the width of the rostrum. Interorbital region short, but much constricted posteriorly. Braincase distinctly longer than broad, its outline in dorsal view nearly rectangular. Temporal ridges strongly developed in adults; fusing in the interorbital region to form a sharp, and eventually a lofty, median crest; well marked on the surface of the braincase, diverging from the interorbital crest and running back for the most part along the upper edges of the squamosals to points above the glenoid articulations and thence converging again, traversing the lateral wings of the parietals and the extremities of the interparietal, to the lambdoid crest. In youth the ridges and the squamosals are widely separated; but with growth they approach each other, the squamosals creeping upwards and inwards over the frontals and parietals (Figs. 1 and 2). Post-orbital squamosal crests long and salient in adult skulls, giving the fore-part of the braincase its rectangular appearance. Occiput nearly vertically truncated in younger stages of growth, becoming more

oblique with age; its upper part being pressed forwards, at the expense of the interparietal, so that the condyles appear wholly or in part in the dorsal view. Diastema long, in profile rather high-pitched behind the incisors. Anterior palatal foramina very small, their length scarcely half that of the diastema, commencing far behind incisors and terminating considerably in front of the molars. Molars very robust and hypsodont, filling great capsules which rise high in the floors of the orbit and braincase, that of  $m^2$  obstructing the mouth of the sphenorbital fissure; presphenoid reduced to a slender rod of bone.

Palate essentially as in *Microtus*; its posterior median sloping septum rather short, broad, and low. Mesopterygoid space rather small. Pterygoid fossæ deep and extensive, their floors considerably dorsal to the ventral surface of the basisphenoid. Auditory bullæ rather small, but little inflated, the basioccipital

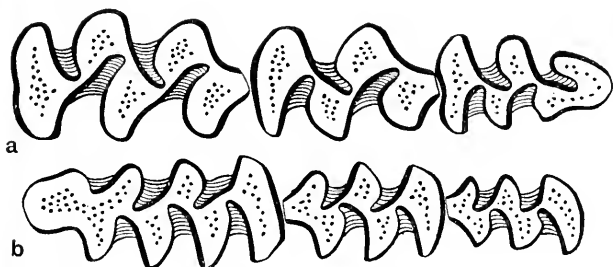


FIG. 109.—Cheek-teeth of *Arvicola amphibius* Linnæus.

Crown views: *a.* right upper, *b.* right lower molars.

remaining relatively wide between the bullæ; cavity of bulla simple, its walls strengthened by a light network of bony threads which thickens posteriorly into a definite bony sponge in the hinder part of the tympanic wall of the bulla; mastoid portion and tegmen tympani not inflated, the tegmen articulating by a squamous facet with the alisphenoid in front; stapedia artery enclosed in a bony tube, which passes through the stapes.

Mandible essentially as in *Microtus*, but the horizontal ramus greatly thickened for the accommodation of the robust teeth; the incisor produces a well-marked hump on the outer surface of the condylar process a little above the level of the dental foramen; above the incisor hump the condylar process is fairly sharply inflected; angular process usually well developed but rather short and stout, its inferior border thickened to form a broad surface for the attachment of the anterior or superficial portion of the *masseter lateralis* muscle. In adults the growing bases of  $m_1$  and  $m_2$  produce rather well-marked swellings on the infero-lateral surface of the ramus, just below the *crista masseterica*, and the capsule of

$m_3$  is a very prominent feature of the inner surface of the jaw. Incisors large but normal. Cheek-teeth robust; enamel pattern (Fig. 109) normal as described above under the genus;  $m_1$  and  $m^3$  with ephemeral complications in youthful stages of wear.

*Geographical differentiation.*—Two subspecies of *A. amphibius* are currently recognized, viz. (1) the typical form inhabiting England and Wales and the Lowlands of Scotland, characterized by lighter brown colour and large size, and (2) *A. a. reta*, a darker and apparently smaller form inhabiting the Highlands of Scotland beyond the Clyde and Tay watersheds. Melanism is frequent in *A. a. reta*, comparatively rare in *A. a. amphibius*; but in the eastern counties of England (Cambridge and Norfolk) there are colonies of black water-voles, the exact status of which is at present doubtful.

Although the habits of this animal are chiefly aquatic they are by no means exclusively so. It is a powerful digger, and many of the chief modifications seen in its skull, dentition and feet are expressions of fossorial and not of aquatic specialization. It may be taken high up on hills or on sandy wastes far removed from any stream or standing water. Like most other Muridæ it will in certain circumstances invade human dwellings. I once killed one accidentally in a cottage in Kent more than a mile distant from a brook.

#### 5a. *Arvicola amphibius amphibius* Linnæus.

1758. *Mus amphibius* Linnæus, Syst. Nat., ed. 10, 1, p. 61.  
 1817. *Leomys aquaticus* F. Cuvier, Dict. des. Sci. Nat., 6, p. 306 (in part); substitute for *amphibius*.  
 1828. *Arvicola aquatica* Fleming, Hist. Brit. Animals, p. 23; the specific name adopted from Leach, Syst. Catal. Spec. Indig. Mamm. and Birds, Brit. Mus., 1816, p. 7 (where it is a *nomen nudum*).  
 1835. *Arvicola amphibia* Jenyns, Man. Brit. Vert. Animals, p. 33 (in part).  
 1837. *Arvicola amphibius* Bell, Hist. Brit. Quadr., ed. 1, p. 321, and ed. 2, 1874, p. 316; Macgillivray, British Quadr., 1846, pp. 68 and 260.  
 1842. *Arvicola americana* Gray, Ann. Mag. N.H., 10, p. 226; described from half-grown individuals supposed to have been taken in South America; co-types B.M., Nos. 42.4.12.6-7.  
 1845. *Arvicola amphibius*, sub-var. *nigricans* de Selys-Longchamps, Atti della sesta Riunione degli Scienziati Italiani, Milano, 1844, p. 322; published without description and hence a *nomen nudum*.  
 1857. *Arvicola amphibius a*, Blasius, Säugethiere Deutschlands, p. 344.  
 1895. *Microtus amphibius* Lydekker, Handbook to the British Mammalia, p. 216.  
 1896. *Microtus (Arvicola) terrestris* Miller, N. Amer. Fauna, No. 12, pp. 66, 67 (in part).  
 1910. *Arvicola amphibius amphibius* Miller, Proc. Biol. Soc. Washington, 23, p. 19; Catal. Mamm. W. Europe, 1912, p. 730; Barrett-Hamilton, Hist. Brit. Mamm., 2, 1914, p. 482.  
 1910. *Arvicola terrestris amphibius* Trouessart, Faune Mamm. d'Europe, p. 194.

*Type*.—Unknown; species based upon the *Mus major aquaticus* of Ray, Syn. Anim. Quadr., 1693, p. 217.

*Type locality*.—England.

*Range*.—England, Wales, and Southern Scotland; exact northern limits of range unknown. Found also in the Isle of Wight and Anglesey.

*Characters*.—Size large, hind-foot commonly between 32 and 35 mm., condylo-basal length 42 mm. or more in adults. Colour moderately dark, black rarely replacing brown upon the upper surface. Melanistic specimens comparatively rare.

For *external and cranial dimensions*, see tables at end of volume.

### 5b. *Arvicola amphibius reta* Miller.

1832. *Arvicola ater* Macgillivray, Mem. Wernerian N.H.S., 6, p. 429; preoccupied by *Hypudæus terrestris*,  $\beta$ , *ater* of Billberg, 827 [= *Arvicola terrestris*].

1835. *Arvicola amphibia*, var.  $\beta$ , *A. ater* Jenyns, Mam. Brit. Vert. An., p. 33.

1910. *Arvicola amphibius reta* Miller, Proc. Biol. Soc. Washington, 23, p. 19; Catal. Mamm. W. Europe, 1912, p. 732; Barrett-Hamilton, Hist. Brit. Mamm., 2, 1914, p. 483.

*Type*.—Unknown.

*Type locality*.—Aberdeen, Scotland.

*Range*.—Scotland, except southern portion; limits of distribution not known.

*Characters*.—Slightly smaller than in *A. a. amphibius*, hind-foot usually between 30 and 32 mm., condylo-basal length in adults usually less than 42 mm. Colour darker, black often replacing brown upon the upper surface. Melanistic specimens are frequent, but black and brown individuals may occur in the same litter.

For *external and cranial dimensions*, see tables at end of volume.

## 6. *Arvicola sapidus* Miller.

(Synonymy under subspecies.)

*Range*.—Iberian Peninsula and Southern France eastwards nearly to the Italian border; northern limit of range unknown, but probably extending at least to the neighbourhood of Paris.

*Characters*.—General size and outward appearance as in *A. amphibius*. Skull distinguished usually by its broader nasals, which at their anterior expansions are together nearly as wide as the rostrum; anterior palatal foramina distinctly larger; auditory bullæ larger, and more conspicuously inflated.

*Geographical differentiation*.—Two subspecies are at present recognized, viz., the typical and lighter-coloured form inhabiting the greater part of Spain and a darker form inhabiting the Pyrenees and Atlantic coast region of South-western France.

*Remarks*.—*A. sapidus* is very closely related to *A. amphibius*,

and, but for convenience' sake in dealing with their respective geographical races, it might well be regarded as a subspecies of the British Water-Vole.

#### 6a. *Arvicola sapidus sapidus* Miller.

1908. *Arvicola sapidus* Miller, Ann. Mag. N.H., [8], 1, p. 195; Trouessart, Faune Mamm. d'Europe, 1910, p. 195.

1910. *Arvicola sapidus sapidus* Miller, Proc. Biol. Soc. Washington, 23, p. 20; Catal. Mamm. W. Europe, 1912, p. 733.

*Type*.—B.M., No. 8.8.4.115; adult female, skin and skull, collected Oct. 7, 1906, by G. S. Miller.

*Type locality*.—Santo Domingo de Silos, Province of Burgos, Spain.

*Range*.—Throughout the Iberian Peninsula.

*Characters*.—General colour not so dark as in *A. amphibius amphibius*, the sides and face a clear yellowish brown without noticeable sprinkling of blackish hairs.

Upper parts yellowish brown varying between "ochraceous buff" and "clay colour," not infrequently tinged with russet; back and crown sufficiently sprinkled with black hairs to produce an evident effect of "lining," the sides and cheeks nearly clear. Under parts pale ochraceous buff more or less darkened by the slaty bases of the hairs. Feet drab grey. Tail brownish, lighter below than above.

For *external and cranial measurements*, see tables at end of volume.

#### 6b. *Arvicola sapidus tenebricus* Miller.

1884. *Microtus musiniani* Lataste, Actes Soc. Linn. Bordeaux, 38, p. 37 (in part); not *Arvicola musignani* de Sélvs-Longchamps.

1908. *Arvicola tenebricus* Miller, Ann. Mag. N.H., [8], 1, p. 196; Trouessart, Faune Mamm. d'Europe, 1910, p. 195.

1910. *Arvicola sapidus tenebricus* Miller, Proc. Biol. Soc. Washington, 23, p. 20; Trouessart, Faune Mamm. d'Europe, 1910, p. x; Miller, Catal. Mamm. W. Europe, 1912, p. 735.

*Type*.—B.M., No. 6.1.21.5; adult male, skin and skull, collected December 30, 1905, by J. F. Davison.

*Type locality*.—Three miles east of Biarritz, Basses-Pyrénées, France.

*Range*.—Pyrenees and Atlantic coast region of South-western France, north to the Garonne; northern limit of range not known; two specimens from La Coruña, Galicia, Spain, appear to be referable to this subspecies rather than to *A. s. sapidus*.

*Characters*.—Colour darker than in *A. s. sapidus*, nearly as in *A. amphibius amphibius*, the sides and face conspicuously sprinkled with black hairs.

Upper parts dull greyish buff, so heavily overlaid with black that the general effect is usually not far from a rather light



grizzled bistre on back and a greyish wood-brown on sides. Cheeks and sides noticeably sprinkled with black-tipped hairs. Under parts slaty grey, washed with pale ochraceous buff on chest and belly. Feet hair brown. Tail blackish above, greyish below; seldom distinctly bicoloured.

For *external and cranial dimensions*, see tables at end of volume.

## 7. *Arvicola terrestris* Linnæus.

(Synonymy under subspecies.)

*Range*.—Widely distributed in Europe and Asia, its range extending from Scandinavia eastwards at least as far as Lake Baikal. Not found in the lowlands of west-central Europe, in the Swiss Alps, Pyrenees, or Iberian Peninsula. Occurring in the Italian Alps and Italy, and thence eastwards through Bosnia and Rumania to the Caucasus, shores of the Caspian and Elburz Mountains in N.W. Persia, whence it ranges probably continuously across Central Asia to the neighbourhood of Lake Baikal.

*Characters*.—Size, in European forms, somewhat smaller than in *A. amphibius* and *A. sapidus*, but Asiatic subspecies are more nearly equal to the two species of Western Europe. Skull slightly more modified for terrestrial and fossorial habits than in *A. amphibius* and *A. sapidus*, but less specialized in this direction than that of *A. scherman*. Auditory bullæ of medium size or small. Cheek-teeth moderately heavy and of normal pattern. Colour variable according to the subspecies; cheek-patches reddish or yellowish and, in most forms, noticeably contrasted with the surrounding parts.

*Geographical differentiation*.—Eight more or less well-marked subspecies of *A. terrestris* are now recognized, but of these three, viz., *A. t. illyricus*, *A. t. musignani* and *A. t. meridionalis*, are still imperfectly known. All the forms are very closely related to each other and the essential characters of the species as a whole shade off through such forms as *A. t. persicus* and *A. t. scythicus* in the direction of *A. amphibius* and *A. sapidus*, and through *A. t. terrestris* towards *A. scherman*; indeed actual intergrading of *A. scherman* and *A. terrestris* may be demonstrated to occur in the neighbourhood of the Baltic. The forms *A. italicus*, *A. illyricus* and *A. musignani* are treated by Miller in his Catalogue as full species; but I can find no character in the existing material that will serve to distinguish any one of them satisfactorily as a species distinct from *A. terrestris*. The presence of such forms as *A. t. scythicus*, *A. t. persicus* and *A. t. rufescens* in Asia and Asia Minor makes it probable that the range of the species is quite continuous from Scandinavia to Italy and the Southern Alps, although it has to make a wide detour to pass round the great area of Central Europe occupied by *A. scherman*.

7a. *Arvicola terrestris terrestris* Linnæus.

1758. *Mus terrestris* Linnæus, Syst. Nat., 1, 10th ed., p. 61.  
 1771. *Mus paludosus* Linnæus, Mantissa Plantarum, pt. 2, p. 522; described from Sweden.  
 1827. *Hypudæus terrestris*  $\beta$ , *ater* Billberg, Syn. Faun. Scand., p. 4; described from Gottland, Sweden.  
 1827. *Hypudæus paludosus*,  $\beta$ , *littoralis*, Billberg, Syn. Faun. Scand., p. 5; described from Småland, Sweden.  
 1827. *Hypudæus paludosus*,  $\gamma$ , *aquaticus*, Billberg, Syn. Faun. Scand., p. 5; described from South Sweden.  
 1857. *Arvicola amphibius a*, Blasius, Säugethiere Deutschlands, p. 344 (in part).  
 1910. *Arvicola terrestris* Miller, Proc. Biol. Soc. Washington, 23, p. 20; Trouessart, Faune Mamm. d'Europe, 1910, p. x; Miller, Catal. Mamm. W. Europe, 1912, p. 738.

*Type*.—Unknown.

*Type locality*.—Upsala, Sweden.

*Range*.—Scandinavia, eastwards into Finland; limits of range not known.

*Characters*.—Size medium, hind-foot 28–31 mm., condylo-basal length 36–39 mm. Colour dark, as in *A. amphibius amphibius*. Upper parts varying between “broccoli brown” and “mars brown” heavily overlaid with black, the general effect where darkest not far from seal brown. Cheeks and sides of head, including the ears, tinged with rusty, the suffusion usually producing a decided contrast with the surrounding parts. Under surface rusty ochraceous buff, sometimes almost tawny, darkened by the under fur, and fading to yellowish grey upon the throat. Feet hair brown to blackish brown. Tail blackish, its under surface usually sprinkled with grey hairs.

Skull distinguished from that of *A. amphibius* chiefly by smaller size and smaller bullæ. Occiput tending to be a little more oblique, and the incisors a little more protruding; these characters apparently better marked in some of the specimens from Sweden and Esthonia than in others from S. Norway. Mandibular angular processes not reduced. Cheek-teeth not peculiar, but rather small and light.

For *external and cranial measurements*, see tables at end of volume.

7b. *Arvicola terrestris italicus* Savi.

1839. *Arvicola amphibius* var. *italica* Savi, Nuovo Giorn. de'Letterati, Pisa, 37, No. 102, p. 202 (p. 5 of separate); for date of publication see de Selys-Longchamps, Études de Micromammalogie, 1839, p. 96, footnote.  
 1839. *Arvicola pertinax* Savi, Nuovo Giorn. de'Letterati, Pisa, 37, No. 102, p. 203 (p. 6 of separate); M.S. synonym of *italica*.  
 1845. ?*Arvicola amphibius* var. *minor* de Selys-Longchamps, Atti della sesta Riunione degli Scienziati Italiani, Milano, 1844, p. 322 (*nomen nudum*).

1910. *Arvicola italicus* Miller, Proc. Biol. Soc. Washington, 23, p. 20; Trouessart, Faune Mamm. d'Europe, 1910, p. x; Miller, Catal. Mamm. W. Europe, 1912, p. 740.

*Type*.—Unknown.

*Type locality*.—Vicinity of Pisa, Italy.

*Range*.—Italian Switzerland and Northern Italy, southwards at least as far as Pisa; details of distribution not known.

*Characters*.—Like *A. t. terrestris*, but teeth slightly larger, anterior palatal foramina larger (both longer and broader), colour not so dark and cheeks less contrasted with the surrounding parts.

Colour of upper parts essentially as in *A. t. terrestris*, but broccoli brown much in excess of black, the latter producing a slight effect of grizzling or "lining," but never sufficiently dominant to make the general colour approach seal brown. Sides pale, buffy, slightly grizzled wood brown, becoming a little more yellowish on cheeks. Under surface pale slate grey, washed with buffy on chest and belly. Feet pale hair brown, sometimes tinged with drab. Tail obscurely bicoloured, dark brown above, greyish below.

Skull presenting a close general resemblance to that of *A. t. terrestris*, but the auditory bullæ are slightly larger and the anterior palatal foramina are longer. The teeth are of normal form, but slightly larger than in *A. t. terrestris*.<sup>1</sup>

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—I can find no good reason for regarding this animal as more than a geographical race of *A. terrestris*, although I have made close studies of its skull and dentition on two occasions separated by an interval of many years.

### 7c. *Arvicola terrestris musignani* de Sélys-Longchamps.

1839. *Arvicola musignani* de Sélys-Longchamps, Rev. Zoologique, p. 8 (January 1839).

1839. *Arvicola destructor* Savi, Nuovo Giorn. de'Letterati, Pisa, 37, No. 102, p. 204 (p. 7 of separate), February 1839 (for date of publication see de Sélys-Longchamps, Études de Micromammalogie, 1839, p. 96, footnote); described from Maremma Grossetana, Tuscany, Italy; de Sélys-Longchamps, Études de Micromammalogie, 1839, p. 93.

1845. ?*Arvicola musignani* var. *futiginosus* de Sélys-Longchamps, Atti della sesta Riunione degli Scienziati Italiani, Torino, 1844, p. 322 (*nomen nudum*).

1857. *Arvicola amphibius* b, Blasius, Säugethiere Deutschland, p. 344.

1910. *Arvicola musignani* Miller, Proc. Biol. Soc. Washington, 23, p. 21; Catal. Mamm. W. Europe, 1912, p. 744.

1910. *Arvicola musignanoi* Trouessart, Faune Mamm. d'Europe, pp. x, 196.

<sup>1</sup> MILLER inadvertently makes conflicting statements about the teeth of this form; in his diagnosis (Catalogue, p. 240), he says teeth "not so heavy" as in *A. terrestris*, but on p. 741 "teeth as in *A. terrestris*, but slightly larger." The latter statement is correct.

*Type*.—Unknown.

*Type locality*.—Vicinity of Rome, Italy.

*Range*.—Central Italy; at present known from the west coast only.

*Characters*.—Distinguished from *A. t. italicus* by its pale and yellowish colour.

Entire animal a light yellowish wood brown, faintly grizzled with black on median dorsal region and darkened by the hair bases on the under surface. Cheeks faintly more yellowish than flanks. Feet light drab. Tail obscurely bicoloured, blackish brown above, yellowish brown below.

Skull indistinguishable from that of *A. t. italicus*; cheek-teeth apparently slightly smaller.

For *cranial and external measurements*, see tables at end of volume.

*Remarks*.—It seems unnecessary to regard this form as more than a geographical race of *A. italicus*, and therefore, like the latter, it is treated here as a subspecies of *A. terrestris*. The material in the Museum is very poor; the only adult skull before me is broken.

**7d. *Arvicola terrestris illyricus* Barrett-Hamilton.**

1899. *Microtus musignani illyricus* Barrett-Hamilton, Ann. Mag. N.H., [7], 3, p. 225

1910. *Arvicola illyricus* Miller, Proc. Biol. Soc. Washington, 23, p. 21; Trouessart, Faune Mamm. d'Europe, 1910, p. x; Miller, Catal. Mamm. W. Europe, 1912, p. 741.

1910. *Arvicola musignanoi illyricus* Trouessart, Faune Mamm. d'Europe, p. 196.

*Type*.—B.M., No. 94.1.5.1; adult male, skin and imperfect skull, collected by Dr. Floericke.

*Type locality*.—Bosnia (no exact locality).

*Range*.—Bosnia; limits of distribution not known.

*Characters*.—Like *A. t. italicus*, but under parts with a decided whitish wash.

For *external and cranial measurements*, see tables at end of volume.

*Remarks*.—As Miller says, the Bosnian Water-Vole is so similar to *A. t. italicus* that the two animals will not improbably prove to be identical.

**7e. *Arvicola terrestris rufescens* Satunin.**

1908. *Microtus terrestris rufescens* Satunin, Mitt. Kauk. Mus., 4, pp. 90, 134.

1924. *Arvicola terrestris rufescens* Ognev, Rodentia of the North Caucasus, p. 40.

*Type*.—Tiflis Museum.

*Type locality*.—Pokun Сырт, upper course of the Podkumok, Karačaj-Territory.

*Range*.—Northern Caucasus.

*Characters*.—Size as in *A. t. terrestris*, hind-foot 32 mm., basilar length 34.2 mm. Ears very small, completely hidden by the fur. Colour of upper parts rusty brown considerably mixed with black, the rusty colour more intense upon the sides of the head, especially under the eyes. Under parts ashy grey, with a thin light rusty suffusion. Feet brownish grey. Tail dark brown above, paler below owing to the mixture of white hairs.

Skull and teeth essentially as in *A. t. terrestris*; zygomatic breadth slightly less. Enamel of incisors more intensely coloured, reddish orange in upper teeth, pale orange in lower.

For *external and cranial measurements*, see tables at end of volume.

### 7f. *Arvicola terrestris meridionalis* Ognev.

1922. *Arvicola amphibius meridionalis* Ognev, Биологич. известия, 1, p. 109 (not seen); Rodentia of the North Caucasus, p. 40, 1924; Бюл. Моск. Общ. Испыт. Прир., 1925, pp. 16 and 41.

*Type*.—Probably in Moscow.

*Type locality*.—Original description not seen.

*Range*.—South-eastern Russia; from the district of Ardatov, Simbirsk (now Government of Samara), the Ural Province, and the Government of Astrakhan southwards to the northern Caucasus.

*Characters*.—Judging from a single specimen, received recently from Prof. Ognev, this subspecies is scarcely to be distinguished from *A. t. scythicus* Thomas; but whether it be distinct or not, I have no doubt that it should be regarded as representing one of the geographical races of *A. terrestris*. Ognev, however, takes another view, and in the third paper cited above he says (at p. 44): "Le campagnol de cette région peut être considérée comme formant une sous-espèce bien différenciée, *A. a. meridionalis*. Il faut remarquer que c'est bien à l'*A. amphibius* telle que l'entend G. S. Miller (1912) que cette sous-espèce doit être rapportée, vu qu'elle possède un grand crâne, massif, dont la partie antérieure et surtout les incisives, ne proéminent pas en avant que cela a lieu chez le *A. terrestris*. Cette sous-espèce se distingue du *A. amphibius* type, (a) par le crâne plus raccourci; (b) par des pommettes plus écartées, malgré un crâne visiblement plus court; (c) enfin parceque, en comparant ses os nasaux avec les dimensions générales du crâne, on constate que proportionnellement leur longueur dépasse celle qui est typique pour l'*A. amphibius* d'Angleterre. La coloration est relativement claire; la teinte générale varie d'un jaune paille brunâtre tirant sur la rouille, jusqu'à un brun marron."

7g. *Arvicola terrestris persicus* de Filippi.

1865. *Arvicola amphibius* var. *persicus* de Filippi, Viaggio in Persia, 1865, p. 344.  
 1876. *Arvicola amphibius*? Blanford, Eastern Persia, 2, Zoology and Geology, p. 61.  
 1907. *Microtus terrestris persicus* Thomas, Ann. Mag. N.H., [7] 20, p. 200.  
 1907. *Microtus terrestris armenius* Thomas, Ann. Mag. N.H., [7], 20, p. 201; type B.M., No. 97.6.4.10 adult male, from Van, Asia Minor.  
 1908. *Microtus terrestris persicus* Satunin, Mitt. Kauk. Mus., 4, pp. 90, 134.

*Co-types*.—Turin Museum.

*Type locality*.—Sultanieh, on the plateau south of the Elburz Mountains; or possibly, according to Thomas, the shores of the Caspian Sea to the north of the Elburz Mountains.

*Range*.—N.W. Persia and Armenia; known from the mountains about Van (altitude 5000 feet), from Dorfe Müzaret, Kars Gebiet (altitude 6000 feet), and from the low-lying southern shores of the Caspian.

*Characters*.—Size large, hind-foot 33 mm., condylo-basal length 41.5 mm. Colour of upper parts dark greyish brown, with a strong mixture of black, especially along the spine, and with a paler rusty shading which becomes more distinct upon the sides. Flanks considerably lighter. Under surface, including the inner surfaces of the limbs, whitish. Hands and feet clad with closely adpressed silvery-white hairs. Tail with a narrow streak of brownish hairs along the dorsum, clothed laterally and below with scanty white hairs.

Skull large, scarcely to be distinguished from middle-sized specimens of *A. amphibius*; the occiput a little more oblique, the nasals slightly more expanded anteriorly in adults, and the anterior palatal foramina slightly larger. Cheek-teeth of normal pattern.

For *external and cranial dimensions*, see tables at end of volume.

*Remarks*.—De Filippi's description although very terse is almost full enough; he says *A. persicus* differs from the European Water-Vole "per il colore che passa al fulvo sui fianchi, ed al bianco nelle parti inferiori. I caratteri osteologici sono assolutamente medesimi." A fuller description of the colour has been given by Satunin. Thomas, studying specimens brought from Van on the Elburz Mountains and from the shores of the Caspian, noticed that in the mountain forms the salient angles of the teeth are remarkably rounded, whereas in those from the low-lying shore the angles are sharp as in normal skulls of *Arvicola*. An examination of the skull of one of de Filippi's types led Thomas to believe that though de Filippi first observed Water-Voles on the high plateau south of the Elburz, he did not obtain his specimen until he had crossed the mountains and descended to the coastal

plain; for the teeth in de Filippi's specimen are of the ordinary angular type. No other character, or at least none that cannot be readily explained by differences of age in the individuals examined, distinguishing the highland from the lowland form is visible in the material available. The difference in the character of the salient angles in the two sets of specimens is certainly striking, but I think it is susceptible of another explanation than that given by Thomas. In prismatic teeth the precise shape of the angles and infolds which form the pattern visible at the grinding surface depends among other things upon the angle at which the plane of wear cuts the prisms. It is possible to get from one and the same tooth very different patterns by slightly altering the plane of wear. The cheek-teeth of *Arvicola* are ever-growing, and they grow in two spirals, one more or less longitudinal, the other transverse. If the animals feed on hard substances or dwell upon a sandy soil their teeth are worn down rapidly; if the food is soft, the wear is slower. In the one case growth at the base may or may not be able to keep pace with the wear on the crown of the tooth; in the other, growth may outstrip the wear; in the two cases supposed the angle of the plane of wear will necessarily be different and the pattern will differ accordingly. A slight difference in station may necessitate a great difference in food and may therefore give rise to a considerable difference in both the exact shape of the salient angles and infolds and in the apparent size of the teeth.

**7h. *Arvicola terrestris scythicus* Thomas.**

1914. *Arvicola terrestris scythicus* Thomas, Ann. Mag. N.H., [8], 13, p. 568.

*Type*.—B.M., No. 14.5.10.154; adult female, collected May 5, 1913, by W. Rückbeil, and presented by the Hon. N. C. Rothschild.

*Type locality*.—Djarkent, Semiretchensk, Central Asia.

*Range*.—Besides the typical series from Djarkent there are a number of specimens in the Museum, collected by G. A. Burney at Irkutsk, and at Alzamai on the banks of the Jenissei River, which appear to be referable to this form. No doubt *A. t. scythicus* has a wide range in Central Asia.

*Characters*.—Size large, hind-foot 34 mm., condylo-basal length 42 mm. General colour about as in *A. a. amphibius* or as in pallid examples of *A. t. terrestris*; the reddening of the cheeks characteristic of *A. t. terrestris* well marked. Tail black, scarcely lighter below, its tip usually with a small white pencil.

Skull equalling that of *A. amphibius* in size, but with the fossorial characters of *A. t. terrestris* intensified, the incisors more protruding and the occiput more oblique than in the typical subspecies.

For cranial and external measurements, see tables at end of volume.

### 8. *Arvicola scherman* Shaw.

(Synonymy under subspecies.)

*Range*.—Central Europe from the Baltic southwards to the Pyrenees and from the coast (probably) eastwards through the Swiss Alps to the Tirol (at least). Limits of distribution unknown.

*Characters*.—Size considerably smaller than in other species of *Arvicola*, hind-foot 22–25 mm., condylo-basal length 33–36.6 mm. External and cranial characters more modified for terrestrial and fossorial habits than in other species. Incisors projecting from the mouth more conspicuously, less concealed by the lips than in normal aquatic species. Palmar and plantar tubercles more or less reduced in size. Skull with incisor teeth straightened and protruding; the rostrum shallow in relation to the cranial depth; the braincase short and broad, moderately angular and ridged in adults; the occiput obliquely truncated, the supraoccipital sloping forwards and upwards, with the crest for the *ligamentum nuchæ* well defined. Angular processes of mandible often reduced. Cheek-teeth rather small and light, but of normal pattern.

*Geographical differentiation*.—Three rather well-marked subspecies are at present recognized, viz., the typical form with a wide range over the lowlands of West-Central Europe, *A. s. exitus*, inhabiting the Swiss Alps and Vosges Mountains, and *A. s. monticola*, its representative in the Pyrenees. Of these the typical form (*A. s. scherman*) is the least specialized, and its habits are partly aquatic, partly terrestrial; it is not improbable that this subspecies will be found to intergrade to the north, probably in the neighbourhood of the Baltic, with *A. terrestris*. In the Alpine *A. s. exitus* and the Pyrenean *A. s. monticola* the specialization is extreme; although, where circumstances render it possible, these subspecies may lead a partly aquatic life, there is no doubt that in many districts their habits are purely terrestrial and fossorial like those of the mole. These mountain forms are much alike externally, but the auditory bullæ are much smaller, flatter and less inflated in *A. s. exitus* than they are in *A. s. monticola*, which in this respect is more like ordinary members of the genus.

The Museum has acquired three or four skulls from Dr. Pfizenmayer which are said to have come from various places in the Caucasus, in the neighbourhood of Tiflis. It is, of course, possible that some such animal occurs in that region; but the skulls are so like normal skulls of *A. s. exitus* that I am inclined to think that some error as to locality has been made. In any case it would not be safe to base any conclusions upon such material.



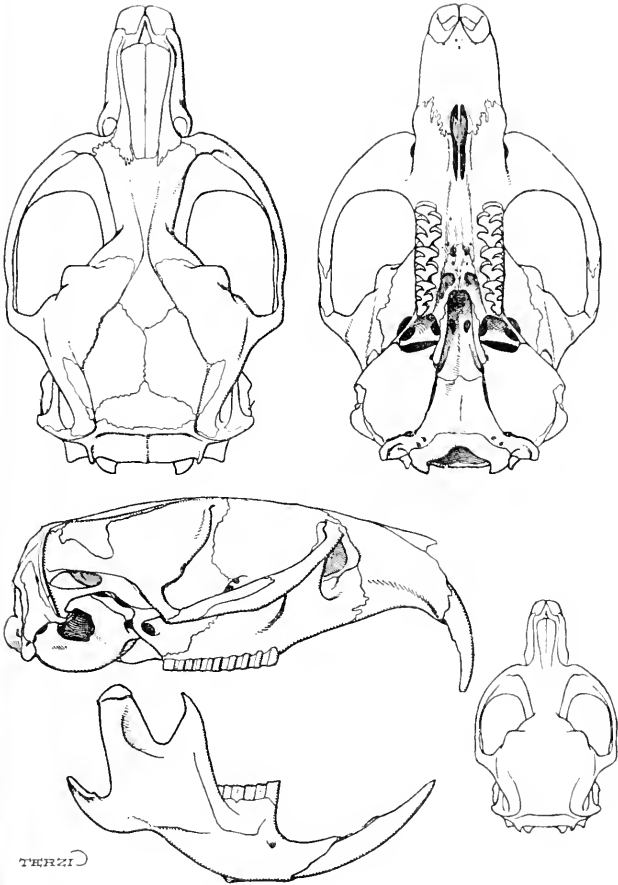


FIG. 110.—*Arvicola scherman*.

Dorsal, ventral, and lateral views of skull; the small figure shows the skull in dorsal view, natural size.

8a. *Arvicola scherman scherman* Shaw.

- 1779 ? *Spalax minor* Leske, Anfangsgrunde d. Naturgesch., 1, p. 168; described from Germany.
1801. *Mus scherman* Shaw, Gen. Zool., 2, pt. 1, p. 75.
1801. *Mus amphibius albus* Bechstein, Gemein. Naturgesch. Deutschlands, 1, 2nd ed., p. 985; described from Thüringen, Germany.
1801. *Mus amphibius canus* Bechstein, Gemein. Naturgesch. Deutschlands, 1, 2nd ed., p. 985; described from Thüringen, Germany.
1804. *Mus terrestris* Hermann, Observ. Zool., p. 59 (not of Linnæus, 1758).
1804. *Mus schermaus* Hermann, Observ. Zool., p. 59; an alternative for *terrestris*, proposed but rejected on the ground that the animal was the same as that of Linnæus; described from Strassburg, Germany.
1822. *Arvicola argentoratensis* Desmarest, Mammalogie, pt. 2, p. 281; described from Strassburg, Germany.
1829. *Lemmus arvalis*  $\beta$ , *buffonii* Fischer, Syn. Mamm., p. 298; described from near Berlin, Germany? (Based on Brant's account (Geschl. d. Muizen, p. 372, 1827) of two specimens in the Berlin Museum supposed to be identical with the dark variety of "Le Campagnol" described by Buffon, Hist. Nat. des Amin., 7, p. 372, 1758.)
1839. *Arvicola amphibius* de Sélvs-Longchamps, Études de Micro-mammalogie, p. 97, pls. i and ii, figs. 1 and 2 (in part; not of Linnæus).
1857. *Arvicola amphibius* c. *Arvicola terrestris* auct., Blasius, Säugthiere Deutschlands, p. 355 (in part).
1910. *Arvicola scherman scherman* Miller, Proc. Biol. Soc. Washington, 23, p. 21; Catal. Mamm. W. Europe, 1912, p. 745.
1910. *Arvicola scherman* Trouessart, Faune Mamm. d'Europe, p. x.

*Type*.—Unknown.

*Type locality*.—Strassburg, Germany.

*Range*.—Continental Europe from the Baltic southwards into Southern Germany and Central France; limits of distribution imperfectly known.

*Characters*.—External form and skull not so highly modified for fossorial life as in the other subspecies. Palmar and plantar tubercles distinctly reduced as compared with those of *A. terrestris*, but not so reduced as in other subspecies of *A. scherman*; sole wrinkled towards the heel, but not distinctly granular, and without evident pubescence. Hind-foot 26–27 mm.; condylo-basal length 35.6–36.4 mm.

Colour of upper surface dark brown, near "Prout's brown" along the spine and between "mars brown" and "broccoli brown" on sides; sometimes broadly suffused with light wood brown, or the sides faintly tinged with dull buffy grey. Cheeks usually like sides, not obviously contrasted with surrounding parts. Under parts slaty grey, more or less washed with dull ochraceous buff. Feet hair-brown to blackish. Tail blackish, or sprinkled with whitish hairs below; never distinctly bicoloured.

Skull much like that of *A. terrestris*, but slightly smaller, the

rostrum a little shallower compared with the depth of the brain-case, with slightly less strongly curved and more protruding incisors, and smaller cheek-teeth.

*For external and cranial measurements*, see tables at end of volume.

*Remarks.*—This appears to be in part the "*Arvicola amphibius*" of de Sélys-Longchamps; he figures (*Études de Micromammal.*, pls. i and ii, figs. 1 and 2) two skulls from Belgium under this name. The Lataste Collection includes three skulls from Belgium collected by de Sélys-Longchamps himself and labelled *A. amphibius*; these agree closely with his figures on the one hand, and I am unable to distinguish them from skulls of *A. s. scherman* on the other. "*A. terrestris*" of de Sélys-Longchamps, cited by Miller in the synonymy of the present subspecies, is a synonym of *A. s. exitus*, being based upon Swiss material.

### **8b. *Arvicola scherman exitus* Miller.**

1839. *Arvicola terrestris* Savi, Nuovo Giorn. de'Letterati, Pisa, 37, p. 300 (p. 3 of separate); described from Geneva, Switzerland. Not *Mus terrestris* Linnæus, 1758.
1839. *Arvicola terrestris* de Sélys-Longchamps, *Études de Micromamm.*, p. 97, pls. i and ii, fig. 6.
1845. ?*Arvicola terrestris* var. *niger* de Sélys-Longchamps, *Atti della sesta Riunione degli Scienziati Italiani*, Milano, 1844, p. 321; type locality Lausanne, Switzerland (*nomen nudum*).
1845. ?*Arvicola terrestris* var. *castaneus* de Sélys-Longchamps, *Atti della sesta Riunione degli Scienziati Italiani*, Milano, 1844, p. 321; type locality Lausanne, Switzerland (*nomen nudum*).
1857. *Arvicola amphibius* e. *Arvicola terrestris* auct., Blasius, *Säugethiere Deutschlands*, p. 355 (in part).
1910. *Arvicola scherman exitus* Miller, *Proc. Biol. Soc. Washington*, 23, p. 21; Tronessart, *Faune Mamm. d'Europe*, 1910, p. x; Miller, *Catal. Mamm. W. Europe*, 1912, p. 746.
1911. *Arvicola scherman exilis* Lydekker, *Zool. Record*, 47 (1910), *Mamm.*, p. 54; accidental renaming of *A. s. exitus*.

*Type.*—B.M., No. 10.8.16.8; adult female, skin and skull, collected by E. H. Zollikofer.

*Type locality.*—St. Gallen, Switzerland.

*Range.*—The Alps (not known from the Italian side) at moderate elevations, and the immediately adjoining lowlands of Switzerland and France; eastwards into the Tirol; northwards into the Vosges Mountains; the limits of its range not known.

*Characters.*—External form and skull highly modified for fossorial habits. Size very small, hind-foot 22-25 mm., condylo-basal length 33 to 35 mm. Incisors projecting from the mouth more conspicuously than in normal aquatic members of the genus. Palmar and plantar tubercles greatly reduced in size, the soles nearly smooth towards the heel. Swimming fringes of hind-foot very slightly developed. Annulation of tail finer than in *A. amphibius* (about 20 instead of 15 to the centimetre).

Colour of upper parts ranging between light "broccoli brown" and ochraceous buff, the face, top of head and spinal region somewhat darkened by blackish hair-tips, which are usually most noticeable over the loins. Sides when brightest clear ochraceous buff, when duller near greyish cream buff. Under parts paler, less slaty grey than in the typical subspecies, the throat near the grey No. 9 of Ridgway; chest and belly washed with cream buff. Feet "ecru drab," sometimes tinged with buffy. Tail whitish throughout, or sprinkled with blackish hairs above; sometimes rather distinctly bicoloured.

Skull smaller than in the typical form and distinguished by its much more marked fossorial specialization. Incisors more projecting or "proödont," rostrum shallower in relation to the depth of the braincase; occiput more obliquely truncated in adults. Auditory bullæ much smaller, their outer faces noticeably but irregularly flattened. Mandibular angular processes usually very small. Cheek-teeth normal, but anterior loop of  $m_1$  usually short and wide.

For *cranial and external dimensions*, see tables at end of volume.

### 8c. *Arvicola scherman monticola* de Sélys-Longchamps.

1838. *Arvicola monticola* de Sélys-Longchamps, Rev. Zoologique, p. 249; Études de Micromammalogie, 1839, p. 92, pls. i and ii, fig. 3.  
 1857. *Arvicola amphibius* e. *Arvicola terrestris* auct., Blasius, Säugethiere Deutschlands, p. 355 (in part).  
 1910. *Arvicola scherman monticola* Miller, Proc. Biol. Soc. Washington, 23, p. 22; Trouessart, Faune Mamm. d'Europe, 1910, p. x; Miller, Catal. Mamm. W. Europe, 1912, p. 749.

*Type*.—Unknown.

*Type locality*.—St. Bertrand de Comminge, Hautes-Pyrénées, France.

*Range*.—Pyrenees and their immediate neighbourhood (known at present from the French side only); Puy-de-Dôme?

*Characters*.—Distinguished from *A. s. exitus* by its larger and more evenly inflated auditory bullæ and by the longer and narrower anterior loop of  $m_1$ .

For *external and cranial measurements*, see tables at end of volume.

### 9. † *Arvicola abbotti* Hinton.

1823. "Water Rat" Buckland, Reliquiæ Diluvianæ, pp. 18, 33, 34, 49, pl. xi, figs. 1-8, 11, 12.  
 1825. *Hypudæus* "Espèce de Campagnol à peu près de la taille du rat d'eau," Cuvier, Oss. Foss., ed. 3, 5, pl. 1, p. 54.  
 1846. *Arvicola amphibia* Owen, British Fossil Mammals, 1846, p. 201. Not *Mus amphibius* Linnæus, 1758.

1847. *Hypudæus spelæus* Cuvier, Giebel, Fauna der Vorwelt, 1, p. 88 (*nomen nudum*).
1869. *Arvicola amphibius* Boyd Dawkins, Q.J.G.S., 25, p. 194; Sanford, *ibid.*, 26, p. 124, 1870; Blackmore and Alston, P.Z.S., 1874, p. 462 (in part).
1890. *Microtus amphibius* Woodward and Sherborn, Cat. Brit. Foss. Vert., p. 365; Newton, Q.J.G.S., 50, 1894, p. 196.
1910. *Arvicola abbotti* Hinton, Ann. Mag. N.H., [8], 6, p. 34; Proc. Geol. Assoc., 21, p. 494.

*Type*.—B.M., No. 11804; adult skull, nearly complete, from the collection of W. J. Lewis Abbott; presented by Sir H. H. Howorth, K.C.S.I., F.R.S.

*Type locality and horizon*.—A deposit filling fissures in the Hythe Beds (Lower Greensand) at Ightham near Sevenoaks, Kent, England. Late Pleistocene.

*Range in time and space*.—Known only from the Late Pleistocene of Britain, where it occurs commonly in the later cavern and fissure deposits.

*Characters*.—A large member of the *A. scherman* group; with skull as large as in *A. amphibius*, the condylo-basal length reaching 41 mm. in adults; the limb skeleton relatively small and light.

Skull (Fig. 108) characterized by its straightened and protruding incisors and sloping occiput; both characters, the result of extreme fossorial specialization, far more pronounced than in any living member of the *A. scherman* group. Occiput, in adults, sloping forwards conspicuously, the interparietal reduced and its posterior margin boldly convex instead of being nearly straight; lambdoidal crest markedly sinuous, and the ridge for the *ligamentum nuchæ* prominent; basioccipital tilted upwards and backwards, forming a marked angle in front with the basi-sphenoid. In younger specimens the occiput is more nearly vertical, the interparietal less reduced, with straighter posterior border, and the basioccipital more nearly horizontal. Post-orbital squamosal crests somewhat more extensive than in *A. amphibius*, but much less salient. Anterior palatal foramina very small in correlation with the relatively broader incisors. Pterygoid fossæ, for origin of *pterygoideus internus* muscles, more extensive, the postero-lateral palatal pits wider and the mesopterygoid fossa narrower correspondingly. Auditory bullæ about as in *A. amphibius*, but with smaller external apertures and a more copious filling of spongy bone.

Mandible with very small angular processes; incisor ascending nearly to the condyle, its growing base marked by a strong hump upon the outer surface of the condylar process, which is sharply inflected above the hump.

Incisor teeth relatively broad. Cheek-teeth very light, but similar to those of *A. amphibius* and other species in pattern.

For measurements, see table at end of volume.

*Remarks.*—The skull characters indicate that *A. abbotti* was highly specialized for fossorial habits; the eyes and external ears, judging from the skull, were smaller than in *A. amphibius*; the masseter and temporal muscles appear to have been as in the living species, but the *pterygoid internus* muscle was more powerful, with a larger fleshy origin and a smaller and more tendinous insertion. Why the limb skeleton should be smaller in proportion to the head it is difficult to say; it may be perhaps connected in some way with more terrestrial and less aquatic habits, but it is a feature seen also in the older genus *Mimomys*.

Buckland noted the profusion in which the remains of "Water Rats" occurred in the Kirkdale cave, and he sent some of his specimens to Cuvier, who determined them as belonging to the same subdivision of the voles as that containing the existing Water-Vole. But with customary astuteness Cuvier remarked: "cependant si l'on excepte les mâchoires et les dents, je trouve tous les autres os un peu plus petits, ce qui me fait soupçonner que l'espèce n'étoit pas la même. Ainsi les fémurs, les tibia que je possède ne sont pas plus grands que dans le schermauss . . . On doit engager les personnes voisines de la caverne, à tâcher de se procurer un crâne assez entier pour donner les caractères; ce sera le seul moyen de déterminer positivement l'espèce." He also notes that a calcaneum and an astragalus figured by Buckland are respectively a little smaller and a little different in shape from those of the Water-Vole. But it was not until 1910 that evidence of the kind demanded by Cuvier was forthcoming, and then not from Kirkdale, but from the Ightham Fissures. At that time I was unaware of Cuvier's suggestion and so no reference was made to it in my description of *A. abbotti*.

Since 1910 I have determined remains of *A. abbotti* from the following Late Pleistocene deposits:—

KENT. *Ightham Fissures*.

The type and several other tolerably complete skulls of younger individuals; a considerable number of fragmentary skulls, mandibular rami, and limb bones.

YORKSHIRE. *Kirkdale Cave, Vale of Pickering*.

1. Part of a skull, a left ramus, and some limb bones (B.M., No. 54).
2. Fragmentary right ramus, some detached teeth, and a right femur, the specimens figured by Buckland (Rel. Diluv., pl. 11, figs. 1-7; B.M., Egerton Coll.).
3. Three other mandibular rami, several detached teeth and some limb bones (B.M., Nos. 35682, 44764, 42357).

Notwithstanding the fragmentary nature of these remains they seem to be referable to *A. abbotti*. The postero-lateral palatal pits are large; the mandibular angle is small; the limb bones are very small and slender, as noted by Cuvier.

DEVONSHIRE. *Kent's Cavern, Torquay*.

1. Anterior part of a skull and part of a left ramus figured by Owen (Brit. Foss. Mamm., p. 201, figs. 76a and b); five other rami

and some limb bones (B.M., Nos. 15081, M. 929, 564, 838, 1123 and 1124).

2. A nearly complete, subadult skull and mandible, collected by Mr. Herron.

DEVONSHIRE. *Brixham Cave, Torquay.*

Part of a left mandibular ramus, probably referable to *A. abbotti* (B.M., No. 48925).

DEVONSHIRE. *Torbryan Cave, Torquay.*

Skull and right ramus, probably of one individual, together with the left mandibular ramus of a larger animal (B.M., No. M. 4650).

DEVONSHIRE. *Happaway Cave.*

A series of mandibular rami, mostly fragmentary. One, nearly perfect, shows the peculiarities of *A. abbotti*. (Pengelly Collection, B.M., No. M. 5807, etc.).

LANCASHIRE. *Dog Holes, Warton Crag.*

Three fragmentary palates; presented by Mr. J. Wilfrid Jackson (B.M.).

These are probably referable to *A. abbotti*.

HEREFORDSHIRE. *Cave in the Valley of the Wye, near Symond's Yat.*

Parts of three skulls and several mandibular rami; collected by Miss D. M. A. Bate (B.M., Nos. 7765, 7773).

HEREFORDSHIRE. *Merlin's Cave, Wye Valley, Symond's Yat.*

A large number of fragmentary skulls, mandibular rami and other remains collected by the Bristol University Spelæological Society, 1924, 1925. (Hinton, Proc. Bristol Univ. Spel. Soc., 2, p. 158.)

SOMERSETSHIRE. *Aveline's Hole, Burrington Combe, Somerset.*

A number of imperfect skulls, mandibular rami, and other remains, representing at least twenty-two individuals; collected by the Bristol University Spelæological Society (Hinton, Proc. Bristol Univ. Spel. Soc., 1, p. 77; 2, p. 36).

GLAMORGANSHIRE. *Gower; Cave deposit.*

Part of a left mandibular ramus, probably referable to *A. abbotti*, but not determinable with certainty (B.M., No. M. 119; Colonel Wood, 1865).

CHANNEL ISLANDS. *Jersey; La Cotte de St. Brelade.*

Some scanty remains, insufficient for precise determination, were obtained in this cave and not improbably represent *A. abbotti* (Hinton, Bull. Ann. Société Jersiaise, 43, p. 356, 1918).

## 10. †*Arvicola antiquus* Pomel.

1853. *Arvicola antiquus* Pomel, Catal. Méthod., p. 25.

Type.—None indicated.

Type locality and horizon.—Brèche de Coudes, Puy-de-Dôme, France; Late Pleistocene.

Range.—Late Pleistocene of France, from the Auvergne northwards to the neighbourhood of Paris. Recorded by Pomel as very common in the Brèche de Coudes, and as occurring in the fluviatile deposits of Neschers, in the terrace deposit of Langy, environs of Paris ("où il a été pris pour l'*Arr. amphibius*"), and in the cave of Brengues (where it was determined at first as *A. terrestris*).

Characters.—Closely related to *A. abbotti* and the living

members of the *A. scherman* group, but its characters are still imperfectly known. Pomel says that the skull closely resembles that of *A. s. monticola* in the form of the frontal, on which the superciliary ridges are in contact but not fused (indicating that his specimen was a subadult skull), but differs in its slightly larger and posteriorly less contracted anterior palatal foramina, in its less flattened nasals, in its larger post-palatal pits and narrower choanæ; "c'était une espèce du type des *Schermaus*, c'est-à-dire s'éloignant beaucoup plus du bord des eaux que les rats d'eau, et peut-être tout-à-fait terrestre comme le *Monticola* d'Auvergne."

This species is represented, in the British Museum, by portions of twelve skulls and a number of mandibular rami from the Pleistocene deposit at Neschers, Auvergne (Croizet Collection). These remains suffice to confirm Pomel's statement that *A. antiquus* is a member of the *A. scherman* group; in size, straightening of the upper incisors, narrowness of nasals, extensive post-palatal pits, and in the form of the mandible this fossil species is much like *A. abbotti*. None of the skulls from Neschers shows the occiput, and in the absence of such a specimen it is impossible to complete the comparison of the French and British fossils.

Parts of fourteen skulls and about sixty mandibular rami from the Pleistocene cave deposit at Bruniquel, Tarn-et-Garonne, are in the Museum and these are evidently to be referred to *A. antiquus* also.

Two left and two right mandibular rami from a Pleistocene cave deposit in the Frou-du-Sureau, near Montaigne, Valley of the Meuse, are referable to the *A. scherman* group and may perhaps belong to *A. antiquus*.

Lastly some fragmentary jaws and detached teeth from the Pleistocene of Mayence (B.M., Nos. 30518, 30519; Hastings Coll.) and other fragmentary remains from the Bromburg Cavern, Posen (B.M., No. 53; Soemmerring Coll.), are not specifically determinable. Remains of "*A. amphibius*" have been recorded from many continental Pleistocene deposits by Nehring, Woldrich and others, but in the absence of material I am unable to say what species or groups these represent.



## EXTERNAL MEASUREMENTS.

Unless otherwise stated all measurements are in millimetres. The tail measurement is the length without the terminal hair; the hind-foot measurement is the length from the heel to the point of the longest toe, exclusive of the claw. Where possible, in order to indicate the relative ages of the individuals measured and in order to control the unsatisfactory head and body measurement, the three chief cranial measurements have been included. Detailed measurements of skulls are given in the appropriate tables.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylar-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>1. Dicrostonyx.</b>									
<i>D. TORQUATUS.</i>									
<i>D. t. torquatus.</i>			3" 1'''	4½'''	7'''*	—	—	—	*With claws 1¼''' (Pallas).
<i>D. t. ungulatus.</i>			131	25*	—	—	—	—	*With pencil (Heuglin).
<i>D. t. ungulatus.</i> Novaya Zemlya.		Old ♂	101.4	14.6	20	27.5	—	—	(G. M. Allen.)
<i>D. CHIONOPES.</i> N. E. Siberia.		♂	115	19	20	—	—	—	(G. M. Allen.)
<i>D. RUBRICATUS.</i> <i>D. r. rubricatus.</i> Alaska.	Average of 5 adults. Maximum.		137	20	22	30.3	—	8.2†	(G. M. Allen.)
<i>D. r. richardsoni.</i> Pt. Churchill, Hudson's Bay.	Average of 5 adults. Maximum.		119	13	19	—	—	—	(E. A. Preble, recorded by G. M. Allen.)
<i>D. EXSUL.</i> St. Lawrence Island.	Type.	♂	135	15	20	32	—	8.3†	(G. M. Allen.)
<i>D. GREENLANDICUS.</i> Discovery Bay, Grant Land.	77.8.6.5		129	17	20	—	—	8†	(G. M. Allen.)
			106	16	14	20.6	18.3	6.6	In alcohol.
			106	15	15	—	—	—	
			100	15	16	—	—	—	
			105	16	16.5	—	—	—	

† Alveolar.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylar basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>DICROSTONYX HUDSONIUS.</b>									
Labrador.	25.9.6.2	♀	106	16	18	—	—	—	
Labrador, Olak.	12.5.6.4		—	—	18	—	—	—	
	12.5.6.5		—	—	17	—	—	—	
Labrador, Hopedale.	61.2.4.1		—	—	18	31.5	20.3	7.3	
"	61.2.4.2		—	—	18	—	—	—	
<b>2. Synaptomys.</b>									
<b>S. (SYNAPTOMYS) COOPERI.</b>									
Michigan, Ann Arbor. Average of 4 adults.			105	17.5	18	—	—	—	(Merriam.)
N. Carolina, Roan Mt.			101	20	19.5	—	—	—	
Massachusetts, Wareham.	7.7.7.1037	♂	123	18.5	18	—	—	—	Miller Coll.
Indiana, Brookville.	78.6.24.2		95	13	16	—	15.5	6.2	
<b>S. (S.) FATIUS.</b>									
Godbout.		♀	87	19	18	—	—	—	(Merriam.)
Quebec, Lake Edward. Average of 2 adults.			106	18	18.7	—	—	—	(Merriam.)
Ontario, North Bay.	7.7.7.4227	♂	112	22	19	25.7	15.8	6.3	Miller Collection; three largest and oldest specimens.
	.4238	♂+♀	112	20	19	—	—	—	
"	.4243	♀	113	19	18	—	—	—	
<b>S. (S.) HELALETES.</b>									
Virginia, Dismal Swamp.	U.S.N.M.	♀	103	22	20	—	—	—	Type (Merriam).
	Average of 4 adults.		97.5	21	20.2	—	—	—	
Kansas, Woodson County.	Average of 6.		99.5	20.5	19	—	—	—	(Merriam.)



Species and locality.	Number.	Sex.	Head and and body.	Tail.	Hind-foot.	Condylo-basal length.	Dental length.	Upper molars (on crowns.)	Remarks.
<b>3. Myopus.</b>									
<i>M. SCHISTICOLOR.</i> Norway, Lidsvold, Akerhus.	84.10.31.2	♀	95	19	15.4	—	—	—	In alcohol.
<i>M. MORULUS.</i> Altai Mts.	U.S.N.M.	♂	86	14	16	22.7	—	6.6†	Type ( <i>Hollister</i> ).
<i>M. SAIANICUS.</i> Syansk Mts.	12.4.1.126	♂	88	14	16	25.8	16.9	7.4	Type.
<i>M. MIDDENDORFFI.</i> Coast of the Sea of Okhotsk.	13180	♂	90	12.8	15.5	26.2	—	7.7†	Vinogradov. (Specimens in Leningrad Museum.)
	13181	♀	95	13	15.1	25.8	—	7.7†	
	13182	♂	86	13.2	16.3	25.2	—	7.5†	
	13179	♂	91	12.5	15	26	—	7.4†	
	13183	♀	87	15.3	15	25	—	7.5†	
	12	♂	96	16.5	15	—	—	—	
	13186	♂	96	16.8	15.8	—	—	—	
<i>M. THAYERI.</i> N.E. Siberia, Kolyma River.	M.C.Zool. Harvard.	♂	99	15	18	25.8	—	7.5†	Type ( <i>Allen</i> ).
		♂	83	20	18	—	—	—	

† Alveolar.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl.-basal length.	Dental length.	Temporal ridges separated by	Remarks.
<b>4. Lemmus.</b>									
LEMMUS LEMMUS.									
Norway. Mölmen.	98.5.2.10	♂	119	—	18	—	—	—	—
	.11	♂	114	—	17	—	—	—	—
Trondhjem.	8.10.5.1	♂	118	12	16	29.2	19.1	0.1	—
"	.2	♂	137	13	20	31.7	—	—	—
"	.5	♂	92	10	15	24	15.4	1.6	Juv.
"	.12	♂	134	12	16	—	19.2	0.3	—
"	.13	♂	123	14	16	—	—	—	—
"	.3	♂	120	13	16	—	—	—	—
"	.4	♀	138	12	17	29.3	19.6	0	Ridges fused.
"	.6	♀	128	12	16	27.9	19	0	" "
"	.7	♀	123	12	16	—	18	0	" "
"	.8	♀	138	12	17	—	—	0	Fused and fairly salient.
"	.9	♀	145	12	20	—	—	—	—
"	.10	♀	130	20	20	26.9	18.1	0.6	—
"	.11	♀	145	17.5	21	—	—	—	—
Sweden. Jemtland.	8.10.19.19	♂	145	18	17	—	20	0	Fused.
"	.20	♂	119	17	14	27.5	17.8	0.7	—
"	.23	♂	143	18	17	30.5	19.7	0	Fused.
"	.24	♂	134	19	18	30.5	19.6	0	"
"	.25	♂	115	18	17	—	19.2	0.8	—
"	.21	♀	112	19	16	27.6	18.6	0	Fused.
"	.22	♀	97	15	14	24	16.3	0.8	Juv.
"	.26	♀	120	19	17	29.3	19.2	0.1	—
"	.27	♀	130	19	18	29.2	19.5	0.3	—
Kola Peninsula.	7.7.7.3620	♀	—	—	—	33	22.3	0	Fused and salient.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylar basal length.	Dental length.	Temporal ridges separated by	Remarks.
<b>LEMUS OBENSIS.</b>									
<i>Type</i> : Berlin Mus.	Brants, "Muizen," p. 56.	—	6"	5'''	9½'''*	—	—	—	* With claws.
	19.7.7.3281	—	—	—	17	30	20.1	0.7	
<b>Taimyrland.</b>									
<i>L. o. norosibiricus.</i>									
New Siberian Archipelago; Kotelmy and Liakhov Islands.	Zool. Mus. Russ. Ac. Sci., No. 7724	♂	125	13	18	34.5	—	?	
(Measurements recorded by Vinogradov, Ann. Mag. N.H., [9], 14, p. 188).	7738	♀	103	8.5	16.8	32	—	?	
	7725	♂	125	13	18	31.4	—	?	
	7728	♂	115.6	12.1	16	32	—	?	
	7726	♀	96	12.5	16	30	—	?	
	7721	♂	—	8.3	14.3	29.7	—	?	
	11711	♂	104.2	7.3	14.3	—	—	—	
	67.1904.1	♂	102	15.8	17	—	—	—	
<i>L. o. chrysogaster.</i>									
Giehiga; W. coast of Sea of Okhotsk.	Amer. Mus. N.H., No. 18762.	—	78	10	14	25	—	—	Immature. <i>Type.</i> Allen, B.A.M.N.H., 19, p. 154.
<b>L. AMURENSIS.</b>									
E. Siberia, Amur. ( <i>Type.</i> )	Zool. Mus. Russ. Ac. Sci., No. 13722.	♀	96	10.6	14	23.2	—	?	Vinogradov, Ann. Mag. N.H., [9], 14, p. 186.
<b>L. PAULUS</b>									
Kolyma River, N.E. Siberia.	Mus. Comp. Zool., Harvard, No. 15288 ( <i>type</i> ).	♂	109	16	17.5	29.5	—	?	(Dry). Allen.
			100	17	19	—	—	—	(Dry).

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl-basal length.	Dental length.	Temporal ridges separated by	Remarks.
<i>L. NIGRIPES.</i>									
St. George Island, Pribilof Islands, Alaska.	U.S. Nat. Mus., No. 59152 ( <i>type</i> ).	♂	130	13	17.5	—	—	—	True.
"	{ 414		—	—	18	—	—	—	HF. measured on skins (dry).
"	{ 416		—	—	19.5	30	19.6	0.3	
"	{ 415		—	—	17.5	—	—	—	
<i>L. ALASCENSIS.</i>									
Point Barrow, Alaska.	U.S. Nat. Mus. $\frac{6.4 \frac{2}{3}}{6.1 \frac{2}{3}}$ ( <i>type</i> ).	♀	100	15	18	—	—	—	
<i>L. YUKONENSIS.</i>									
Yukon River, Alaska.	U.S. Nat. Mus. 98849	♀	113	17	19.5	—	—	—	
"	17.10.6.7		127	9	17.8	31.1	20.5	0	Ridges fused.
"									
<i>L. MINUSCULUS.</i>									
Kakhtul River, Alaska.	U.S. Nat. Mus. Average of 10.	♂	119	12	19	—	—	—	
"	Average of 5.	♀	110	12	18.5	—	—	—	
"									
<i>L. HELVOLUS.</i>									
Alberta ( <i>type</i> ). <sup>1</sup>	42.10.7.11		114	15.2	16*	—	17.6	?	* On skin.
<i>L. TRIMUCRONATUS.</i>									
Point Lake ( <i>type</i> ).	42.10.7.13	♂	—	—	15*	—	—	—	* On skin.
Repulse Bay (Dr. Rae)	48.3.13.2		—	—	17.5	—	—	—	
"	.3		—	—	16*	—	18.2	—	* On skin.
Cumberland, Baffin Land (5 skins).	17.1.19.10		—	—	16	—	—	—	
"	.8 and .11		—	—	17	—	—	—	
"	.9 and .12		—	—	18	—	—	—	

♂ <sup>1</sup> Richardson records the dimension of this specimen as Head and body 4'' 6''; tail 7''; hind-foot from heel to end of claw 8''; but the measures were probably taken on the stuffed skin (Fauna Bor. Amer., p. 129, 1829).

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylobasal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>5. Evotomys.</b>									
a. <i>glareolus</i> group.									
<i>E. GLAREOLUS.</i>									
<i>E. g. glareolus.</i>									
Holland.		♂	102	51	17.6	—	—	—	
Denmark, Zealand.		♂	98	44	16.5	—	—	—	
Brunswick.	Average of 10 adults.		102.5	47.3	17.1	—	—	—	
	Maximum.		111	54	17.6	24.6	14	5.3	Old, long roots.
	Minimum.		98	40	16.6	—	—	—	
Harz Mts.		♂	108	45	16.6	—	—	—	
"		♂	102	52	17	—	—	—	
France, Pas-de-Calais.		♂	101	57	17.5	—	—	—	
"		♂	97	59	18.5	—	—	—	
Seine-et-Marne.		♂	103	54	17.6	—	—	—	
"		♂	108	47	17.8	—	—	—	
<i>E. g. britannicus.</i>									
Reigate, Surrey	Average of 20.	♂	91	46.2	16.2	—	—	—	All sexually mature. Weight in grammes : average 18.6; range 16-23.5.
( <i>L. E. Adams</i> ).	Maximum.		100	55	17	—	—	—	
	Minimum.		85	42	15	—	—	—	
Great Britain	Average of 36 adults.	♂	93	43	16.25	—	—	—	Old, long roots. All sexually mature. Weight in grammes : average 19.8; range 14.5-26.
(various localities).	Maximum.		104	55	18	24.2	13.4	5.1	
Reigate, Surrey	Average of 20.	♀	92.6	47.5	16.3	—	—	—	
( <i>L. E. Adams</i> ).	Maximum.		105	55	17	—	—	—	
	Minimum.		81	40	15.5	—	—	—	
Great Britain	Average of 38 adults.	♀	93	43	16.25	—	—	—	
(various localities).	Maximum.		117	51	18	—	—	—	





Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl.-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>Evotomys glareolus sobrus.</i>									
Croatia.	21.12.1.16	♀	101	46	18	24.4	13.9	5.2	Type, long roots.
	.15	♀	93	43	18	23.4	13.5	5.2	Short roots.
<i>E. g. saianicus.</i> Syansk Mts.	12.4.1.85	♀	95	50	16	23	13	4.9	Type, long roots.
E. CENTRALIS.									
Thian Shan Mts.	5.12.4.14	♂	85	35	16	22.9	13.2	5	Type.
<i>b. nageri</i> group.									
E. NAGERI.									
<i>E. n. nageri.</i>									
Switzerland, Vitznau, Lucerne ( <i>O. Thomas</i> ).	5.8.3.22	♂	107	58	19.2	25.8	14.7	5.4	Long roots.
	.23	♂	108	58	18.4	25.5	14.6	5.6	" "
	.24	♀	108	55	18.5	—	—	—	—
	.25	♀	105	56	18.5	—	—	—	—
	.25	♂	103	62	19.6	—	—	—	—
Locarno, Ticino ( <i>O. Thomas</i> ).	5.8.2.15	♂	103	55	19.3	24.9	13.8	5.3	Long roots.
	.16	♂	108	59	19.5	—	—	—	—
	.17	♀	106.3	64.5	18.8	—	—	—	—
Uri, Andermatt.	Average of 10 adults.		112	72	19	—	—	—	—
	Maximum.		101	59	18.6	—	—	—	—
	Minimum.		103	57	18	—	—	—	—
<i>E. n. italicus.</i>									
N. Italy, Pass of Brennero, Alto Adige.		♂	107	62	19	—	—	—	Recorded by G. B. dal Piaz.
		♂	112	55	18	—	—	—	
		♂	100	60	20	—	—	—	
		♂	100	50	19.4	—	—	—	
		♀	108	60	19.2	—	—	—	
		♀	110	54	19	—	—	—	
		♀	107	52	18.5	—	—	—	
		♀	110	57	19	—	—	—	
		♀	110	57	19.3	—	—	—	

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylodental basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>E. n. vesanus.</i>									
Bavaria, Mittelberg.	8.11.30.12	♀	102	60	18	25.4	14.4	5.2	Type, long roots.
	.13	♀	105	55	18	—	14.7	5	" "
	.14	♀	95	51	18	22.8	12.8	4.5	Cement spaces closed.
<i>E. n. hallucalis.</i>									
Calabria, S. Italy.	6.8.4.9	♂	115	66	21	25.6	14.8	5.7	Type, short roots.
<i>E. n. rascoviæ.</i>									
France, Montréjeau, Haute Garonne.	U.S.N.M.	♂	107	53	19	25	—	5.8†	Type. † Alveolar.
Caterille, Haute Garonne.		♀	97	44	18.8	—	—	—	—
L' Hospitalet, Ariège.		♂	112	54	19.6	—	—	—	—
" "		♀	110	60	18.8	—	—	—	—
Porté, Pyrénées Orientale.		♀	110	55	19	—	—	—	—
" "		♀	112	56	19	—	—	—	—
<i>E. n. norvegicus.</i>									
W. Norway, Bergen. U.S. Nat. Mus.	84674	♀	108	57	18.6	26.2	—	5.8†	Type.
Granvin, Hardanger.	5.8.5.2	♀	105	55	21	24.5	13.9	5	Old, long roots.
" "	.1	♀	106	55	21	—	—	—	—
Bergen, Opheim.	7.7.7.4463	♂	97	45	20.5	—	—	—	—
" "	.4462	♀	99	57	21	—	—	—	—
E. GORKA.									
Croatia.	26.3.7.1	♀	117	54	19	26.6	15.2	5.4	Type, adult, long roots.
E. SKOMERENSIS.									
Skomer Island.	3.7.4.1	♂	113	56	17	25.5	14.5	5.5	Short roots.
	.2	♂	110	56	19	—	—	—	—
	.3	♂	108	59	18	25	14.4	5.4	Type, adult, moderate roots.
	.4	♂	107	54	18	—	—	—	—
	.5	♂	105	53	18	—	—	—	—
	.6	♀	110	54	18	—	—	—	—
	.7	♀	109	55	18	—	—	—	—

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl. basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>EYOTOMYS CÆSARIUS</i> . Jersey.	3.2.11.2	♂	96	49	18	25.6	14.6	5.5	Type, adult, short roots.
	8.9.2.12	♂	109	50.5	20	27	15.7	6.1	Old, long roots.
	.13	♂	111	48	19	26	14.9	5.9	" " "
	19.8.3.1	♂	115	50	20	25.8	15.4	6.2	" " "
	8.9.2.16	♀	107	54	20	25.7	15.4	6	" " "
	19.8.3.5	♀	116	49	18	26.1	15.5	6.3	" " "
	.6	♀	113	49	19	25.4	14.9	5.9	" " "
	14.1.30.4	♂	108	44	18	25.3	14.1	5.6†	Type, old, long roots.
	.135	♂	110	44	19.5	25.3	14	5.7†	Old, long roots.
	.136	♂	103	44	18	24.9	—	5.6†	" " "
<i>E. ALSTONII</i> . Mull.	.128	♂	105	45	18.5	—	—	—	" " "
	.130	♀	100	42	18	24.1	—	5.2†	" " "
	14.1.30.5	♂	110	45	18	25.2	14.5	5.8	Type, adult, short roots.
	.80	♂	112	48	20	—	14.5	5.7	Adult, short roots.
	.81	♂	114	50	20	25.4	14.6	5.9	" " "
	.201	♀	97	42	20	—	—	—	" " "
<i>E. ERICA</i> . Raasay.	200	♀	120	54	19	—	—	—	" " "
	6.3.6.172	♂	100	51	19.5	—	—	—	Type, adult, short roots.
<i>E. PONTICUS</i> .	.173	♂	102	54	19	24.5	13.7	4.8	" " "
	8.3.2.18	♀	112*	48	19	24.5±	13.6	5	Type, cement spaces closed.
<i>E. FRATER</i> .									
<i>e. rutilus</i> group.									
<i>E. BAIKALENSIS</i> . E. of Lake Baikal.	Moscow Univ. Mus.	Max.	101	36.7	18.3	25.5	—	5.2†	Recorded by Ognev.
		Min.	96.3	36	17.2	—	—	—	

\* Measured on skin.

† Alveolar.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylobasal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>E. LATICEPS.</i>									
Irkutsk.	Moscow Univ. Mus.	♀	103	41.2	17.7	24.8	—	5†	Recorded by Ognev.
<i>E. PARVIDENS.</i>									
Irkutsk.	Moscow Univ. Mus.	♀	96	38.7	16.2	24.2	—	4.7†	Recorded by Ognev.
<i>E. RUTILUS.</i>									
<i>E. r. rutilus.</i>	U.S. Nat. Mus. 49.11.16	—	98	23	18	—	—	—	Recorded by Miller, from a well-made skin;
Lappmark.		—	—	—	17	—	—	—	caudal pencil 12.
Jenissei, Alzamai.	14.11.1.77	♂	98	35	16	—	13.5	4.3	Old, roots above alveoli.
"	.73	♀	98	31	16	—	13.1	4.3	Adult, short roots.
"	.74	♀	95	29	16	23	12.7	4.4	Adult, roots well developed.
Malta, Irkutsk.	.71	♂	100	31	16.5	—	13.7	4.8	Old, roots protruding.
"	.72	♀	97	38	16.5	—	13.2	4.5	Adult, short roots.
Mantchuria, Klunglan Mts.	10.5.1.67	♂	90	28	17	22.1	12.6	4.4	Cement spaces closing.
"	.68	♀	93	34	16.5	—	12.8	4.6	Old, long roots.
<i>E. r. russatus.</i>									
Syansk Mts.	12.11.1.87	♂	97	39	18	23.7	13.1	4.5	Old, long roots.
N.E. Altai.	14.6.12.2	♂	85	33	16.2	21.9	12.2	4.3	Old, long roots.
<i>E. WOSSENSKII.</i>									
Kamtschatka.	8.4.8.1	Max.	—	—	17	—	—	—	
"	.8	Min.	—	—	16	—	—	—	
"	Co-type.	—	87	36	19.5*	—	—	—	* With claws.
<i>E. JOCHELSONI.</i>									
N.E. Siberia, Verkhne	Am. Mus.	♀	85	22	17	22	—	—	Type, recorded by J. A.
Kolymsk.	19538	—	80	—	17	—	—	—	Allen.
"				† Alveolar.					

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl.-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>EVOTOMYS AMURENSIS.</i> Saghalien.	7.2.5.76	♂	102	38	17	22.9	13.5	4.4	Old, long roots.
	7.2.5.89	♂	106	44	18.5	—	—	—	—
	7.2.5.99	♂	105	50	17.5	—	—	—	—
	.73	♂	100	40	18	—	—	—	—
	.93	♀	104	49	19	—	—	—	—
<i>E. MIKADO.</i> Japan, Hokkaido.	6.1.4.206	♀	104	34	17	—	13±	4.5	<i>Type</i> , short roots.
	7.2.7.91	♂	97	43	18	24.6	13.5	4.4	Old, long roots.
	.96	♂	102	45	18	—	—	—	—
	.97	♂	107	48	18	24.3	14.2	4.9	Old, long roots.
	.99	♀	102	47	18	24	13.8	4.9	" " "
<i>d. rufocanus</i> group. <i>E. RUFOCANUS.</i> <i>E. r. rufocanus.</i> Lappland, Norway.	11.1.1.153	♂	114	37	18	—	—	—	<i>m</i> <sup>2</sup> with well-developed roots.
	11.1.2.114	♀	125	30	16	26.6	15.8	6.2	<i>m</i> <sup>2</sup> with well-developed roots.
	98.5.2.5	♂	—	25	16	24.5±	14.4	5.8	<i>m</i> <sup>2</sup> cement spaces closing.
	84.10.31.4	♂	—	—	18	26.1	15.4	6.1	<i>m</i> <sup>2</sup> with short roots.
	90.8.1.15	♂	—	—	19	26.9	15.7	6.1	<i>m</i> <sup>2</sup> well-developed roots.
Sweden. Syansk Mts. 100 miles W. of Lake Baikal.	12.4.1.82	♂	95	36	18	22.8	13.3	5.3	<i>m</i> <sup>2</sup> growing.
	.80	♂	80	30	18	26.6	15.5	5.9	<i>m</i> <sup>2</sup> long roots.
	.81	♂	98	36	18.5	26.1	15.2	5.9	" "
	.79	♂	105	37	18	—	15.2	5.8	" "
	.83	♂	99	35	18	20.5	11.9	5.1	<i>m</i> <sup>2</sup> partly in germ.
Irkutsk.	14.11.1.85	♂	65	24	17	—	13	5.3	<i>m</i> <sup>2</sup> growing.
	.80	♂	77	26	17	—	—	—	—
	.82	♀	77	26	16	—	—	—	—

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylar basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>E. RUFOCANUS (continued).</i>									
<i>E. r. rufocanus (continued).</i> Irkutsk.	14.11.1.84	♀	90.5	29	17	23.8	14.1	5.4	$m^2$ cement spaces about to close.
	15.9.3.35	♂	93	28	17	—	—	—	$m^2$ still growing.
	.37	♀	97	29	17	24.5	14.4	5.6	$m^2$ "
	.36	♀	98.5	29	17	—	14.2	5.6	$m^2$ cement spaces about to close.
	14.11.1.86	♀	102	35	17.5	24.7	14.3	5.2	Old; roots appearing at alveolar margin.
	.81	♂	110	30	17	25.9	15.4	5.7	Old; roots visible at alveolar margin.
	15.3.9.39	♂	111	36.5	17.5	26.4	15.1	5.3	Old; roots visible at alveolar margin.
	14.11.1.79	♂	111.5	37.5	18	27.2	15.4	6	Old; roots visible at alveolar margin.
	15.3.9.40	♀	115	40	17.5	—	—	—	Old; roots visible at alveolar margin.
	14.11.1.78	♂	116	37	17	—	15.1	5.7	$m^2$ cement spaces just closing.
	15.3.9.38	♂	117	33.5	18	—	—	—	$m^2$ with long roots.
	14.11.1.83	♀	117.5	32	17	—	—	—	$m^2$ cement spaces closing Old.
Kamtschatka.	8.4.8.9	—	—	—	18	26±	15.1	5.6	$m^2$ Growing.
	.10	—	—	—	19	25±	14.5	5.7	"
	.11	—	—	—	18	—	14.9	5.6	"
<i>E. r. shanensis.</i> Shansi, 100 miles N.W. of Tai-Yuen-Fu.	8.8.7.86	♂	70	25	15.5	21.2	12.8	5.2	"
	.88	♂	85	24	16	22.8	13.6	5.3	"
	.92	♀	82	27	17	23.1	14	5.3	"
	.82	♂	82	28	17	23.4	13.8	5.4	"
	.84	♂	88	31	18	24.3	14.3	5.7	"
	.87	♂	90	23	18	24.5	14.6	5.8	"

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyllo-basal length.	Dental length. (on crowns).	Upper molars (on crowns).	Remarks.
<i>EVOTOMYS RUFOCANUS (continued).</i>									
<i>E. r. shanensis (continued).</i>									
Tai-Yuen-Fu.	8.8.7.91	♂	85	29	18	24.6	14.6	5.8	Growing.
	.90	♀	93	29	17	24.6	15	6.1	"
	.93	♀	100	31	18	25.1	15	5.8	"
	.85	♂	98	98	18	25.7	15.2	5.8	"
Mountains 12 miles N.W. of Ko-lan-chow.	9.1.1.199	♀	99	33	19	25.9	15.5	6.1	Type.
	.198	♀	100	34	18.5	26.3	15.7	6.3	"
	.200	♀	102	37	18	26.3	15.9	6.2	"
	.197	♀	102	37	18	26.7	15.8	6.3	"
100 miles N.W. of Tai-Yuen-Fu.	8.8.7.83	♂	104	32	18	—	15.4	5.8	m <sup>2</sup> with moderate roots.
Imperial Tombs 65 miles E. of Pekin.	8.8.7.81	♀	104	25	18.5	27.3	15.7	5.7	Growing.
Mountains 12 miles N.W. of Ko-lan-chow.	9.1.1.191		63	23	15.5	19	—	—	"
(Series referred to "Caryomys inez"; arranged in order of age.)	.194	♀	90	32	16	22.2	13.2	5.5	"
	.185	♂	88	31	16	22.4	13.1	5.3	"
	.182	♂	88	32	15.5	23	13.5	5.7	"
	.188	♀	90	35	15.5	23.1	13.4	5.7	Type of "C. inez."
	.193	♀	88	35	16	23.3	13.8	5.8	"
	.184	♂	92	32	16	23.6	13.7	5.5	"
	.189	♀	90	33	15.5	23.7	13.6	5.5	"
"Caryomys nux."	10.5.2.85	♀	91	39	15.5	22.9	13.6	5.3	"
S.E. Shen-si, Shang-chow district.	.78	♂	94	37	16	23.1	13.7	5.4	"
(Arranged in order of age.)	.75	♂	84	35	15.5	23.2	13.4	5.4	"
	.82		—	—	—	23.4	13.5	5.6	"
	.79	♂	93	39	16.5	23.4	13.6	5.4	Type of "C. nux."
	.81	♂	93	42	16.5	23.6	13.6	5.3	"
Ching Ling Mountains.	.87	♂	85	35	16	22.4	12.9	5.1	"



Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylobasal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>E. RUFOCANTUS</i> (continued).									
<i>E. r. shansicus</i> (continued).									
“ <i>Caryomys eva</i> .”								<i>m</i> <sup>2</sup>	
Tau-chow, Kansu.	12.8.5.49	♀	—	—	—	20.8	12	4.6	Growing.
(Arranged in order of age.)	.52	♂	84	46	16	21.6	12.2	4.7	”
	.55	♀	86	47	15	21.8	12.5	4.9	”
	11.2.1.223	♂	92	50	16	22	12.8	5.5	”
	11.6.1.55	♂	88	50	16.5	22.9	13.1	4.9	”
		♂	83	60	16	22.8	13.1	5.1	”
Tai-pei-San, Shansi.	11.9.8.138	♀	83	50	16.5	21.4	12.3	5	”
“ <i>Caryomys alcinous</i> .”	.133	♂	85	48	16.5	22	12.8	5.2	”
Sze-chwan, Wei choe.	.135	♂	86	52	17	22.3	13	5.1	”
(Arranged in order of age.)	.134	♂	86	54	17	22.4	13.3	5.4	”
	.137	♂	—	—	—	22.4	13.2	5.1	”
	.136	♀	90	56	17	23.4	13.9	5.6	”
“ <i>Caryomys aquilus</i> .”	13.9.13.10	♀	102	55	19	23.3	13.6	5.3	”
Hupeh, China.	7190	♂	101	59	20	23.8	—	6 (alveolar).	<i>Type.</i>
<i>E. r. regulus</i> .	6.12.6.102	♀	84	31	17.5	21.9	13.3	5.5	Growing.
Korea.	.97	♂	87	36	18	22.4	13.3	5.2	”
(Arranged in order of age.)	.94	♂	84	37	17	22.9	13.4	5.2	”
	.101	♀	90	38	18	22.9	13.3	5.3	”
	7.6.3.59	♀	87	39	17.5	23.6	13.8	5.4	”
	6.12.6.96	♂	92	35	18	23.6	13.8	5.4	”
	6.12.6.110	♂	93	34	18.5	23.7	14.3	5.5	”
	7.6.3.58	♀	88	37	18	23.8	13.8	5.3	”
	6.12.6.108	♀	100	39	19	23.9	14.2	5.4	”
	7.6.3.60	♀	91	42	19	24	14	5.3	”
	6.12.6.93	♂	94	42	18.5	24	14.3	5.5	”

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylo-basal length.	Dental length. (on crowns).	Upper molars (on crowns).	Remarks.
<i>EVOTOMYS RUFOCANTUS (continued).</i>									
<i>E. r. regulus (continued).</i>									
Korea. (Arranged in order of age.)	6.12.6.106	♀	95	39	18	24.3	14.1	5.6	Growing.
	.95	♂	96	35	19	24.3	14.5	5.5	"
	.92	♂	108	42	18	25.3	14.8	5.4	"
	7.6.3.61	♂	105	45	20	25.5	14.7	5.6	"
	6.12.6.98	♀	111	42	19	25.6	14.9	5.8	"
	.103	—	—	—	—	25.7	15.4	5.8	"
	13.5.27.54	♀	97	35	20	25.7	15.3	5.7	With roots.
	.56	♀	116	34	20	25.8	15	6	"
	7.6.3.57	♀	110	49	18.5	26.1	15.3	5.9	Growing.
	.53	♂	108	47	18.5	26.3	15.5	6	"
6.12.6.100	♀	110	41	19	26.3	15.4	5.8	"	
13.5.27.53	♂	99	37	20	26.3	15.4	6	With roots.	
6.12.6.105	♀	110	47	19	26.5	15.5	5.5	Growing.	
.89	♂	116	45	18.5	26.6	15.8	6	Cement spaces closed.	
<i>E. r. smithii.</i>									
Japan.									
(Arranged in order of age.)	7.6.3.54	♂	112	49	20	27.8	16.1	6	Growing.
	6.1.4.345	♀	83	36	—	20.6	11.7	4.5	Growing.
	.341	♀	84	42	17.5	21	12.7	4.8	"
	.352	♀	83	43	18	21.1	12.7	5	"
	.325	♂	86	44	17	21.6	12.4	4.7	"
	.342	♀	90	40	18	22.4	13.3	5.2	"
	7.2.7.68	♀	82	40	19	22.4	13.1	5.2	"
	6.11.2.14	♀	91	46	16	22.5	13.6	5.3	"
	6.1.4.338	♂	94	49	18	22.5	13.2	5.1	"
	.318	♀	94	45	18.5	22.7	13.2	4.9	"
	.337	♂	97	44	17	22.8	13.2	4.9	"
	.331	♂	95	42	17	22.9	13.2	5.3	"
	.326	♂	99	44	17.5	23	13.6	5.2	"
	.340	♀	100	44	17.5	23.1	13.5	5.2	"
			48	17.5	23.2	13.4	5.3	"	

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylodental length.	Dental length. (on crowns).	Upper molars	Remarks.
<i>E. RUFOCANUS (continued).</i>									
<i>E. r. smithii (continued).</i>									
Japan.									
(Arranged in order of age.)									
	6.1.4.336	♂	105	49	19	23.4	13.5	5.3	Growing.
	.304	♂	97	35	19	23.5	14.3	5.5	"
	6.11.2.13	♀	101	49	17	23.5	13.6	5.4	"
	6.1.4.344	♀	101	46	18.5	23.5	13.6	5.5	"
	.332	♂	97	46	16.5	23.6	13.5	5.2	"
	5.3.3.49	♂	" 79 "	54	17.5	23.7	13.8	5.1	Type.
	6.1.4.305	♂	99	37	19.5	23.7	14.2	5.5	"
	.339	♂	100	50	17.5	23.7	13.7	5.2	"
	.312	♂	95	45	18	23.9	13.9	5.1	"
	.335	♂	99	44	18	23.9	14	5.7	"
	.329	♂	100	49	17	23.9	14	—	"
	.323	♂	100	49	18.5	24	14.1	5.6	"
	.315	♂	100	46	18.5	24.2	14.1	5.6	"
	7.2.5.67	♂	" 89 "	41	20	24.2	14.4	5.9	"
	6.1.4.321	♂	93	45	19	24.5	14.2	5.5	"
	.317	♀	97	47	17.5	24.5	14.6	5.6	"
	.322	♀	101	51	18	24.5	14.7	5.5	"
	.350	♀	102	47	18.5	24.6	14.3	5.7	"
	7.2.7.69	♂	90	43	19	24.8	14.6	5.6	"
	7.2.7.69	♂	90	43	19	24.8	14.6	5.6	Cement spaces about to close.
	.71	♂	92	45	20	24.8	15	5.7	Cement spaces about to close.
	.72	♂	93	43	19	24.9	15	5.5	Cement spaces just closed.
	.79	♀	90	46	19.5	25	14.8	5.6	Growing.
	7.2.5.68	♂	95	40	20	25	15	5.6	"
	7.2.7.80	♀	102	48	19	25.1	15.1	5.8	Cement spaces closed.
	7.2.5.55	♂	103	42	20	25.2	14.8	5.6	Growing.
	8.12.1.65	♂	107	63	18	25.4	14.6	5.4	" Type of <i>C. nigatae</i> .

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylar basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>EVOTOMYS RUFOCANUS (continued).</i>									
<i>E. r. smithii (continued).</i>									
Japan.	10.1.1.27	♂	—	—	—	25.7	15.3	5.8	Growing.
(Arranged in order of age.)	6.1.4.307	♂	120	54	18.5	25.7	14.5	5.7	Type of <i>C. andersoni</i> .
	7.2.5.71	♀	104	44	20	25.8	15.5	6	Growing.
	.72	♀	105	47	20	25.8	15.3	6	"
	.63	♀	107	54	20	25.8	15.4	6	"
	.61	♂	109	46	21	25.9	15.2	5.9	"
	.66	♂	104	45	21	26	15.5	6	Cement spaces closed.
	7.2.7.67	♂	105	48	20	26	15.5	6.2	"
	7.2.5.59	—	—	—	—	20.1	15.6	6	Cement space about to close.
	86.11.2.3	—	—	—	—	20.1	15.7	6.1	Short roots.
	7.2.5.60	♂	102	44	20	20.2	15.4	5.8	Growing.
	6.1.4.300	♀	115	51	21	20.2	15.4	5.8	Cement spaces closed.
	7.2.7.77	♀	100	52	20	20.3	15.5	6.1	"
	7.2.5.66	♂	104	45	21	20.4	15.7	5.8	"
	7.2.7.82	♂	107	56	20	20.4	15.6	6.1	Roots beginning.
	.83	♀	108	52	20	20.4	15.9	5.9	"
	7.2.5.58	♀	113	52	20.5	20.6	15.8	6.1	Growing.
	7.2.5.62	♂	115	53	22	20.6	16.2	6.1	Cement spaces closing.
	.69	♀	113	49	20	20.9	16	6.1	Roots beginning.
	6.1.4.298	♂	119	47	20	20.9	16.2	6.2	Short roots. Type of <i>C. bedfordiæ</i> .
	7.2.5.54	♂	115	55	22	27	15.8	6	Cement spaces closed.
	7.2.5.56	♀	122	49	22	27.1	16.1	6	Growing.
	.64	—	—	—	—	27.1	16	6.1	Cement spaces closed.
	6.1.4.299	♂	119	49	21	27.1	15.7	5.8	Roots beginning.
	7.2.7.78	♀	110	55	20	27.5	16.4	6.2	Long roots.
	6.1.4.297	♂	117	43	21	27.8	16.5	6.2	Roots beginning.
	7.2.5.70	♀	113	60	21	28.4	16.9	6.2	Long roots.
	.53	♂	118	52	21	28.5	17.1	6.6	"

EXTERNAL AND CRANIAL MEASUREMENTS OF AMERICAN SPECIES OF *EVOTOMYS*.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylar basal length.	Zygomatic breadth.	Mastoid breadth.	Nasals.	Upper molars alveolar.	Authority and remarks.
<i>E. CAURINUS</i> , British Columbia.	U.S. Nat. Mus., No. 89460	♂	101	34	18	—	13.3	10.8	6.2	4.9	Bailey. Type.
	Average of 5 adults.		99	36	18	—	—	—	—	—	"
<i>E. PHÆUS</i> , Alaska.	Average of 9 adults.		104.7	51	19	24.8	13.8	11.1	7.2	5.1	Swarth.
	Maximum.		106	58	20	25.5	14.8	11.8	7.8	5.2	"
	Minimum.		103	46	19	23.2	13	10.5	6.8	5	"
<i>E. WRANGELI</i> , Wrangel Island, Alaska.	Average of 4 adults.		110	37	20	—	13.5	11	8	5.5	Bailey.
<i>E. DAWSONI</i> , <i>E. d. dawsoni</i> , Canada, Yukon.	Average of 8 adults.		111	33	20	—	14	12.2	7.5	5	Bailey.
<i>E. d. insularis</i> , Hawkins Island, Alaska.	Average of 6 adults.	♂	111	32	19.5	—	14.6	—	7	5	Heller. Type.
			113	32	19.5	—	14.4	—	7	5	"
<i>E. ORCA</i> , Alaska.	U.S. Nat. Mus., No. 98028	♀	108	30	20	—	—	—	—	—	Merriam. Type.
	Average of 6 adults.		108	32	20	—	—	—	—	—	No skull measurements recorded.
<i>E. GAPPERI</i> , <i>E. g. gapperi</i> , New York, Elizabethtown.	Average of 10 adults.		102	39	18.3	—	—	—	—	—	G. S. Miller in Bailey.
New York, Peterboro.	Average of 10 adults.		105	40	18.3	—	—	—	—	—	"
Ontario, Ernsdale.		♂	—	—	—	—	13.3	11.2	6.5	5	Bailey. Old.

EXTERNAL AND CRANIAL MEASUREMENTS OF AMERICAN SPECIES OF *EVOTOMYS* (continued).

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylyo-basal length.	Basal length.	Zygomatic breadth.	Mastoid breadth.	Nasals.	Upper molars, alveolar.	Authority and remarks.
<i>E. g. ochraceus</i> , New Hampshire, Mt. Washington.	E.M., No. 7.7.7.131	♀	108	40	19	23.7	22	13	11.3	6.7	5	Miller. <i>Type</i> .
<i>E. g. rhoadsi</i> , New Jersey.	Average of 3 young adults.		103.3	36	20	—	21.5	13.5	11.3	7	5.2	Bailey.
<i>E. g. loringi</i> , N. Dakota.	Average of 18 adults and type skull.		98.5	34.5	17.9	—	21.5	12.8	10.9	6.8	5	Bailey. [Skull of <i>Type</i> .]
<i>E. g. alabasacæ</i> , Canada.	Average of 10 adults.		105	40.6	18	—	—	—	—	—	—	Preble.
Ft. Chipewyan, Mackenzie, Ft. Smith.	Average of 10 adults.		104	38	18	—	—	—	—	—	—	"
Mackenzie, Ft. Resolution.	Average of 10 adults.		104.2	38.5	19	—	—	—	—	—	—	"
<i>E. g. galici</i> , Colorado.	Average of 6 adults. Topotype adult.	♂	101.4 100	43.6 40	18.2 18	— —	— 22.3	— 13	— 11	— 6.5	— 5	Bailey. "
<i>E. g. saturatus</i> , British Columbia.	Average of 15 adults and skull of average-sized adult.		104	45	18.2	—	22.3	13.5	11.2	6.5	5	"
<i>E. BREVICAUDUS</i> , S. Dakota.	U.S. Nat. Mus., No. 1471 Topotype.	♂	94	31	19	—	21.2	12.5	11.3	6.6	5.4	Bailey. <i>Type</i> .
<i>E. CAROLINENSIS</i> , N. Carolina.	Average of 4 adults and skull of "fully adult ♀."		98	32	19	—	21.8	12.8	11	7	5.3	"
			105	44	20.2	—	23.5	14.4	12	7.5	6	"

V. L.	Species and Locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl. basal length.	Basal length.	Zygomatic breadth.	Mastoid breadth.	Nasals.	Upper molars.	Authority and remarks.
	<i>E. LIMBIS.</i> New Mexico.	U.S. Nat. Mus., No. 141335	♂	120	42	20	—	24.5	14.7	12	8	5.3	Bailey. <i>Type.</i>
		Average of 4 adults.	♂	102.5	39.5	19.6	—	—	—	—	—	—	"
	<i>E. UNGAVA.</i> (Canada, Ungava.	U.S. Nat. Mus., No. 8114	♂	95	39	19	—	22.8	13.5	11	7	5	" <i>Type.</i>
	<i>E. IDAHOENSIS.</i> Idaho.	U.S. Nat. Mus., No. 31783	♀	105	48	20	—	23.5	13.3	11.6	8	5.4	" <i>Type.</i>
		Average of 4 adults.		104	44	20.2	—	—	—	—	—	—	"
	<i>E. MAZAMA.</i> Oregon.	Average of 4 adults.	♂	105	52	18.7	—	23.3	14.2	12.4	7.2	5	Bailey. [Skull of <i>Type.</i> ]
	<i>E. OBSCURUS.</i> Oregon.	U.S. Nat. Mus., No. 80413	♂	108	47	17	—	21.8	13.3	11.5	—	4.5	Bailey. <i>Type.</i>
	<i>E. CALFORNICUS.</i> N. California.	U.S. Nat. Mus., No. 43716	♂	111	50	21	—	22.8	14	12.3	7.5	5.3	" <i>Type.</i>
		Adult.	♂	108	55	20	—	—	—	—	—	—	"
	<i>E. OCCIDENTALIS.</i> Washington.	U.S. Nat. Mus., No. 4341	♂	100	45	18	—	22	12.5	11	7	4.7	" <i>Type.</i>
		Average of 3 adults.		99	47	18.3	—	—	—	—	—	—	"
	<i>E. NIVARIUS.</i> Washington, Olympic Mts.	Average of 3 adults.	♀	100	50	18	—	21	13	11.5	6.5	5	Bailey. [Skull of <i>Type.</i> ]
	<i>E. PROTEUS.</i> Labrador, Hamilton Inlet.	Bangs Coll., No. 4081	♀	118	53	21	—	—	—	—	—	—	Bangs. <i>Type.</i>
		Average of 20 adults.		113	48.8	20.5	—	—	—	—	—	—	"

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl.-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>6. Eothenomys.</b>									
<i>E. MELANOGASTER.</i>									
<i>E. m. melanogaster.</i>	11.2.1.227	♂	96	—	16	24.5	14.7	6	
	.230	♂	96	43	17	—	—	—	
W. Sze-chwan.	.233	♀	96	36	17	—	—	—	
<i>E. m. cachinus.</i>									
N. Burma.	20.8.7.14	♀	108	56	19	25.9	16.2	6.4	Type.
<i>E. m. eleusis.</i>									
N. Yunnan.	11.9.8.111	♂	98	55	17	24.4	14.5	5.5	Type.
	.116	♀	92	50	18	—	—	—	
<i>E. m. aurora.</i>									
Hupeh, China.	Harvard Coll.	♂	105	43	18.5	25.8±	—	6†	Type (Allen).
<i>E. m. milctus.</i>									
W. Yunnan.	14.10.23.32	♂	114	48	19	25.3	15.1	6	Type.
<i>E. m. confinis.</i>									
S. Yunnan.	22.12.1.1	♂	106	59	19	25.2	15.3	5.8	Type, adult.
<i>E. m. colurnus.</i>									
N.W. Fokien.	0.5.8.38	♂	110	35	17.5	25.6	15.2	6.3	Type.
<i>E. m. macronotus.</i>									
W. Sze-chwan.	Harvard Coll.	♀	105	39	19	26±	—	6.7†	Type (Allen).
<i>E. m. tibonotus.</i>									
Assam.	21.12.5.54	♂	105	34	17	24.9	15.5	6.1	Type, adult.
<i>E. FIDELIS.</i>									
N.W. Yunnan.	22.12.1.8	♀	126	49	18.5	27.6	16.8	6.6	Type, adult.
	.6	♂	133	40	19	—	17.3	6.3	

† Alveolar.





Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>8. Alticola.</b>									
ALTICOLA.									
A. ARAGURUS.	9.4.3.100	♀	93	50	19	24.6	14.3	5.4	Type, subadult.
A. HISSAR Mts.	81.3.1.22	♂	115	52	19	26.5±	16.2	5.5	In alcohol.
A. BLANFORDI.		♂	99	48	19.3				
A. b. blanfordi.	26.3.9.1	♂	100	51	19	25	14.7	5.5	Type, young adult.
Gilgit.									
A. b. tahalius.									
Lahul.									
A. ROYLEI.									
A. r. roylei.	2002		—	—	17.7	25.8	15.8	6.2	Type.
Kumaon.	Average of 10 adults.		108	36	18.7	—	—	—	Weight 1¼-1½ ozs.
Pindar Valley.	Maximum.		113	39	20	27.2	16.6	6.6	
	Minimum.		102	33	18	—	—	—	
A. r. cautus.									
Lahul.	26.3.9.2	♂	118	44	19	27.3	16.5	6.2	Type.
	Average of 16 adults		109.5	40	18.6	—	—	—	
	from type locality.								
	Maximum.		118	44	19	27.3	—	—	
	Minimum.		98	36	18	—	—	—	
A. ALBICAUDA.	U.S. Nat. Mus. No.	♀	108	32	18	26.4	—	6.6†	Miller.
Baltistan.	5032♀								
	5031♂								

† Alveolar.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condyl. basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>ALITICOLA ALBICAUDA</i> ( <i>continued</i> ).									
Skardu, Nahr Nulla.	5.10.8.5	♂	107	32	20	—	14.8	5.4	
<i>A. MOYNTOSA</i> .									
Central Kashmir.	U.S. Nat. Mus., No. $\frac{29147}{35567}$	♂	92	32	18	24±	—	6	Type, half-grown (Miller).
	13.1.19.20	♀	126	58	20	27.9	16.6	6.1	
	10.1.18.60	♂	103	47	21	27.8	16.4	6.2	
	5.1.5.12	♂	105	45	19	—	14.8	5.6	Type of " <i>A. imitator</i> ."
	7.12.28.2	♀	124	45	20	26.7	15.8	6	
<i>A. GLACIALIS</i> .									
Baltistan.	U.S. Nat. Mus., No. 176071	♀	116	40	20	27	—	6.6†	Type. † Alveolar.
<i>A. PHASMA</i> .									
Kara Korum Mts.	12.4.1.120	♂	101	40.5	20	27	15.8	6	Type.
	Average of 7 adults.	♂	97	39	19.2	—	—	—	
	Maximum.		101	41	20	—	—	—	
	Minimum.		88	36	19	—	—	—	
<i>A. WORTHINGTONI</i> .									
<i>A. w. worthingtoni</i> .									
Thian Shan Mts.	5.12.4.11	♀	101	33	18	26	14.9	5.6	Type.
	.9	♂	110	34	18	25.7	14.8	5.5	
<i>A. w. subulatus</i> .									
Djarkent.	14.5.10.186	♀	95	40	20	25.1	14.5	5.5	Type.
<i>A. w. semicanus</i> .									
Central Mongolia.	Amer. Mus. N.H., No. 57805	♂	110	30	19	28.7	—	6.7†	Type. † Alveolar.
<i>A. STOLICZKANUS</i> .									
Kuenlun Mts.	Calcutta.		101	25	18	29±	—	—	Co-type; recorded by Blanford.



Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylobasal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>9. Hyperacrius.</b>									
<i>H. FERTILIS.</i>									
<i>H. f. fertilis.</i> Pir Panjal (type).	U.S. Nat. Mus., No. 5014, 5015, 5016	♀	114	27	15.6	24.6±	—	6.4†	
Pir Panjal	4.5.4.10	♀	114	25	—	—	15.3	5.4	
Tulhian.	8.7.6.106	♂	106	28	16	—	—	—	
Kishtwar.	8.7.6.94	♀	104	30	16	24.3	15.7	5.7	
Kaghan Valley.	12.11.26.14	♂	103	22	15	24.8	16	6.1	
"	12.11.26.15	♀	111	26	16	—	—	—	
"	12.11.26.16	♂	108	26	16	—	—	—	
<i>H. f. brachelix.</i> Nagnarg. (type).	U.S. Nat. Mus., No. 63445	♀	93	18	16	—	—	—	
Laycock.	5.1.5.10	♀	105	29	16.5	24.8	15.7	5.7	
Zogi-La.	5.1.5.7	♂	102	—	14	—	—	—	
H. AITCHISONI.	6.10.3.12	♀	96	21	15	24.7	16.1	5.7	
Gulmerg (type).	96.11.2.3	♂	102	33	18	—	—	6.4	
Murree, Punjab.	Average of 14.	♂	106.5	39	18.4	—	—	—	Three males, with the head and body measurement ranging between 104 and 116 mm., weighed 1.5 ozs. each.
	Maximum.	♂	116	45	19	29.1	18.8	7.2	
	Minimum.	♂	99	33	18	—	—	—	
	Average of 14.	♂	108	37.5	18	—	—	—	
	Maximum.	♀	116	44	19.5	28.6	18.4	7.1	
	Minimum.	♀	100	33	17	—	—	—	

† Alveolar.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylo-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<b>10. Arvicola.</b>									
<i>A. AMPHIBIUS.</i>									
<i>A. a. amphibioides.</i>									
Surrey, Esher.	6.8.18.1	♂	200	120	38	43.8	27.5	9.6	Skull shown in Pl III.
Northants.	11.1.2.58	♂	204	114	32	43.7	28.3	10.5	
Hampton Wick.		♂	205	135	33.5	44	28.1	10	
England (various localities).	Average of 23 sexually mature.	♂	201.3	124	34	—	—	—	
	Maximum.		219	149	39	—	—	—	
	Minimum.		185	106	29	—	—	—	
	Average of 22 sexually mature.	♀	187.1	116.5	32.7	—	—	—	
	Maximum.		220	144	37	—	—	—	
	Minimum.		170	92	28	—	—	—	
<i>A. a. retā.</i>	5.5.12.1	♂	199	125	32	41.9	26.7	9.7	
Inverness-shire.		♀	194.5	109	30.5	—	—	—	
Fife.	6.11.18.5	♂	174	113	31	41.4	—	—	
"	.6	♂	157	95	29	39.5	—	—	
"		♀							

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylor-basal length.	Dental length.	Upper molars (on crowns).	Remarks.
<i>A. SAPIDUS.</i>									
<i>A. s.apidus.</i>									
Burgos.	8.8.4.115	♀	187	123	34	41.9	27.1	10.1	Type.
Spain, Castellon.	8.2.9.160	♂	203	123	33	44.4	—	—	
	.163	♂	220	127	33	43	27.8	10.4	
<i>A. s. tenebricus.</i>									
France, Biarritz.	6.1.21.5	♂	193	112	34	41.4	26.3	9.5	Type.
<i>A. TERRESTRIS.</i>									
<i>A. t.terrestris.</i>									
Norway.	8.8.9.21	♂	183	107	31	38.4	—	—	
<i>A. t.italicus.</i>									
Switzerland, Locarno.	2.7.1.2	♂	179	102	29	38.2	24.6	9.4	
	2.7.1.5	♀	171	98	27.5	38.2	24.7	9.4	
<i>A. t. musignani.</i>									
Italy, Rome.	11.1.2.37	♂	210	95	30	—	24.9	8.9	
<i>A. t.illyricus.</i>									
Bosnia.	94.1.5.1	♂	—	—	30	—	25	9.1	Type.
Rumania.	4.4.6.66	♂	146	94	28	—	—	—	
<i>A. t. rufescens.</i>									
Tiflis Mus.		♀	185	93	—	—	—	9	Saturin.
		—	138	91	32	—	—	8.3	„
<i>A. t. meridionalis.</i>									
			185	130	33.4	41.7	—	10.3†	Ognev.
<i>A. t. persicus.</i>									
Armenia, Van.	97.6.4.10	♂	195	126	29	40.9	26.2	9.6	Type of <i>A. armenius.</i>
<i>A. t. scythicus.</i>									
Semretchensk.	14.5.10.154	♀	200	130	34	41.2	26.6	9.4	Type.
Central Asia, Jenissei.	14.11.1.64	♀	195	100	30	39	25.8	9.1	
	.62	♂	192	100	31	41.7	26.6	9.1	

† Alveolar.

Species and locality.	Number.	Sex.	Head and body.	Tail.	Hind-foot.	Condylor-basal length.	Dental length. (on crowns).	Upper molars (on crowns).	Remarks.
<i>A. SCHEMANN.</i>									
<i>A. s. scherman.</i>	8.11.2.56	♀	152	64	25	32.3	—	—	
Germany, Ingelheim.	.57	♂	165	73	26	33	21.5	7.9	Ridges 1.1 mm. apart.
	.53	♂	161	84	25	35.3	22.8	8.5	" nearly fused.
	.58	♀	169	81	24	37.2	24.	8.4	" " "
<i>A. s. exitus.</i>	10.8.16.8	♀	138	64	24	33.8	—	8.6†	Type.
Switzerland, St. Gallen.	2.8.4.48	♂	153	69	28	—	—	—	
"	10.8.16.1	♀	200	55	26	—	—	—	
"	10.8.16.5	♂	214	75	27	—	—	—	
"	5.11.18.21	♀	135	57	23	—	—	—	
France, Haute Savoie.	6.6.4.20	♀	147	66	24	—	—	—	
<i>A. s. monticola.</i>	6.6.4.22	♀	145	64	24	—	—	—	
France.	.18	♀	128	69	24	33.6	—	—	
	.15	♂	144	63	23	—	—	—	



CRANIAL MEASUREMENTS:—

Dicrostonyx.

	<i>D. torquatus</i>		<i>D. rubricatus</i>				<i>D. rubricatus</i>		<i>D. exsul</i> Type. (G. M. Allen.)
	Petschhara, Russia. 7.7.7.3621.	[Russian] "Lapland". 49.11.1.11.	<i>D. chinopes</i> , Type. (G. M. Allen.) E. Siberia.	Ft. Anderson.	Griffin Point, Alaska. (G. M. Allen.)	48.3.13.7. (Dr. Rae.)	Wellington Channel 55.1.31.6.	Ft. Churehill. (G. M. Allen.) +	
1. Condyle-basal length.	29.1	28.5	27.5	25	30.3	20.3	31.0	32	20
2. Zygomatic breadth.	19.2	19.4	18	16.8	20.7	3.6	19.5±	20	21.3
3. Interorbital constriction.	3.9	3.5	3	3.8	4	14.8	3.8	4.5	4.6
4. Occipital breadth.	14	14±	13.8	==	13.8	==	15.2	14.8	==
5. " depth (median).	7.1	—	==	==	7±	==	7.8	==	==
6. Condyle to <i>m</i> <sup>3</sup> .	11	10.5±	==	9.2	10.1	==	11.6	==	==
7. " to front of bulla.	8.6	8.4	==	8.1	8.4	==	9.3	==	==
8. Nasal length.	8.6	8.6	8.8	7.5	7.6	==	9.1	9.2	9.2
9. " width.	3.8	3.3	—	2.9	3.5	==	4.2	==	==
10. Dental length.	18.6	18.6	—	16.2	17.6	==	19.6	==	==
11. Diastema.	9.2	9.4	9	7.9	8.8	==	9.4	==	10.9
12. Upper molars (crowns).	6.7	7.1	—	6.4	6.8	==	7.7	==	==
13. " (alveolar).	7.4	7.6	7	6.8	7.2	==	8.3	8.3	8
14. Mandible.	19.8	—	—	18.2	19.2	==	19.5	==	==
15. Lower molars (alveolar).	6.8	—	6.8	6.5	6.8	6.9	7.8	7.5	7.9
			Sub- adult.		Adult.				

CRANIAL MEASUREMENTS:—	<i>D. groenlandicus.</i>			<i>D. hudsonius.</i>			<i>†D. gulielmi.</i>			<i>†D. henschi.</i>		
	Discovery Bay.	Fleobers Beach.	Labrador.	(G. M. Allen.) Max. ♂	Hutton Cave. Co-types.	Langwith Cave.	Type.	Ightham Fissures.	Lea Valley.			
<b>Dicrostonyx (continued).</b>												
1. Condyllo-basal length.	29.2	29.6	12	61	61	31.5±	32	28.6	20.3			
2. Zygomatic breadth.	18.6	18.5	5.6	2.4	2.4	21	21.3	19.8	19			
3. Interorbital constriction.	3.7	3.9	4.1	4.1	4.1	4.1	4.8	4	4.3			
4. Occipital breadth.	14.6	14	14	14	14	16	16	14±	14			
5. " depth (median).	7.3	7.2	7.7	7.7	7.7	7.7	7.7	6.8	6.8			
6. Condyle to <i>m</i> <sup>3</sup>	11.2	11.4	10.7	10.7	10.7	10.7	10.7	10.4	10.4			
7. " to front of bulla.	8.6	8.6	8.7	8.7	8.7	8.7	8.7	7.6	7.6			
8. Nasal length.	8.6	9	9.4	9	9.3	9.3	10	8.7	8.8			
9. " width.	3.5	3.5	3.4	3.8	4.3	4.3	4.3	3.1	3.6			
10. Dental length.	18.3	18.3	19.3	19	20.3	18.5±	18.5±	18.8	18.9±			
11. Diastema	9.4	9.3	9.5	10	10.5	10.5	10.5	9.2	9.5			
12. Upper molars (crowns).	6.8	6.6	7.1	6.9	7.3	7.1	7.1	7.2	7.3			
13. " (alveolar).	7.4	7.3	7.9	7.5	7.9	7.6	7.6	7.4	7.7			
14. Mandible.	19.8	19.8	20.3	21.3	21.8	21.5	21.5	21	21			
15. Lower molars (alveolar).	6.7	6.7	7.4	7.3	7.7	7.7	7.8	7.4	7.4			

Newborn.

## CRANIAL MEASUREMENTS :—

## Synaptomys.

	<i>S. (S.) cooperi</i> .		<i>S. (S.) fatuus</i> .		<i>S. (S.) healdetes</i> .		<i>S. (Mictomys) borealis</i> .				
	Largest recorded by Indiana.	Massachusetts.	New Jersey.	1717, 1827.	<i>helaldetes</i> .	Rhoads.	<i>gossii</i> .	Type.	Halkett.	Metlakatla, B. Columbia.	(2)
1. Condyllo-basal length.	24	24.4	—	25.7	27.8	—	—	23.5	23.8	—	—
1a. Basilar length.	22.6	22.6	24	—	17.7	—	—	—	—	—	—
2. Zygomatic breadth.	16.2	16.6	16	16	—	—	—	14.5	13.4	15.4	—
3. Interorbital constriction.	3.4	3.6	3.4	3.2	—	—	—	3.1	3.2	2.8	—
4. Occipital breadth.	—	—	—	12.5	—	—	—	11.4	11	—	—
5. " depth (median).	—	—	—	6.4	—	—	—	5.8	5.8	—	—
6. Condyle to <i>m</i> <sup>3</sup> .	—	—	—	10.2	—	—	—	9.3	9.4	—	—
7. " to front of bulla.	—	—	—	8	—	—	—	8	7.5	—	—
8. Nasal length.	7	8	7.4	7.1	—	—	—	5.7	6.7	7.6	—
9. " width.	—	—	—	2.9	—	—	—	2.6	2.6	2.7	—
10. Dental length.	—	—	—	15.8	—	—	—	14.7	14.6	15.2	—
11. Diastema.	7	7	7	6.8	—	—	—	6.7	6.3	7.1	—
12. Upper molars (crowns).	6.6	7.2	6.8	6.3	—	—	—	6.1	6.1	7.2	—
13. " (alveolar).	16.2	17	17	15.7	—	—	—	7.4	6.6	6.7	7.5
14. Mandible.	—	—	—	6.3	—	—	—	15	15.4	16.7	—
15. Lower molars (alveolar).	—	—	—	—	—	—	—	—	—	—	—
15a. " (crowns).	6.2	6.8	6.4	6.3	—	—	—	5.9	5.9	6.7	—

<sup>1</sup> Temporal ridges separated in interorbital region by 0.2 mm.

<sup>2</sup> Temporal ridges fused.

\* Topotype of *S. stonci*.

CRANIAL MEASUREMENTS:—		<i>Synaptomys</i> (continued).					
		<i>S.</i> ( <i>M.</i> ) <i>dalli</i> .	<i>S.</i> ( <i>M.</i> ) <i>urangeli</i> .	<i>S.</i> ( <i>M.</i> ) <i>andersoni</i> , <i>chapmani</i> .	<i>S.</i> ( <i>M.</i> ) <i>truci</i> .	<i>S.</i> ( <i>M.</i> ) <i>innuitus</i> , <i>mediotimus</i> .	<i>S.</i> ( <i>M.</i> ) <i>sphagnicola</i> .
		Type. (Allen.)	Type. (Allen.)	Type. (Allen.)	Type. (Merriam.)	Type. (Bangs.)	Type. (Preble.)
1.	Condyllo-basal length.	=	=	=	=	=	=
1a.	Basilar length.	=	=	=	=	=	=
1b.	Basal length.	23		24.5		24.4	26
2.	Zygomatic breadth.	14.5		15.2		15.6	16
3.	Interorbital constriction.	3		3		3.6	2.8
4.	Occipital breadth.	11.5		11.5		11.8	12
5.	" depth (median).	=		=		=	=
6.	Condyle to <i>m</i> <sup>3</sup> .	=		=		=	=
7.	" to front of bulla.	=		=		=	=
8.	Nasal length.	6		6.6		6.6	8
9.	" width.	=		=		=	=
10.	Dental length.	=		=		=	=
11.	Diastema.	=		=		=	=
12.	Upper molars (crowns).	=		=		=	=
13.	" " (alveolar).	6.6		7		7.4	7
14.	Mandible.	=		=		=	=
15.	Lower molars (alveolar).	=		=		17.6	17.6
15a.	" " (crowns).	=		=		6.8	6.8
			None recorded.				
			None recorded.				
			None recorded.				



CRANIAL MEASUREMENTS:—  <b>Lemmus.</b>	<i>Lemmus</i>								
	79 9 25 64 ♂	79 9 25 65 ♂	79 9 25 63 ♀	8 10 5 6 ♀	8 10 5 1 ♀	8 10 5 4 ♀	8 10 5 2 ♂	8 10 5 8 ♀	8 10 19 21 ♀
1. Condyllo-basal length.	23.2	28.3	28.7	27.9	29.2	29.3	31.7	=	27.6
2. Zygomatic breadth.	14.8	18.8	19.2	19.1	19.2	19.5	20.6	22†	18.1
3. Interorbital constriction.	3.6	4.2	3.8	3.6	3.7	3.5	3.9	3.9	3.6
4. Occipital breadth.	11.8	14.4	14.1	13.8	13.3	14	15.3	15.4	13.7
5. „ depth.	6.1	6.7	6.3	6.7	6.9	6.9	7	7.4	6.5
6. Condyle to $m^3$ .	7.8	10.1	10.1	9.8	10.2	10.6	11.6	11	9.5
7. „ to bulla.	6.5	8.5	8.5	8.3	8.4	8.7	9.3	9.1	8.3
8. Nasal length.	6.4	7.7	7.7	8.3	8.4	8.2	9.1	=	7.8
9. „ width.	3	3.3	3.6	3.3	3.5	3.7	3.7	=	3.1
10. Dental length.	15.3	18.7	19.5	19	19.1	19.6	20.7	=	18.6
11. Diastema.	7.4	8.8	9.5	9.1	9.4	9.5	10.4	=	8.5
12. Upper molars (crowns).	5.8	7.1	7.3	7.4	6.9	=	7.4	8.1	7.5
13. „ „ (alveolar).	6.6	7.6	7.9	7.9	7.7	7.6	8.2	8.5	7.8
14. Mandible.	16	18.3	19	19.2	19.3	19.4	21	21	19
15. Lower molars (alveolar).	6.3	7.4	7.3	7.3	7.1	7.5	7.2	8.1	7.4
Temporal ridges separated in interorbital region by:	1.6	0.8	0.8	0	0.1	0	0	0	0

CRANIAL MEASUREMENTS:—  <b>Lemmus.</b>	<i>L. o. novosibiricus.</i>						
	Vinogradov, Ann. Mag. N.H., [9], 14, p. 188.						
	77 24 ♂	77 38 ♀	77 25	77 28 ♂	77 26 ♀	77 21 ♂	75 53
1. Condyllo-basal length.	34.5	32	31.4	32	30	29.7	29
2. Zygomatic breadth.	22.3	21.7	21.2	21.2	20.2	20	18.8
3. Interorbital constriction.	4.5	4.1	4.2	4.4	4.2	4.3	4.3
4. Occipital breadth.	18.1	16.4	16.4	16.4	15.7	15.5	15.7
5. „ depth.	—	—	—	—	—	—	—
6. Condyle to $m^3$ .	—	—	—	—	—	—	—
7. „ to bulla.	—	—	—	—	—	—	—
8. Nasal length.	9.5	8.6	8.2	8.6	7.9	8.2	7.6
9. „ width.	—	—	—	—	—	—	—
10. Dental length.	—	—	—	—	—	—	—
11. Diastema.	11.4	10.7	10.5	10.8	10.2	9.9	9.3
12. Upper molars (crowns).	—	—	—	—	—	—	—
13. „ „ (alveolar).	9.8	9.5	9.5	9.2	8.8	8.1	8.2
14. Mandible.	22.6	21.5	21.9	21.8	21.2	20.1	19.6
15. Lower molars (alveolar).	9	8.8	8.6	8.2	8.6	7.6	7
Temporal ridges separated in interorbital region by:	?	?	?	?	?	?	?

<i>lemmus.</i> Norway.					Kola 7 Penin- sula.	<i>L. o. "crassidens."</i> "Portugal."					<i>L. obensis.</i>			Waigatsch.	
8 10	8 19	8 19	8 19	8 19		<i>Type.</i>					19 7 7	47 8 17			
27 ♀	26 ♀	19 ♂	23 ♂	24 ♂	34	20	3	2	1	4	5	32	82	11	
29.2	29.3	=	30.5	30.5	33	29.1	29.2	29.9	30.1	=	30	=	=	=	=
19.8	19.4	19.7	20.3	20.6	22.8	18.9	19.2	20	=	21	19.9	21.4	25.6		
4	4	4	3.9	3.9	3.7	3.7	4.2	3.8	3.6	=	4.1	4.1	3.6		
14.4	14	=	14.7	14.9	16.2	14.5	14.8	14.1	15.2	=	15.3	=	=		
7	6.7	=	7	7	7.3	6.6	6.9	6.8	6.6	=	7	=	=		
10.3	10.7	=	10.9	11.1	11.4	10.1	9.6	10.5	10.6	=	10.3	=	=		
8.4	8.7	=	8.9	9	9.7	8.4	8.6	8.7	8.9	=	9	=	=		
8	8	8.4	8.5	8.7	9.8	8.4	8.4	8.3	=	=	7.8	8.2	=		
3.8	3.5	3.7	3.9	3.6	4.5	3.5	3.5	3.3	=	=	3.4	3.9	5.2		
19.5	19.2	20	19.7	19.6	22.3	19.4	19.9	20	19.9	21.3	20.1	20.3	23		
9.1	9.5	10.1	9.7	9.7	11	9.3	9.5	9.4	9.4	10.2	9.5	9.3	11.5		
7.5	7.3	7.3	7.6	7.3	8.5	7.7	8.1	8.2	8	8.6	8.4	8.3	8.8		
8	8	7.5	8	8	9.2	8.5	8.9	8.6	8.4	8.9	9	8.7	8.8		
—	18.8	20.1	20	20.7	22.6	20.1	20.2	20.1	20.1	21.6	20	21	=		
—	7.4	7.4	7.6	7.8	8.6	7.8	8.1	7.9	8.2	8.2	8	8	=		
0.3	0.1	0	0	0	0	0	0	0	0	0	0.7	0	0		

<i>L. o. chrysogaster,</i> Allen, Bull. A.M.N.H., 19, p. 154.	<i>L. amurensis,</i> Vinogradov, <i>op. cit.</i>	<i>L. paulus,</i> type, Allen.	<i>L. nigripes,</i> St. George Island.	<i>L. minusculus,</i> Osgood.	<i>L. yukonensis,</i> 17, 10, 6, 7.	<i>L. helveticus,</i> type, 42, 10, 7, 11.	<i>L. trimacronatus,</i> type, 42, 10, 7, 13.
25	26.2	29.5	30	28.5±	31.1	=	=
16.5	18±	20.2	19.6	19	20.7	17.3	=
4	3.3	3.8	4.3	—	3.8	=	=
13	13.7	15.5	15.6	15	16.5	=	=
—	—	—	7.2	—	7.5	=	=
—	—	—	10.6	—	11.5	=	=
—	—	—	9	—	10	=	=
6	7.3	8.8	8.9	8.9	8.7	8	8.6
—	—	—	3.8	—	3.9	3.4	3.1
—	—	—	19.6	—	20.5	17.6	=
—	8	9.1	9.5	8.8	9.2	8.1	=
—	—	—	8.2	—	8.8	6.7	8.5
7	7.2	8.2	8.5	8	9.1	7.2	9
—	—	—	19.6	—	20.2	18	20.8
—	7	7.5	8.1	—	8.7	6.5	8.3
Juv.	Type.	?	0.3	?	0	?	?

CRANIAL MEASUREMENTS :—		<i>E. glareolus</i>											
		<i>harrisoni</i> , Pleistocene, Ightham.		Denmark,		<i>glareolus</i> , Germany, Rhineland.		Great Britain.		<i>reinvalldi</i> , Esthonia.		<i>succicus</i> , Sweden, Norway, Mölmén.	
	Type.	98 6.7 15	98 6.7 13	98 11.2 48	8 11.2 46	7.7 44 Type.	7.7 44 Type.	7.7 44 Type.	7.7 44 Type.	11.6 4 Type.	11.6 4 Type.	98 5.2 4	98 5.2 4
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
A.— <i>glareolus</i> group.													
1. Condyllo-basal length.	22.8	23	23.7	24.1	24.6	22.5	23.4	24.2	23	23	24.5	—	24.1
2. Zygomatic breadth.	13.4	13.2	13.4	13.5	14.1	—	13.5	14	12.7	13.1	13.1	—	13.6
3. Interorbital constriction.	3.9	3.8	3.9	3.9	3.7	3.5	3.8	3.9	3.7	3.6	3.6	3.8	4
4. Occipital breadth.	11.4	11.2	11.3	11.1	11.4	10.7	11	11.2	10.6	11.4	11.4	—	10.6±
5. " depth (median).	6	6.1	6.1	6	6.1	5.7	6	6	5.8	6.4	6.4	—	6±
6. Condyle to <i>m</i> <sup>3</sup> .	10	9.7	9.9	10.6	10.7	9.9	10.2	10.6	10.1	10.9	10.9	—	10.4
7. " to front of bulla.	7.5	7.3	7.4	7.9	8.2	7.4	7.2	7.6	7.3	7.8	7.8	7	8
8. Nasal length.	6.9	7.1	6.9	7	7	6.5	6.7	6.8	6.3	7.9	7.9	7	6.7
9. " width.	2.8	2.8	2.9	2.8	2.9	2.5	3	2.7	2.7	2.8	2.8	—	2.8
10. Dental length.	12.8	13.4	13.4	13.6	14	12.6	13.3	13.4	12.9	13.6	13.6	—	14
11. Diastema.	6.2	6.5	6.6	7	7	6	6.4	6.5	6.4	7.4	7.4	6.8	6.8
12. Upper molars (crowns).	4.9	5.1	4.9	5.2	5.3	4.8	4.8	5.1	4.4	4.5	4.5	—	5
13. " (alveolar).	5.1	5.4	5.3	5.5	5.4	5.1	5.3	5.5	5.2	4.8	4.8	5.2	5.7
14. Mandible.	—	14.5	14.1	14.3	14.5	14	14.6	14.5	14.1	14.7	14.7	14.2	14.5
15. Lower molars (alveolar).	—	5.1	5.1	5.4	5.4	4.6	5	5.1	4.9	4.5	4.5	5	5.4
	Long roots.	Moderate roots.	Long roots.	Moderate roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Short roots.	Long roots.	Moderate roots.	Moderate roots.



## CRANIAL MEASUREMENTS:—

	<i>E. glareolus</i>									
	<i>isticus</i> , Rumania, 4 4.6 72 Type, ♂	<i>helveticus</i> , Haute-Savoie, 2 6.7 1 5 11 18 40 Type, ♂	*	*Barcelon- ette, 5 8 5 4 ♀	<i>sobrius</i> , Croatia, 21 12.1 16 Type, ♀	<i>saianicus</i> , Nyansk Mts., 12 4.1 85 Type, ♀	<i>E. centralis</i> , 12 4.1 14 Type, ♂			
A.— <i>glareolus</i> group.										
1. Condylar-basal length.	22.9	23.6	25.4	25.5	24.4	23	22.1	22.9		
2. Zygomatic breadth.	13	13.5	13.7	13.9	13.9	12.8	12.4	13		
3. Interorbital constriction.	3.7	3.7	3.8	3.7	3.9	3.5	3.5	3.9		
4. Occipital breadth.	11.5	11.3	11.5	11.4	11.7	10.8	10.5	11.2		
5. " depth (median).	6.2	6	6.4	6.1	6.3	5.9	5.8	=		
6. Condyle to <i>m</i> <sup>3</sup> .	9.8	9.9	10.8	11.2	10.7	10.1	9.5	9.6		
7. " to front of bulla.	7.6	7.5	7.7	8.1	7.6	7.1	7	7		
8. Nasal length.	6.5	6.7	7.4	8.1	7.3	6	5.4	6.8		
9. " width.	3	3	3	3.3	3.2	2.3	2.5	2.6		
10. Dental length.	13.3	13.7	13.8	14.4	13.9	13	12.6	13.2		
11. Diastema.	6.5	6.2	6.8	7.1	6.7	6.6	6.1	6.3		
12. Upper molars (crowns).	4.9	5.1	5	5.2	5.2	4.9	4.7	5		
13. " " (alveolar).	5.3	5.6	5.5	5.7	5.5	5.1	4.9	5.7		
14. Mandible.	14	14.2	15.2	14.8	14.7	14.3	13.7	14.7		
15. Lower molars (alveolar).	5.1	5.4	5.5	5.5	5.2	4.9	4.8	5.5		
	Adult Long roots, Moderate roots, Moderate roots,	Adult moderate roots, Long roots,	Old long roots, Long roots,	Long roots, Long roots,	Long roots, Long roots,	Long roots, Long roots,	Aged, Long roots,	Cement spaces closed.		

\* ? *E. nageri*.

	† <i>E. kennardi</i> .			<i>E. nageri</i> .			<i>E. gorka</i> .									
	CRANIAL MEASUREMENTS:—			<i>vesanus, hallucalis, vasconie, norvegicus.</i>			<i>norvegicus.</i>									
	Type.			Italy.			France.			Norway.			Croatia.			
	Type.			Passo del Brennero, (Dal Piaz.)			Haute Ariège, Garonne.			Bergen.			Hardanger.			
<b>Evotomys (continued).</b>	Type.			Type.			Type.			Type.			Type.			
<b>B.—<i>nageri</i> group.</b>	Type.			Type.			Type.			Type.			Type.			
1. Condyllo-basal length.	23.7	25±	25.4	24.8	24.3	25.6	25	25.6	26.2	24.5	26.6	26.6	24.5	26.6	26.6	
2. Zygomatic breadth.	13.2	13.8	13.1	14.1	14.6	13.1	14	13.9	14.6	13.4	13.7	13.7	13.4	13.7	13.7	
3. Interorbital constriction.	3.7	4	3.7	4	4	4.2	4	4.1	4	3.8	4	4	3.8	4	4	
4. Occipital breadth.	11.2±	11.3	11.1	11.8	11.6	11.5±	11.6	11.6	12	11.1	12	12	11.1	12	12	
5. " depth (median).	6.5	6.4	6.1	6.3	6.6	6.5	6.6	6.6	6.6	6	6.6	6.6	6	6.6	6.6	
6. Condyle to <i>m</i> <sup>2</sup> .	10.2	11	11.1	10.9	—	10.2	—	11.2	—	10.8	11.2	—	10.8	11.2	11.2	
7. " to front of bulla.	7.9	8	8	7.8	—	—	—	7.9	—	7.9	8.3	—	7.9	8.3	8.3	
8. Nasal length.	6.4	8.2	7.6	7.6	7.2	7.8	7.4	7.7	8	6.9	7.8	—	6.9	7.8	7.8	
9. " width.	2.5	3.2	2.8	3.2	—	3.4	—	3.1	—	3.2	3.2	—	3.2	3.2	3.2	
10. Dental length.	13.4	14.6	14.4	13.8	—	14.4	—	14.5	—	13.9	15.2	—	13.9	15.2	15.2	
11. Diastema.	6.4	6.9	7	6.8	7.2	7.5	8	7.2	8	7.8	7.7	—	7.8	7.7	7.7	
12. Upper molars (crowns).	5.2	5.6	5.2	5.3	—	5.2	—	5.2	—	5	5.4	—	5	5.4	5.4	
13. " (alveolar).	5.6	5.8	5.4	5.5	5.3	5.4	5.8	5.8	5.8	5.4	5.7	—	5.8	5.7	5.7	
14. Mandible.	—	15.8	15.7	14.6	15	15.4	15	15	15	15.3	15.6	—	15.3	15.6	15.6	
15. Lower molars (alveolar).	—	5.6	5	5.3	5.2	5.2	5.6	5.6	5.6	5.1	5.7	—	5.1	5.7	5.7	
	Short roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Short roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Adult long roots.

CRANIAL MEASUREMENTS:—		<i>E. skomerensis</i> , Skomer Island.		<i>E. caesarius</i> , Jersey.		<i>E. abstoni</i> , Mull, Hebrides.		<i>E. erica</i> , Raasay, Hebrides.		<i>E. ponticus</i> , Asia Minor.		<i>E. frater</i> , Thian Shan.	
	Type.	♂	♀	Type.	♂	♀	Type.	♂	♀	Type.	♂	♀	Type.
<b>Evotomys (continued).</b>													
B.— <i>nageri</i> group.													
1.	Condylar-basal length.	25	25.5	25.6	24.2	26.8	25.3	24.1	25.3	25.2	25.4	24.5	24.5±
2.	Zygomatic breadth.	14.5	14.8	14	13.6	15.2	13.9	13.5	14.3	14.7	15	12.9	13.5
3.	Interorbital constriction.	4	3.9	4.1	4	3.8	3.8	3.9	3.7	3.8	3.8	4.1	4
4.	Occipital breadth.	12.3	12.5	11.6	11.3	12.3	11.5	11.4	12.1	11.8	11.9	11.4	11.1
5.	„ depth (median).	6.4	6.9	6.6	6.3	6.7	6.4	6	6.6	6.4	6.6	6.4	6.4
6.	Condyle to <i>m</i> <sup>3</sup> .	10.7	10.9	11.2	9.9	11.2	11	9.9	10.8	10.7	10.8	10.8	10.5
7.	„ to front of bulla.	7.9	8.2	8	7.7	8.1	7.7	7.4	8.2	7.8	8.2	7.9	7.6
8.	Nasal length.	8	7.8	7.1	7.1	8.3	7.5	6.8	7.8	7.1	7.4	7	6.8
9.	„ width.	2.8	3	3.1	3	3.2	3	2.8	3.2	2.8	3	3.1	2.9
10.	Dental length.	14.3	14.5	14.6	—	15.5	14.1	—	14	14.5	14.6	13.7	13.6
11.	Diastema.	6.7	6.9	6.7	6.7	7.2	7.1	6.3	7.7	6.7	6.7	6.8	6.6
12.	Upper molars (crowns).	5.4	5.5	5.5	—	6	—	—	—	5.8	5.9	4.9	5
13.	„ „ (alveolar).	5.8	5.7	6.1	6	6.4	5.6	5.2	5.7	6.2	6.3	5.4	5.5
14.	Mandible.	15.6	15.7	15.6	15	16.7	15.6	15.1	15.7	16.1	16.4	14.5	15
15.	Lower molars (alveolar).	5.6	5.7	5.7	6	6.2	5.4	5.4	5.4	6.1	6.1	5.3	5.5
		Moderate roots.	Short roots.	Short roots.	Cement spaces closed.	Long roots.	Long roots.	Long roots.	Long roots.	Short roots.	Short roots.	Short roots.	Cement spaces closed.

## CRANIAL MEASUREMENTS:—

	<i>E. rutilus</i> .										Type.	<i>E. amurensis</i> .	<i>E. mikado</i> .					
	<i>E. baikalensis</i> .	<i>E. laticeps</i> .	<i>E. parvidens</i> .	Finnmark.	Gyansk Mts.	Jenissei.	N.E. Altai.	Kingghan Mts.	<i>E. wosnessenskii</i> .	<i>E. jochelsoni</i> .			(Allen.)	♂	♀	♂	♀	♀
C.— <i>rutilus</i> group.	3940																	
1. Condylø-basal length.	25.5	24.8±	24.2	23	23.7	—	23	21.9	—	23.2	22*	22.9	23.7	24.5	—	24.6	24.3	24
2. Zygomatic breadth.	14.6	14.1	13.6	12.4	13.1	13.7	13	12.8	12.6	13.2	—	13.1	13.7	13.7	12.6	13.8	13.4	13.2
3. Interorbital constriction.	4	4.1	4.3	4.1	3.9	3.8	3.7	3.8	3.7	3.9	—	3.9	3.9	4	4	3.8	4	4.1
4. Occipital breadth.	12	12.7±	11.9±	11.2	11.4	—	10.9	11.1	—	11.3	11	10.7	11.5	11.3	—	11.6	11.1	10.9
5. " depth (median).	6.5	7.2	6.4	6.5	6	—	6	6	—	5.9	—	5.9	6.2	6.1	—	6.1	6	6.1
6. Condyle to <i>m</i> <sup>3</sup> .	11	—	10.5	9.8	10.4	—	10.2	9.7	—	10.1	—	9.7	10	10.6	—	11.2	10.3	10.5
7. " to front of bulla.	7.1	—	—	7.4	7.9	—	7.4	7.3	—	7	—	7	7.2	7.6	—	7.8	7.6	7.5
8. Nasal length.	8.2	—	7.6	6.8	7.5	6.9	6.8	6.3	6.2	6.9	6.3	7	7	7.1	6.5	7.2	6.9	7.1
9. " width.	—	—	—	2.7	2.9	2.8	2.6	2.7	2.8	2.8	—	2.8	2.7	2.6	2.7	2.9	2.8	2.9
10. Dental length.	—	—	—	13.1	13.1	13.5	12.8	12.2	12.7	13.4	—	13.5	14	13.8	13±	13.5	14.2	13.8
11. Diastema.	—	—	—	7.1	7	7.5	6.5	6.1	6.5	6.9	—	7.1	7.7	7.3	6.8	7.5	7.5	7.2
12. Upper molars (crowns).	—	—	—	4.3	4.5	4.3	4.4	4.3	4.6	4.6	—	4.4	4.8	4.7	4.5	4.4	4.9	4.9
13. " (alveolar).	5.2	5	4.7	5	4.8	4.6	4.9	4.7	4.8	5	—	4.7	5.1	5	5	4.8	5.2	5.1
14. Mandible.	13.8	—	14.1	—	14.3	14.4	13.6	13	13.5	14.1	—	13.8	14.8	14.6	13.8	14.4	14.7	14.2
15. Lower molars (alveolar).	5.2	—	—	—	4.7	4.6	4.6	4.5	4.8	4.8	—	4.7	4.8	4.6	4.9	4.8	5.2	5
					Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	Long roots.	* Total length.	Old, long roots.	Old, long roots.	Old, long roots.	Moderate roots.	Long roots (sculle).	Long roots.	Long roots.



CRANIAL MEASUREMENTS: — *E. r. shanensis* (continued), *E. rufocanus* (continued), *E. r. smithi*.

	"Caryomys."										<i>E. r. regulus</i> .				<i>E. r. smithi</i> .				
	"Caryomys inez."		"C. nutz."		"C. eva."		"C. alpinus."		"C. aquilus."		Korea.		"Crasomys nitidus."		"C. ander- soni."		Japan.		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
	Type.		Type.		Type.		Type.		Type.		Type.		Type.		Type.		Type.		
<b>Evotomys</b> (continued).	9	9	10	11	11	11	13	6	6	6	5	6	8	6	6	6	6	7	7
1. Condylar-basal length.	23-1	23-6	23-5	23-4	22-9	23-4	23-8±	23-3	26-7	26-3	22-9	23-7	24-5	25-4	25-7	26-9	27-1	28-4	28-5
2. Zygomatic breadth.	14-5	14-4	14-4	14-3	13-2	13-7	13-5	13-3	14-8	14-8	13-5	14-5	14-6	14-4	14-5	15-7	15-1	15-9	16-5
3. Interorbital con- striction.	4-3	4-4	4-7	4-1	4-1	4-1	3-5	4	4-2	4-3	4	3-8	3-8	3-7	3-5	3-8	4	3-8	3-8
4. Occipital breadth.	11-9	11-6	12-3	11-9	11-1	11-2	11-6	—	12-5	12-4	11-5	10-8	11-8	11-8	12-1	12-6	12-5	12-5	13-1
5. " " depth (median).	6-1	6-1	5-9	6	6-1	5-7	—	—	6-7	6-6	6-3	6-3	6-3	6-6	6-4	6-7	6-6	6-8	7-1
6. Condyle to m <sup>2</sup> .	9-7	10	9-9	10	9-8	9-7	—	10-2	11	11-1	9-5	9-8	9-9	10-8	11-2	11-2	11-4	11-7	11-9
7. " " to front of bulia.	7-3	7-3	7-3	7-5	7	7-1	—	7-2	8-2	8	7-4	7	6-8	7-9	8	8-1	8-2	8-6	8-7
8. Nasal length.	6-5	6-5	6-8	7-2	6-9	6-6	—	6-9	8-2	7-9	6-4	7-1	7-2	7-4	7-8	7-7	8	8-1	8-4
9. " " width.	2-8	2-5	2-8	3-4	2-6	2-9	—	2-9	3-5	3-1	2-6	3-1	2-8	3-1	3-1	3-1	3	3-4	3-3
10. Dental length.	13-4	13-7	13-8	13-6	13-1	13-9	—	13-6	15-8	15-4	13-4	13-8	14-7	14-6	14-5	16-2	15-7	16-9	17-1
11. Diastema.	5-7	6-3	6-2	6-2	6-4	6-4	6-6	6-4	7-4	7-3	6	6-5	7-2	7-2	6-8	7-5	7-5	8-1	8-2
12. Upper molars (crowns).	5-6	5-5	5-6	5-5	4-9	5-6	—	5-3	6	5-8	5-2	5-1	5-5	5-4	5-7	6-2	5-8	6-2	6-6
13. " " (alveolar).	5-9	5-8	5-8	5-8	5-3	6	6	5-7	6-6	6-4	5-9	5-4	5-9	5-8	6-1	6-7	6-3	6-8	6-9
14. Mandible.	14-6	15	15	14-6	14	14-5	—	14-6	16	15-9	14-4	14-5	15-6	15-4	15-8	16-7	17	16-6	—
15. Lower molars (alveolar).	5-5	5-9	5-7	5-5	5	5-7	5	5-4	6	6-1	5-5	5-3	5-7	5-6	5-8	6-5	6-2	6-4	—
	Growing	Growing	Growing	Growing	Growing	Growing	Growing	Growing	Cement spaces closed.	Growing	Young.	Growing	Growing	Growing	Growing	Short Roots.	Roots beginning	Old, long Roots.	Old, long Roots.

*E. glareolus britannicus.**E. gapperi.*  
*E. g. gapperi.**E. g.*  
*ochraceus.*  
Mt.Washington,  
N. Hamp-  
shire.  
7 7 7  
7 7 7  
131 2542  
Type.Maine,  
Campbell,  
Id. 7.7.1918.Massachusetts,  
2459 2016 2299New York,  
1346 1629 2459Ontario,  
7.7.3264.England,  
Chingford, Essex.Scotland,  
Loch Awe,  
Forrose.Scotland,  
Loch Awe,  
Forrose.Scotland,  
Loch Awe,  
Forrose.Scotland,  
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Forrose.Scotland,  
Loch Awe,  
Forrose.Scotland,  
Loch Awe,  
Forrose.Scotland,  
Loch Awe,  
Forrose.**Evotomys.** Comparison of  
*E. gapperi* with *E. glareolus*  
*britannicus.*

1. Condylar-basal length.	22.9	23.4	22.7	23.3	23.6	23.7	24.2	24.1	23.8	24.2	23.8	24.3	23.5	24	23.7	24.7
2. Zygomatic breadth.	13.8	13.5	13.3	13.1	13.8	14	13.4	13.1	13.7	13.2	13.8	13.5	12.5	12.5	13.2	13.9
3. Interorbital constriction.	4	3.8	3.7	3.8	3.9	3.9	3.9	3.8	4.1	4.2	4	3.8	3.8	3.8	4.1	4.3
4. Posterior border of inter- parietal to front nasal suture.	15.6	15.9	15.9	16.1	16.2	16.2	16.5	17	15.9	16.8	15.9	16.4	16	16.8	16.1	17.2
5. Posterior border of inter- parietal to coronal suture.	7.2	7.1	7.1	7	7.5	7.4	7.6	7.8	7.4	8	7	7.7	7.5	8.3	7	8
6. Occipital breadth.	11.4	11	—	10.8	11.4	11.2	11.2	11.6	11.4	11.7	11.4	11.3	11.5	11.3	11.4	11.9
7. " " depth (median).	5.9	6	—	5.9	6.1	6.1	6	5.9	6.1	6.2	6.4	6	6	5.7	6.2	6.6
8. Condyle to <i>m</i> <sup>3</sup> .	9.7	10.2	9.7	10	10.3	10.3	10.6	10.8	10.5	11	10.5	10.5	10	11.1	10	10.5
9. " " to front of bulla.	7.2	7.2	7.3	7.5	7.4	7.5	7.6	8.2	7.8	7.9	7.7	7.8	7.3	7.7	7.3	7.8
10. Nasal length.	6.6	6.7	6.5	6.7	6.9	6.9	6.8	7.1	6.8	7.2	7.2	6.8	6.6	6.8	6.7	6.9
11. " " width.	2.7	3	2.7	2.5	2.8	2.9	2.7	2.5	2.7	2.6	2.8	2.9	2.7	2.8	2.8	2.8
12. Dental length.	13.1	13.3	13	13.3	13.1	13.3	13.4	13.2	13.5	13.2	13.3	13.7	13.5	12.9	13.8	14.1
13. Diastema.	6.3	6.4	6.1	6.4	6.3	6.3	6.5	7	6.8	7	7	7	6.7	7	7.1	7.2
14. Upper molars (crowns).	5	4.8	5	5.1	4.9	5.2	5.1	4.7	4.8	4.7	4.5	5	4.8	4.2	4.8	5.1
15. " " (alveolar).	5.4	5.3	5.2	5.5	5.4	5.5	5.5	4.9	5.2	5	5	5.3	5.3	4.5	5.1	5.4

For reduced values of these measurements see p. 466.

CRANIAL MEASUREMENTS :—		<i>E. glareolus britannicus.</i>				<i>E. gapperi.</i>				<i>E. g. gapperi.</i>				<i>E. g. ochraceus.</i>			
		Scotland.		England.		New York.		Massachusetts.		Maine, Campbelllo.		Washington, N. Hampshire.		Type.		Type.	
		Loch Awe.	Fortrose.	Chingford, Essex.	Ontario.	New York.	Massachusetts.	Maine, Campbelllo.	Washington, N. Hampshire.	Id.	Id.	Id.	Id.	Id.	Id.	Id.	Id.
		100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
1 =	Dimension 1 =	60.2	57.7	58.5	56.2	55.6	58.2	57.8	55.7	55.1	56.5	55.5	56.7	57.5	52.1	55.7	56.2
2 =		17.5	16.2	16.3	16.3	16.6	16.5	16.1	16.2	16	16.9	17.7	16.4	16.2	15.8	17.3	17.4
3 =		68	68	70	69	68.8	68.3	68.2	70.7	66.8	69.3	66.8	67.4	68.2	70	68	69.6
4 =		31.4	30.3	31.2	30	31.8	31.2	31.4	32.4	31.1	33	29.4	31.6	31.9	34.6	29.5	32.4
5 =		49.7	47	—	46.3	48.4	47.2	46.2	48.2	47.9	48.3	47.9	46.5	49	47.2	48.1	48.1
6 =		27.5	25.6	—	25.3	25.9	25.7	24.8	24.5	25.6	25.6	26.9	24.7	25.6	23.8	26.2	26.7
7 =		42.3	43.6	42.6	42.9	43.7	43.5	43.8	44.9	44.1	45.3	44.1	43.2	42.6	46.3	42.3	42.5
8 =		31.4	30.8	32.1	32.2	31.4	31.6	31.4	34.1	32.8	32.6	32.3	32.1	31.1	32.1	30.8	31.6
9 =		28.8	28.6	28.6	28.7	29.3	29.1	28.1	29.5	28.6	28.9	30.2	27.9	28.1	28.3	28.3	27.9
10 =		11.8	12.8	11.9	10.7	11.9	12.3	11.2	10.4	11.3	10.7	11.7	11.9	11.5	11.7	11.8	11.3
11 =		57.2	56.9	57.3	57	55.6	56.2	55.4	54.8	56.7	54.6	55.9	56.2	57.5	53.8	58.3	57.1
12 =		27.5	27.3	26.8	27.4	26.7	26.6	26.8	29.1	29.4	28	29.4	28.8	28.5	29.2	30	29.1
13 =		21.8	20.5	22.1	21.8	20.8	22	21.1	19.5	20.2	19.4	18.9	20.5	20.4	17.5	20.3	20.7
14 =		23.6	22.6	22.9	23.6	22.9	23.2	22.7	20.4	21.9	20.6	21	21.8	22.6	18.8	21.3	21.9
15 =		Long	Long	Long	Long	Long	Long	Long	Aged.	Short	Long	Moderate	Short	Long	Aged.	Long	Long

**Evotomys.** Comparison of *E. gapperi* with *E. glareolus britannicus*.

Reductions :



*E. melanogaster.*

CRANIAL MEASUREMENTS:—	<i>E. m. melanogaster.</i>		<i>E. m. caehinus.</i>		<i>E. m. lewis.</i>		<i>E. m. aurora.</i>		<i>E. m. mitus.</i>		<i>E. m. confini.</i>		<i>E. m. colurus.</i>		<i>E. m. micron.</i>		<i>E. m. albus.</i>		<i>E. m. tibonotus.</i>		<i>E. fidlis.</i>		<i>E. proditor.</i>		<i>E. olitor.</i>		
	Type.	♂	Type.	♂	Type.	♂	Type.	♂	Type.	♂	Type.	♂	Type.	♂	Type.	♀	Type.	♂	Type.	♂	Type.	♂	Type.	♂	Type.	♀	Type.
1. Condyllo-basal length.	24.5	24.4	25.9	24.4	—	25.3	25.2	25.6	—	24.9	27.6	—	27.3	27.1	23.7	—	27.3	27.1	23.7	—	27.3	27.1	23.7	—	27.3	27.1	23.7
2. Zygomatic breadth.	14.8	14.7	16	14.7	14.8	15.4	14.9	15.5	15.6	15±	16.3	17.2	16.4	16.6	14	—	16.3	16.4	16.6	14	16.3	16.4	16.6	14	16.3	16.4	16.6
3. Interorbital constriction.	4.2	4.3	4.6	4.3	4.3	4.8	4.4	4.1	4.2	4.4	4.6	4.4	4.4	4.6	3.9	—	4.4	4.4	4.6	3.9	4.4	4.4	4.6	3.9	4.4	4.4	4.6
4. Occipital breadth.	12.5	12.3	12.1	12.3	—	12	11.5	11.7	—	11.4	12.2	12.8	11.9	12	10.8	—	11.4	12.2	12.8	11.9	12	11.9	12	10.8	11.4	12	10.8
5. " depth (median).	6.4	6.2	6.8	6.2	—	7	6.7	6.2	—	6.3	7.1	—	7.1	7.3	6	—	6.3	7.1	—	7.1	7.3	6	—	7.1	7.3	6	—
6. Condyle to <i>m</i> <sup>3</sup> .	10.1	10.5	10	10.5	—	10.4	10.2	10.6	—	10.2	11.5	—	11.1	10.7	9.8	—	10.2	11.5	—	11.1	10.7	9.8	—	10.2	11.5	9.8	—
7. " to front of bulla.	7.8	7.6	7.2	7.6	—	7.8	7.3	7.6	—	7.4	7.8±	—	8.2	8	7.2	—	7.4	7.8±	—	8.2	8	7.2	—	8.2	8	7.2	—
8. Nasal length.	7.1	7.4	7.8	7.4	7.4±	7.4	7.9	7.6	8	7.5	7.7	8.7	7.7	7.6	6.5	—	7.5	7.7	8.7	7.7	7.6	6.5	—	7.5	7.7	8.7	7.7
9. " width.	3.1	3.1	3.4	3.1	3.2	3.2	3.1	3.1	3.1	3.7	3.4	3.5	3.4	3.5	2.5	—	3.7	3.4	3.5	3.4	3.5	3.4	3.5	2.5	3.7	3.4	3.5
10. Dental length.	14.7	14.5	16.2	14.5	14.8	15.1	15.3	15.2	16	15.5	16.8	17.3	16.8	16.9	14.2	—	15.5	16.8	17.3	16.8	16.9	14.2	—	15.5	16.8	17.3	16.8
11. Diastema.	6.7	6.9	7.5	6.9	6.9	6.9	7.5	6.6	7.5	7.5	7.8	8.1	8.1	8.3	6.8	—	7.5	7.8	8.1	8.1	8.3	6.8	—	7.5	7.8	8.1	8.3
12. Upper molars (crowns).	6	5.5	6.4	5.5	5.7	6	5.8	6.3	6.4	6.1	6.6	6.9	6.5	6.4	5.5	—	6.1	6.6	6.9	6.5	6.4	5.5	—	6.1	6.6	6.9	6.5
13. " (alveolar).	6.2	5.8	6.8	5.8	5.9	6.4	6.3	6.7	6.6	6.7	6.9	7.4	6.9	6.7	5.8	—	6.7	6.9	7.4	6.9	6.7	5.8	—	6.7	6.9	7.4	6.9
14. Mandible.	16	15.4	16.8	15.4	15.1	16	16.8	16	17.4	16.5	17	18.5	18	18	14.7	—	16.5	17	18.5	18	18	14.7	—	16.5	17	18.5	18
15. Lower molars (alveolar).	6	5.7	6.5	5.7	5.8	6.3	6.4	6.2	6.5	6.5	6.5	6.9	6.8	6.7	5.5	—	6.5	6.9	6.8	6.7	6.5	5.5	—	6.5	6.9	6.8	6.7



CRANIAL MEASUREMENTS:—	Subgenus ALTICOLA.															
	<i>A. argurus.</i>			<i>A. b. blanfordi.</i>			<i>A. blanfordi</i>			<i>A. r. roylei</i>			<i>A. r. cautus.</i>			
Alticola.	♂		♀		♂		♀		♂		♀		♂		♀	
	Type.	type.	Type.	type.	Type.	type.	Type.	type.	Type.	type.	Type.	Type.	Type.	Type.	Type.	Type.
1. Condyllo-basal length.	24.6	26.5±	26.5±	25.3	25	25.1	25.4	25.4	25.4	27.1	15.8	25.4	27.2	27.3	27	27
2. Zygomatic breadth.	—	14.1	14.2	—	14.5	—	14.5	—	14.5	—	15.6	14.7	15.8	15.7	15.5	15.5
3. Interorbital constriction.	3.8	3.8	4.1	4	3.9	3.9	3.7	4	3.7	4	4	4.1	4.1	4	4.1	4.1
4. Occipital breadth.	11.9	12.3	12.2	12.7	12.3	12	11.8	12.2	12.2	12.5	12.2	12.1	12.8	12.5	12.4	12.4
5. " depth (median).	6.9	—	—	6.6	7	—	7	7	7	6.8	6.4	6.7	6.7	7	6.7	6.7
6. Condyle to <i>m</i> <sup>3</sup> .	10.4	—	—	10.3	10.5	10.3	10.5	10.5	10.5	—	10.1	10.3	10.9	10.8	10.7	10.7
7. " to front of bulla.	7.7	—	—	7.8	8	7.6	8	8	8	—	7.5	7.5	8	7.6	—	—
8. Nasal length.	7.3	8.5	8.4	8.3	7.3	7.4	7	7.8	8.3	7.7	7.7	7.7	7.8	8.3	8	8
9. " width.	2.8	3.2	3.1	3	3.2	3	3.2	3.1	3.3	3.3	3	3.2	3.5	3.4	3.1	3.1
10. Dental length.	14.3	15	16.2	14.7	14.7	14.6	14.9	15	15.8	15.8	15.8	15.1	16.6	16.5	16.4	16.4
11. Diastema.	7.2	7.4	8.7	7.2	7.3	7.3	7.3	7.3	7.7	7.7	7.6	7.3	8	8.4	7.8	7.8
12. Upper molars (crowns).	5.4	5.7	5.5	5.8	5.5	5.3	5.8	5.7	5.7	5.7	6.2	5.9	6.6	6.2	6.3	6.3

adult

CRANIAL MEASUREMENTS:—		Subgenus ALTICOLA (continued).																	
		<i>A. albicauda.</i>		<i>A. montosa.</i>		<i>A. glacialis phasma.</i>		<i>A. v. worthingtoni</i>		<i>A. worthingtoni</i>		<i>A. v. A. w. sub- scmi- luteus. canus.</i>							
	Type.	5	13	5	7	10	12	12	5	5	12	12	12	14	5	10	(G. M. Allen.)	Type.	Type.
1. Condyllo-basal length.	26.4±	—	27.9	—	26.7	27.8	27	27	26	25.7	26.8	25	25.1	28.7	25.1	28.7			
2. Zygomatic breadth.	15	—	15.3	—	14.9	16	14.8	14.9	14.7	14.9	15.2	14.8	13.2	16.7	13.2	16.7			
3. Interorbital constriction.	4.4	4.1	3.5	—	4	4.2	4	4.1	4.2	4.1	4.1	4	4	—	3.8	4			
4. Occipital breadth.	13.4	—	12.9	—	12.3	12.6	12.8	12.6	12.5	12.3	13	12.3	12.3	14.4	12.3	12.3			
5. " depth (median).	7.6	—	—	6.9	—	6.6	7	7.3	—	—	—	7	7.1	—	7.2	—			
6. Condyle to <i>m</i> <sup>3</sup> .	—	—	11.5	—	11	11.4	—	11.3	10.9	10.9	10.9	11.5	10.4	—	10.4	—			
7. " to front of bulla.	—	—	8.3	8	7.8	8.2	—	8.2	8.5	8	8.6	7.8	8	—	8	—			
8. Nasal length.	7.8	7.6	8.3	7.7	7.8	8.5	8	8.2	7.3	7.9	7.9	7.4	7.7	—	7.4	—			
9. " width.	3.8	3.4	3.5	3.3	3.4	3.4	—	3.1	2.8	3.1	3.2	3	2.9	—	3.2	—			
10. Dental length.	—	14.8	16.6	14.8	15.8	16.4	—	15.8	16.1	14.9	14.8	15.4	14.7	—	14.5	—			
11. Diastema.	7.8	7.6	8.3	7.2	7.6	8.1	8	8.1	7.5	7.5	8	7.2	7.4	—	7.4	—			
12. Upper molars (crowns).	—	5.4	6.1	5.6	6	6.2	—	6	5.6	5.5	5.5	5.5	5.6	—	5.5	—			

\* Type of *A. imitator*.

		Subgenus ALTICOLA ( <i>continuel</i> ).				Subgenus PLATYCRANIUS.												
<i>A. stoliczkanus</i> .		<i>A. stracheyi</i> .				<i>A. lama</i> .				<i>A. acrophilus</i> .				<i>A. (Platycranus) strelzovi</i> .				
(Blanford.)		Co-type.				Type.				Type.				Type.				
1. Condyllo-basal length.	29±	24±	26·7	—	27	27·6	28±	—	—	28±	27·8	27·9	28·8	29·1	—	—	—	—
2. Zygomatic breadth.	—	14·4	—	15·4	15·5	15·5	16	15	—	16·4	16·6	15·7	16·6	16·5	—	—	—	—
3. Interorbital constriction.	3·5	3·7	—	4·1	3·7	4	4	4·4	4·4	5	4·3	4·3	4·6	4·3	—	—	—	—
4. Occipital breadth.	—	12·5±	12·7	—	12·6	12·6	13·4	12·5±	—	13	13·8	13·2	14·2	13·8	—	—	—	—
5. " depth (median).	—	—	7	—	6·5	6·7	8	—	—	8·4	6·7	6·3	6·5	6·2	—	—	—	—
6. Condyle to <i>m</i> <sup>3</sup> .	—	—	10·9	—	10·9	11·4	—	—	—	—	—	11·9	12·7	12·7	—	—	—	—
7. " to front of bulla.	—	—	8·3	—	7·7	8·3	—	—	—	—	—	8·6	8·3	8·6	—	—	—	—
8. Nasal length.	9·5	7·9	8·2	9·3	8·5	8·6	9	8·6	8·3	8·8	8	8·1	8·2	8·8	—	—	—	—
9. " width.	3	3·4	3·4	3·6	3·5	3·7	4	3·3	3·2	3·8	3·5	3·3	3·4	3·5	—	—	—	—
10. Dental length.	—	14·8	16	16·7	16·2	16·3	—	16·2	15·8	—	15·7	15·9	16·1	16·6	—	—	—	—
11. Diastema.	8·5	7·3	8·3	8·4	8·4	8·4	9	8·2	8·3	8·8	7·9	8·1	8·5	9·1	—	—	—	—
12. Upper molars (crowns).	7†	5·8	5·6	6·1	5·9	6	—	6	5·7	—	5·7	5·9	5·8	5·8	—	—	—	—

\* Paratype of *A. crictulus*.

† ? Alveolar.

CRANIAL MEASUREMENTS:—

**Alticola** (*continuel*).

*H. weynaci.**H. aitchisoni.**H. fertilis.**H. f. brachidix.*

96

11.2

7

28.5

28.6

29.1

	<i>H. f. fertilis.</i>	<i>H. f. brachidix.</i>	<i>H. aitchisoni.</i>	<i>H. weynaci.</i>
(Miller.)	5 4	5 6	3	11 21 4305 4311 4307 4267
Type.	♀ ♂	♀ ♂	♂	♀ ♂ ♀ ♂ ♀ ♂

**Hyperacrius.**

	<i>H. f. fertilis.</i>	<i>H. f. brachidix.</i>	<i>H. aitchisoni.</i>	<i>H. weynaci.</i>
1. Condyllo-basal length.	24.3 24.8 24.9	— 24.7 24.8	—	26.7 27 28.2 28.5
2. Zygomatic breadth.	15.3 15.7 15.6	— 16.1 15.6 16	—	17.2 16.8 18 18.4 18.3 18.8 18.7 19
3. Interorbital constriction.	3.5 3.9 3.6	3.5 3.8	3.6	4.2 4.1 4.2 4.1 4 4.1 4.4 4.2
4. Occipital breadth.	— 11.7 11.8 12.1	— 11.8 11.8	—	12.2 12.5 13 13 13.2 13 13.3 —
5. " depth (median).	— 6.5 6.4 6.5	— 6.3 6.4	—	7.3 7.1 7.3 7.8 — 7.8 7.4 —
6. Condyle to <i>m</i> <sup>3</sup> .	— 9 9.1 9.1	— 9.2 9.6	—	9.8 10.2 10.2 10.7 — 10.6 10.8 —
7. " to front of bulla.	— 6.6 6.7 6.6	— 6.9 7	—	7.2 7.6 7.3 7.9 — 8.2 —
8. Nasal length.	7 7.1 7.1 7.2	7.2 6.3 7	8.6	7.6 8 8.5 8.6 8.4 8.5 8.5 8.3
9. " width.	3.2 2.6 3 2.9 3	3 2.7 2.8	3	3 3 3 3.3 2.9 3.1 3.1 3.2
10. Dental length.	— 15.3 15.7 16 16	15.5 16.1 15.7	—	17.3 17 18.4 18.4 17.8 18.4 18.8 18.9
11. Diastema.	7.6 7.9 7.6 7.7	7.6 7.8 7.8	—	8.5 8.7 9.2 9 8.3 9.2 9.2 9.3
12. Upper molars (crowns).	— 5.4 5.7 6.1 5.8	5.8 5.7 5.7	6.4	6.5 6.1 6.8 6.8 7.1 7 7.1 7.2
13. " (alveolar).	6.4 6 6.1 6.5 6.3	6.1 6.1 6.1	6.8	6.8 6.5 7.3 7.4 7.4 7.4 7.4 7.5

CRANIAL MEASUREMENTS:—

CRANIAL MEASUREMENTS:—		<i>D. bogdanovi</i> .		Reductions.	
		22	23		
		7.5	11.1		
		1	8	22	23
		♂	♂	7.5	11.1
	Juv.		Adult.	1	8
	Type.				
<b>Dolomys.</b>					
1.	Condylar-basal length.	26.5	32.6	100	100
2.	Zygomatic breadth.	15.7	18.5	59.3	56.8
3.	Interorbital constriction.	4.5	4.7	17	14.4
4.	Occipital breadth.	13	15.3	49.1	46.9
5.	"    depth (median).	7.6	8.8	28.7	27
6.	Condyle to <i>m</i> <sup>2</sup> .	10.2	12.8	38.5	33.3
7.	"    to front of bulla.	8.2	10.1	31	31
8.	Nasal length.	7.7	10	29.1	30.7
9.	"    width.	3.3	4.4	12.5	13.5
10.	Dental length.	16.5	20	62.3	61.4
11.	Diastema.	7.1	9.2	26.8	28.2
12.	Upper molars (crowns).	6.7	7.6	25.3	23.3
13.	"    (alveolar).	7.6	8.1	28.7	24.8
14.	Mandible.	17.5	20	63.1	61.4
15.	Lower molars (alveolar).	7.4	7.9	27.9	24.2





*A. terrestris* (continued).

## CRANIAL MEASUREMENTS:—

	<i>A. t.</i>		<i>A. s.</i>		<i>A. s.</i>		<i>A. s.</i>		<i>A. s.</i>		<i>A. abbotti.</i>	
	<i>rufescens.</i>	<i>meridionalis.</i>	<i>cus. cus.</i>	<i>schermani.</i>	<i>cus.</i>	Vosges.	Pyrenees.	Kent's Cavern.	Ignlham.	Torbryan Cave.		
	97	14	5	19	19	19	19	19	19	19	19	19
	6.4	5.10	8.3	8.16	7.7	7.7	7.7	7.7	7.7	7.7	7.7	7.7
	10	15.4	8	18.49	18.18	18.15	18.15	18.15	18.15	18.15	18.15	18.15
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
	40.9	41.2	33.7	33.8	34.7	34.7	34.7	34.7	34.2	34.2	34.2	34.2
1. Condyllo-basal length.	23.8	24.5	21±	20.4	21.7	21.7	22.2	22.2	22.3	22.3	22.3	22.3
2. Zygomatic breadth.	5.2	4.6	4.2	5	4.6	4.6	4.4	4.7	4.8	4.8	4.8	4.8
3. Interorbital constriction.	—	17.5	15.6	15.4	15.5	15.5	16.3	15.9	—	18.1	17.5	17.3
4. Occipital breadth.	—	10	10.4	9	9	9.4	9.1	9.3	10.1	10.6	10	10.1
5. " depth (median).	—	15.8	15.8	11.7	12.2	12.2	12.8	11.8	15.6	14.6	14.5	14.6
6. Condyle to <i>m</i> <sup>3</sup> .	—	10.9	11.4	8.6	9	9.4	9.4	8.9	12±	11.1	11.2	11.3
7. " to front of bulla.	10	12.2	11.2	11.3	8.8	9.4	10±	9.5	—	10.4	10.2	—
8. Nasal length.	—	—	—	—	—	—	—	—	—	—	—	—
9. " width.	4.5	5.5	4.4	3.9	3.8	3.8	3.8	3.6	—	4.6	4.1	4.3
10. Dental length.	—	26.2	26.6	22.5	22.6	22.6	22.8	22.8	25.7	26.6	—	—
11. Diastema.	13	13.2	13.2	11.7	11.5	11.5	12.3	11.6	14	13.8	12.7	11.9
12. Upper molars (crowns).	—	—	9.6	9.4	8.1	8.1	7.8	8.2	9.1	—	—	—
13. " (alveolar).	9	10.3	10.2	9.9	8.2	8.6	8.3	8.7	9.5	9.5	9.4	9.4
14. Mandible.	25	—	26.6	27.5	23.8	23.8	23.5	23.5	—	25.1	26	24.5
15. Lower molars (alveolar).	9	—	9.9	10	8.9	8.9	8.3	8.5	—	8.7±	9.4	10.3

\* Type of *A. armenicus*.



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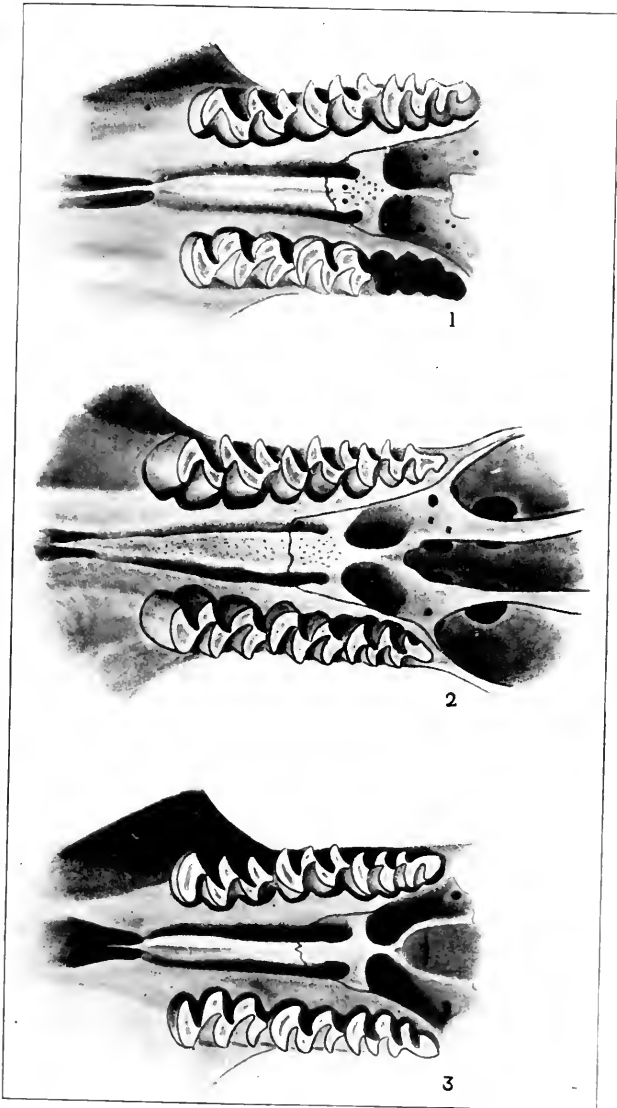


## EXPLANATION OF PLATE I.

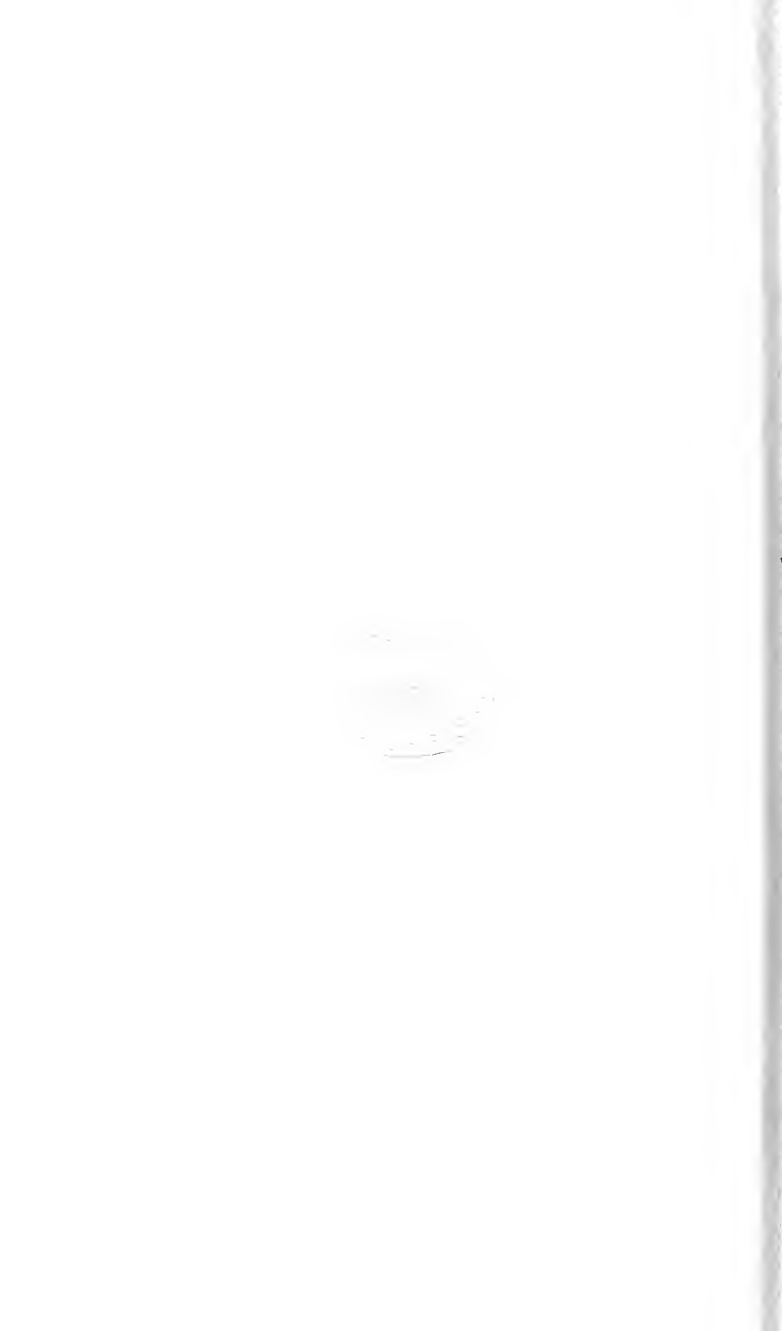
### Palates of *Microtus*.

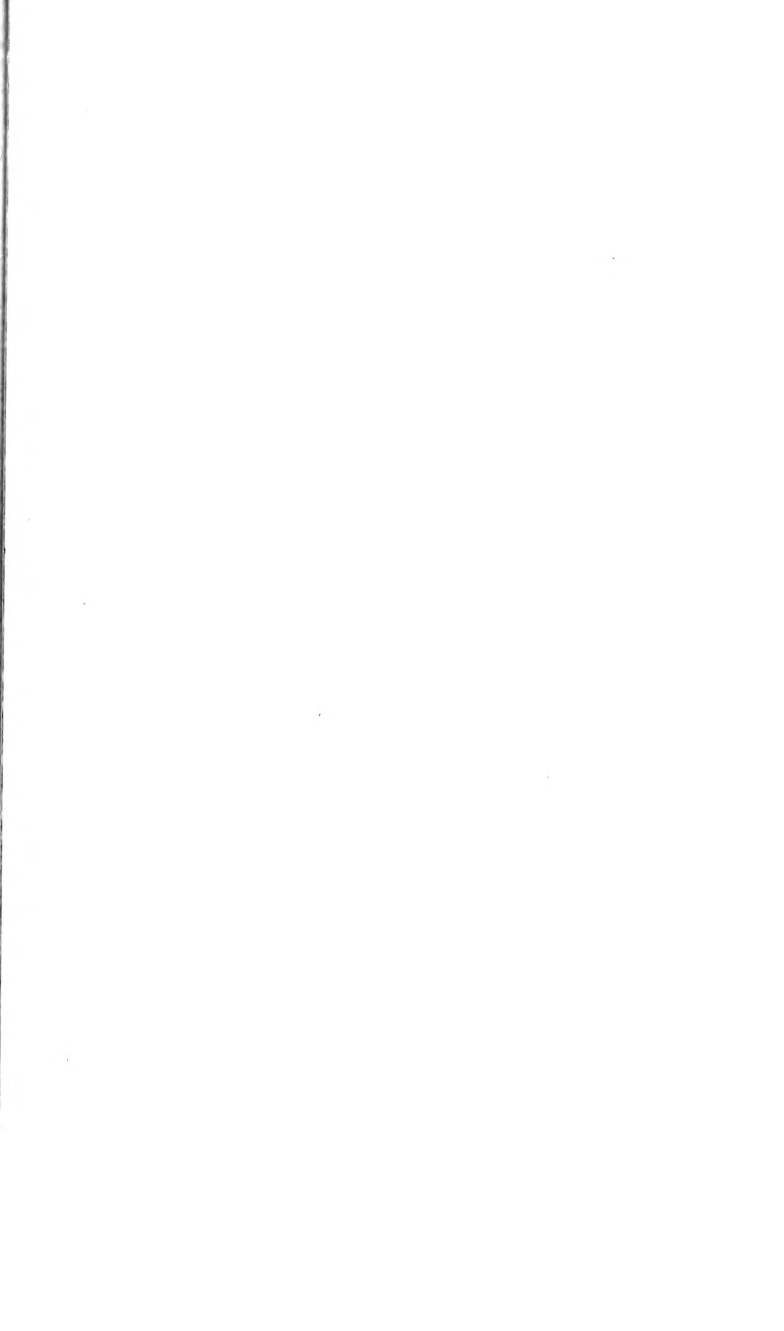
1. *Microtus* sp. Pleistocene, later Middle Terrace deposits of the Thames, Crayford, Kent.
2. *Microtus (Stenocranius) angustus* Thomas. Recent. Mongolia. (Type and only known specimen, *B.M. No.* 8.3.5.63.)
3. *Microtus (Stenocranius) anglicus* Hinton. Pleistocene fissure deposit, Ightham, near Sevenoaks, Kent. (Type.)





Palates of *Microtus*.



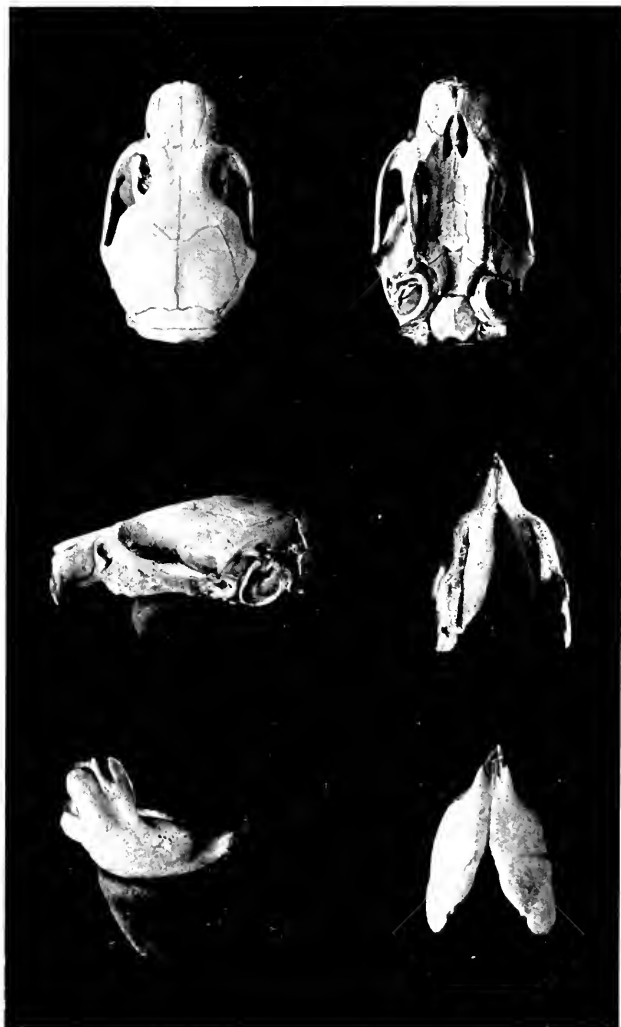


## EXPLANATION OF PLATE II.

### *Ondatra zibethica* Linnæus.

Dorsal, ventral, and lateral views of skull and mandible of new-born animal (enlarged). The condylo-basal length of this skull is 27 mm. The Plate should be compared with Figs. 44-46, which represent an adult skull of *Ondatra zibethica*, and with Figs. 1-7, which represent successive stages of growth in the skull of *Arvicola amphibius*.

The unworn  $m_1$  shown in Fig. 58 and described at p. 115 belongs to the specimen represented in this Plate.



*Ondatra zibethica* Linnæus.





EXPLANATION OF PLATE III.

*Arvicola amphibius* Linnæus.

Skull and limb-skeleton of old individual; the cheek-teeth are still growing and the epiphyses of the limb bones are still free. (Condylo-basal length 43.8 mm.)





*Arvicola amphibius* Linnaeus.

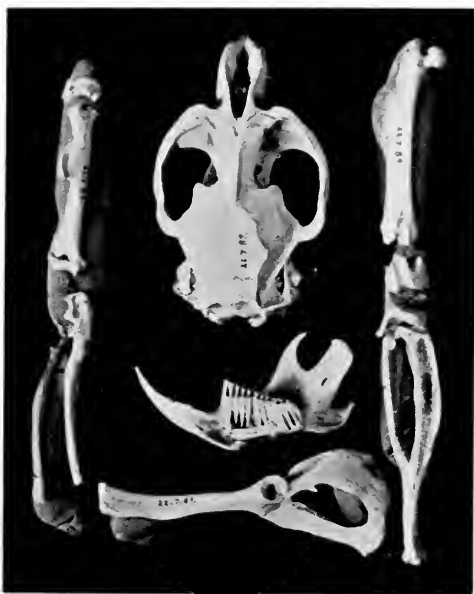
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EXPLANATION OF PLATE IV.

*Arvicola terrestris* Linnæus.

Skull and limb-skeleton of the oldest individual of the genus examined; the cheek-teeth are still growing and the epiphyses of the long bones are still free. (Condyl-basal length 43·8 mm.).



*Arricola terrestris* Linnaeus.



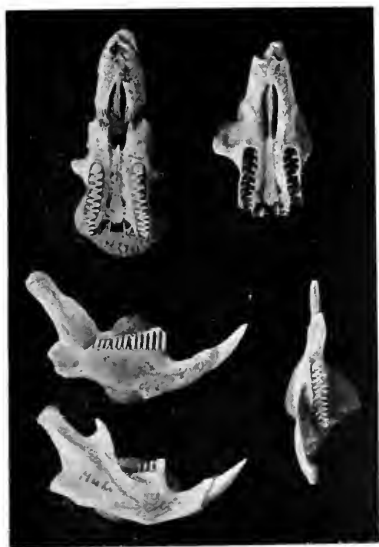


EXPLANATION OF PLATE V.

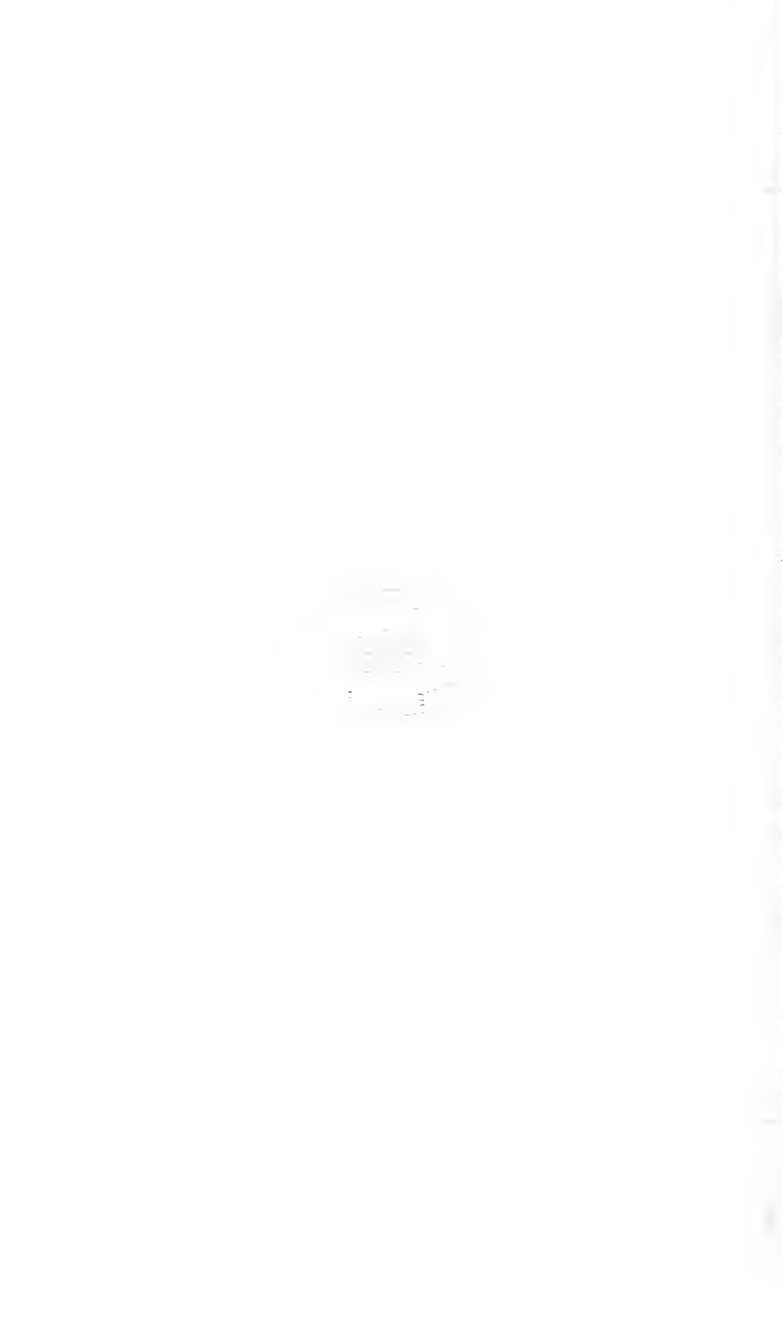
*Dicrostonyx golicmi* Sanford.

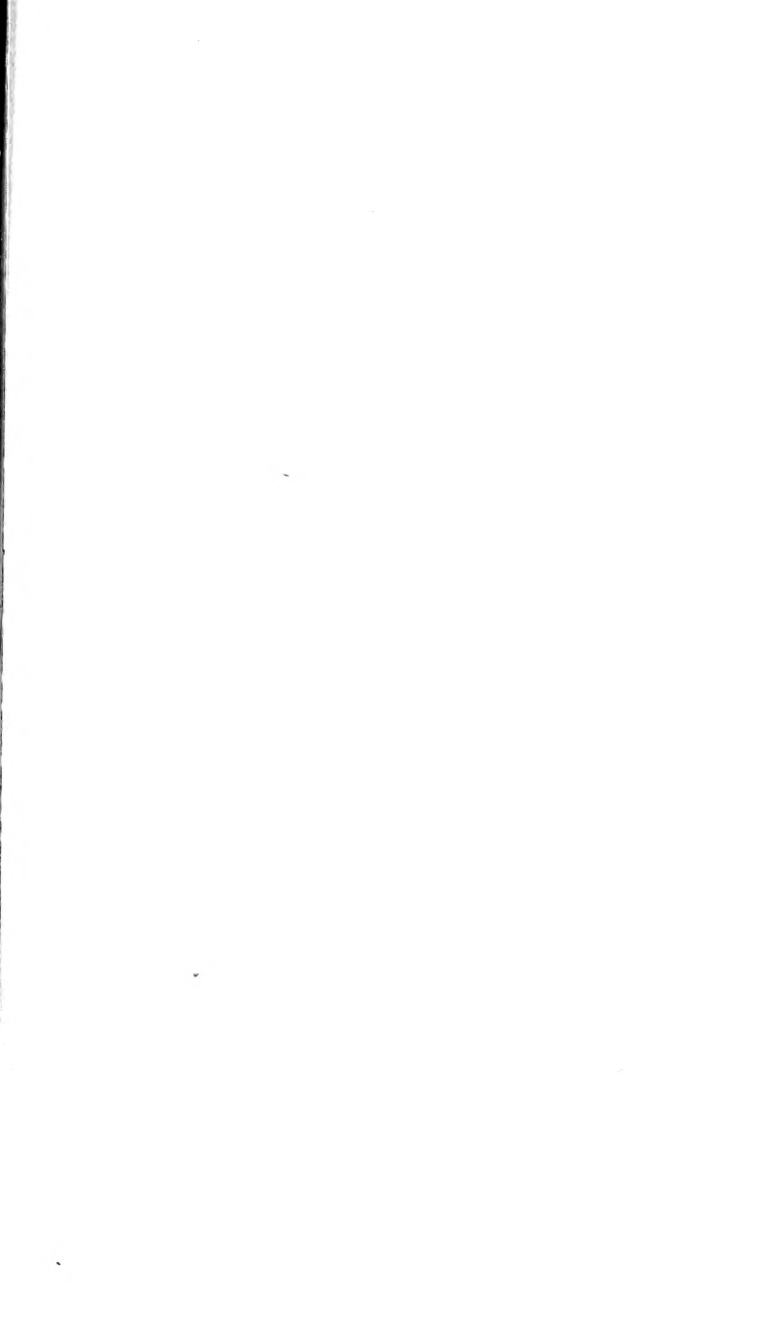
Fragmentary skulls and mandibular rami from a Pleistocene deposit in Hutton Cave, Somersetshire. These remains, in Taunton Museum, were described by Sanford in 1870 and are the co-types of the species. The upper molars of the more perfect skull are shown in Fig. 71, 4.





*Dicrostonyx gulielmi* Sanford.





EXPLANATION OF PLATE VI.

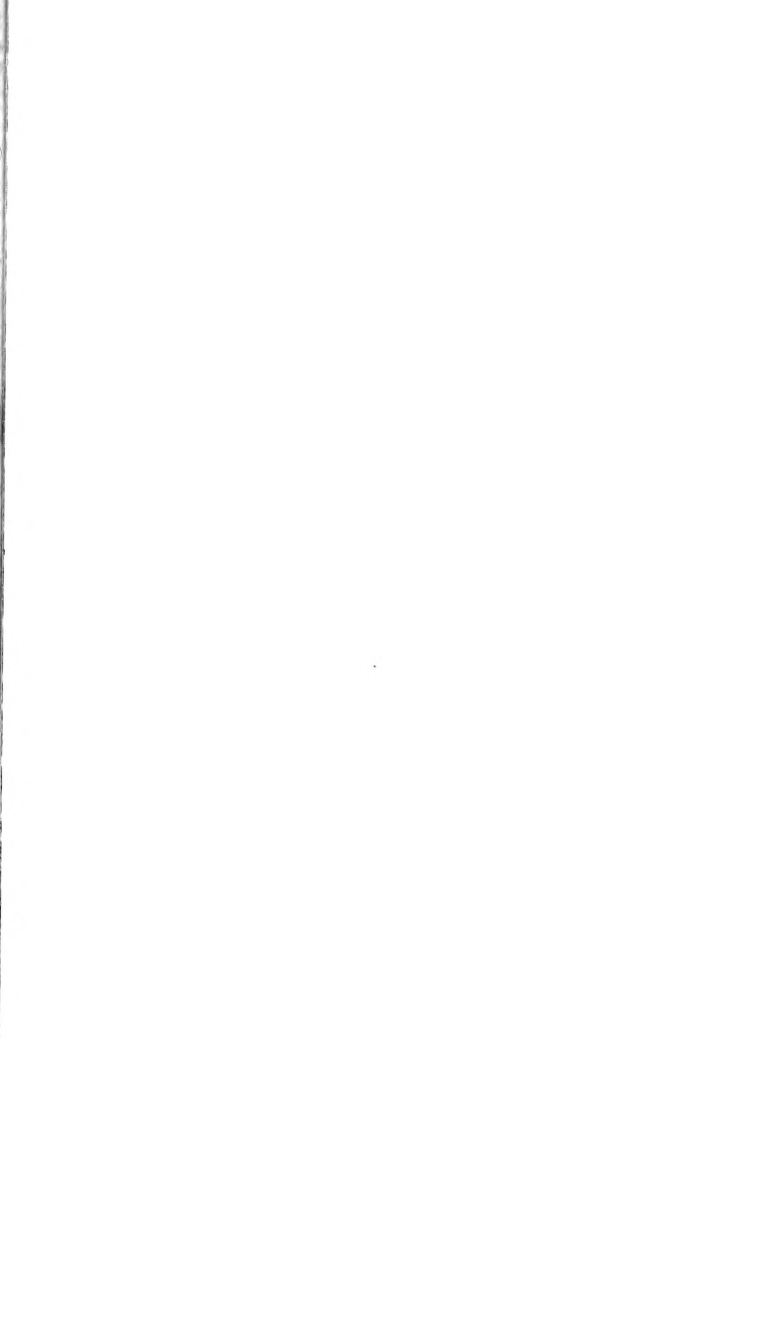
Skulls of *Lemmus*.

- a. *Lemmus lemmus*, Kola Peninsula ; adult.
- b. *Lemmus obensis*, Waigatsch ; old.



Skulls of *Lemmus*.





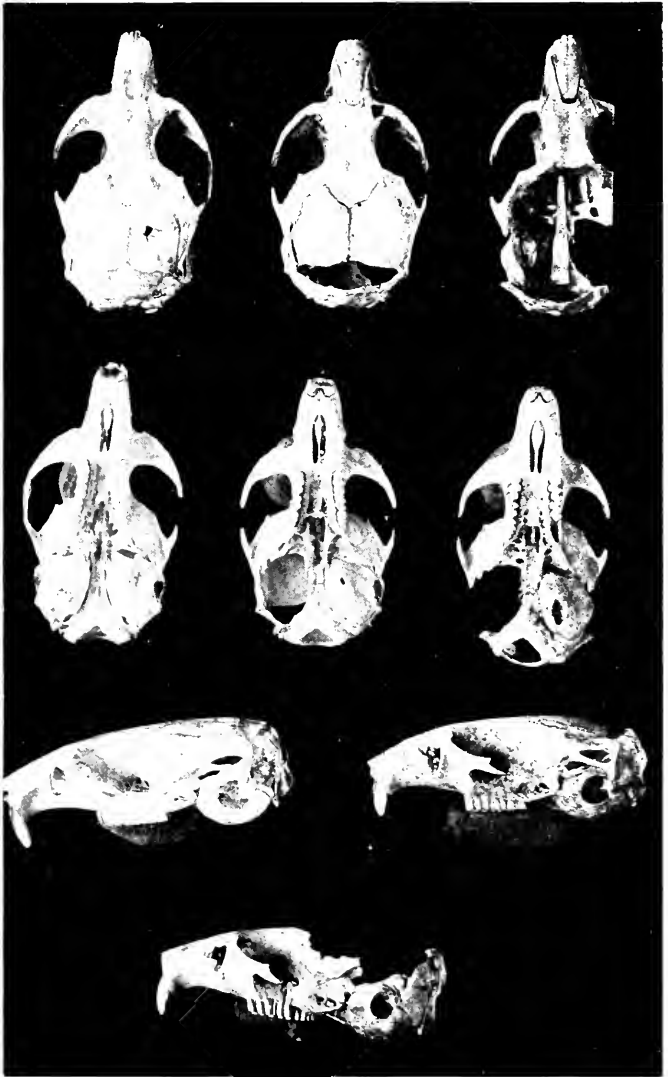
## EXPLANATION OF PLATE VII.

### Skulls of British *Evotomys*.

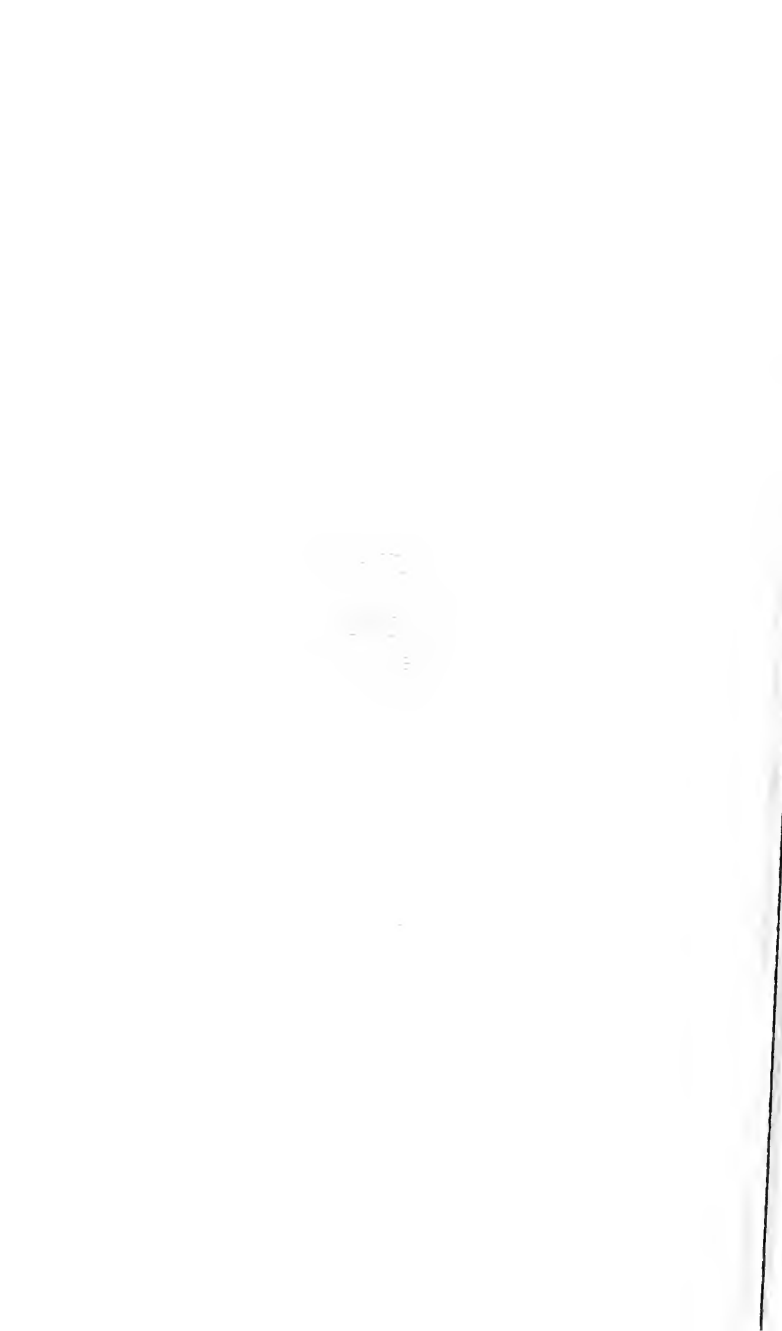
From left to right :—

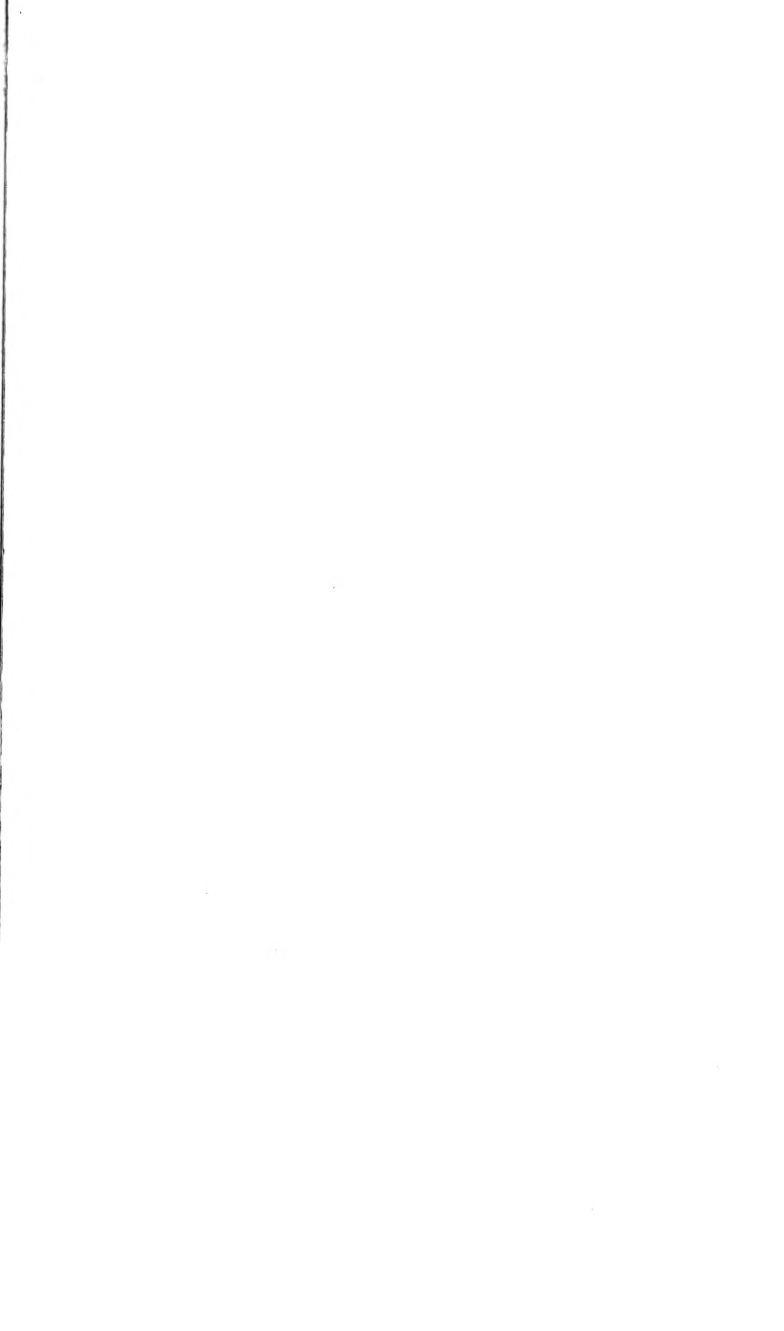
1. *E. glareolus britannicus*, adult male; Chingford, Essex. Condylο-basal length 24·2 mm.
2. *E. harrisoni*, adult (Type); Pleistocene, Ightham, Kent. Condylο-basal length 22·8 mm.
3. *E. kennardi*, young adult (Type); Pleistocene, Ightham, Kent. Condylο-basal length 23·7 mm.





Skulls of British *Eutamias*



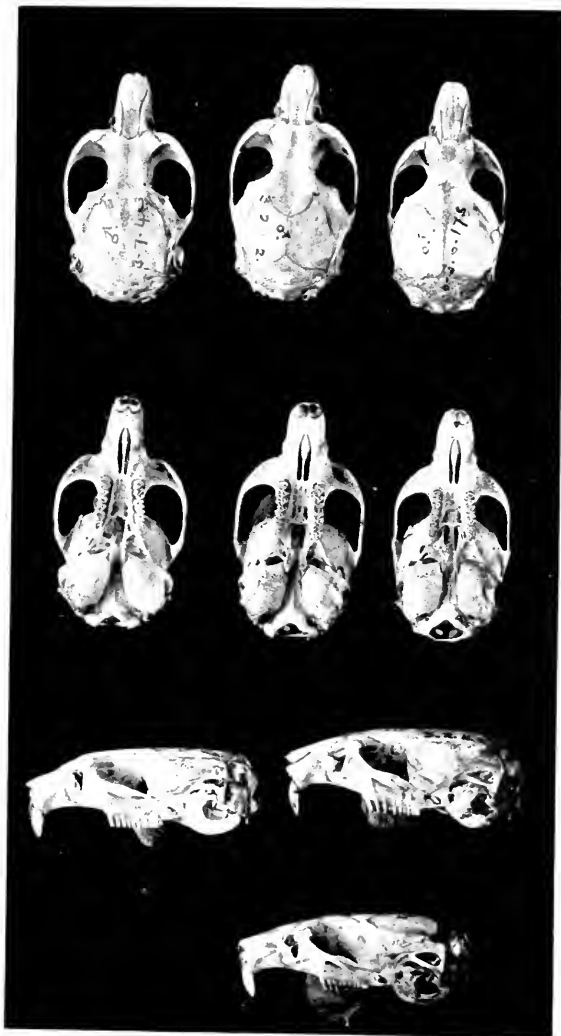


EXPLANATION OF PLATE VIII.

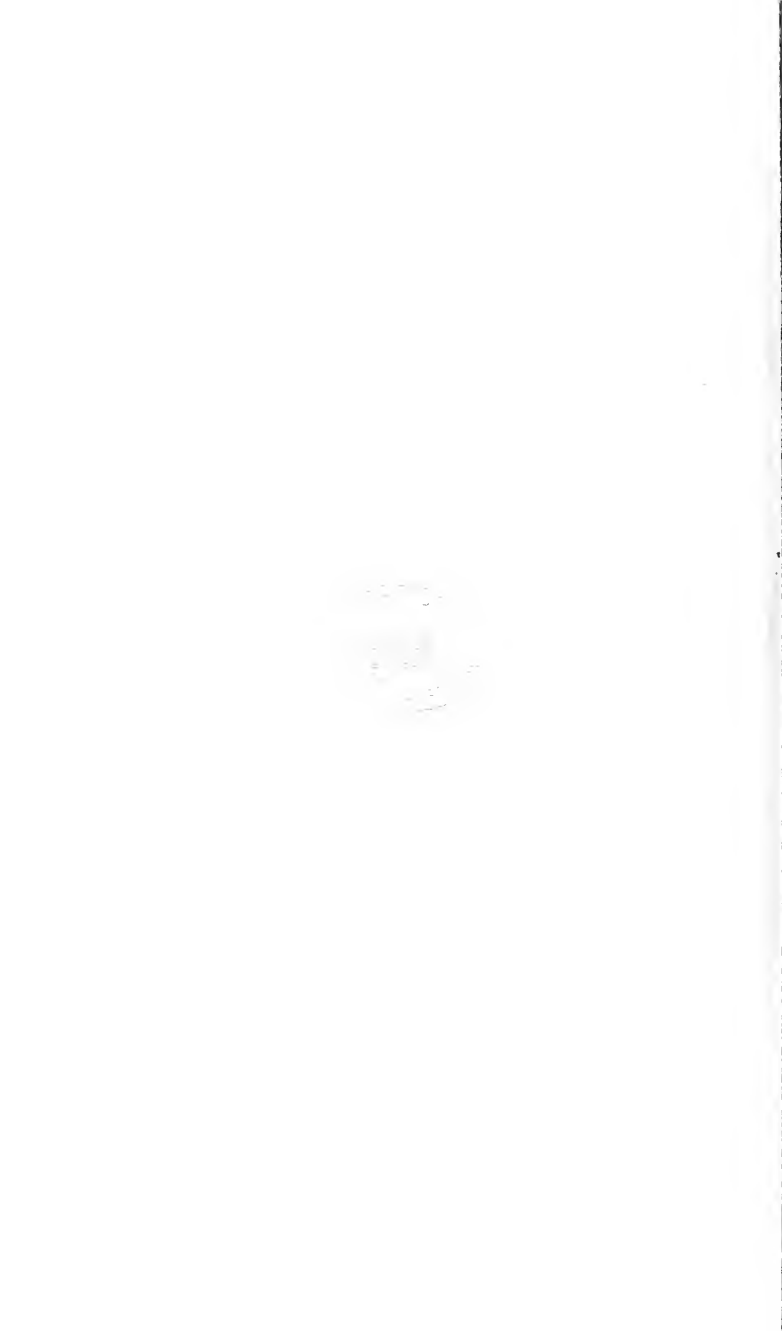
Skulls of *Evotomys*.

From left to right :—

1. *E. skomerensis*, adult male (Type). Condyllo-basal length 25·2 mm.
2. *E. cæsarius*, adult male (Type). Condyllo-basal length 25·6 mm.
3. *E. ponticus*, adult male (Type). Condyllo-basal length 24·6 mm.



Skulls of *Erotomys*.



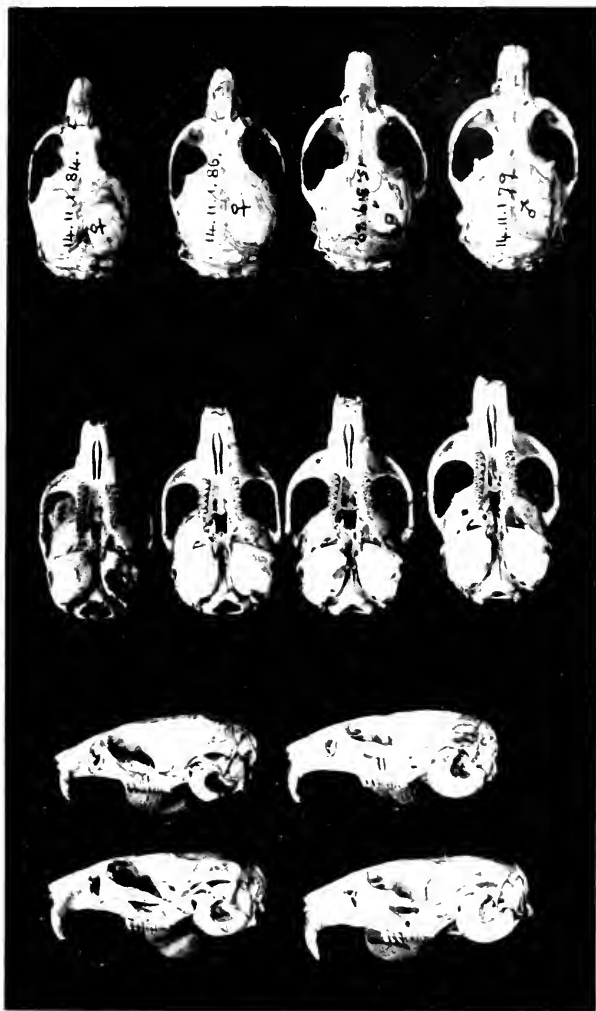


EXPLANATION OF PLATE IX.

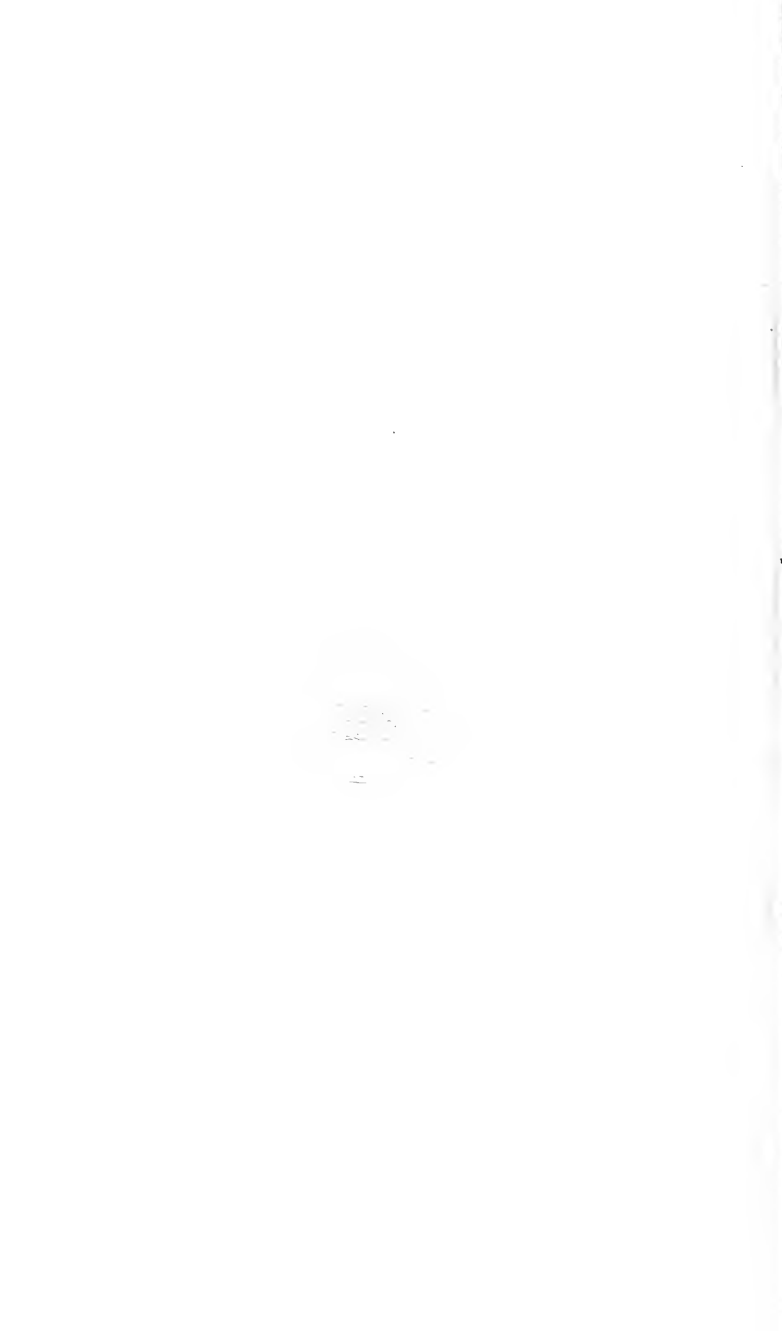
Skulls of *Evotomys rufocanus rufocanus*, Irkutsk, Siberia.

Four successive stages of growth. Condylö-basal lengths 23.5, 24.7, 26.4  
and 27.2 mm.





Skulls of *Eutamias rufocanus rufocanus*.



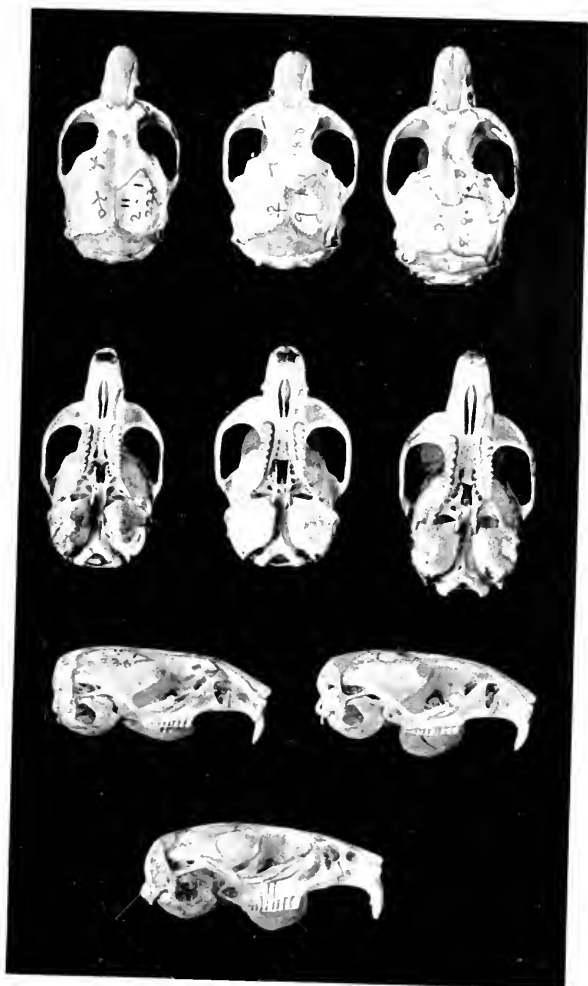


EXPLANATION OF PLATE X.

Skulls of *Evotomys rufocanus shanensis*.

From left to right:—

1. Young male (Type of "*Caryomys eva*"). Condyllo-basal length 22·9 mm.
2. Young female (Type of "*Caryomys inez*"). Condyllo-basal length 23·1 mm.
3. Subadult male (Type). Condyllo-basal length 25·7 mm.



Skulls of *Eutamias rufocanus shansicus*.





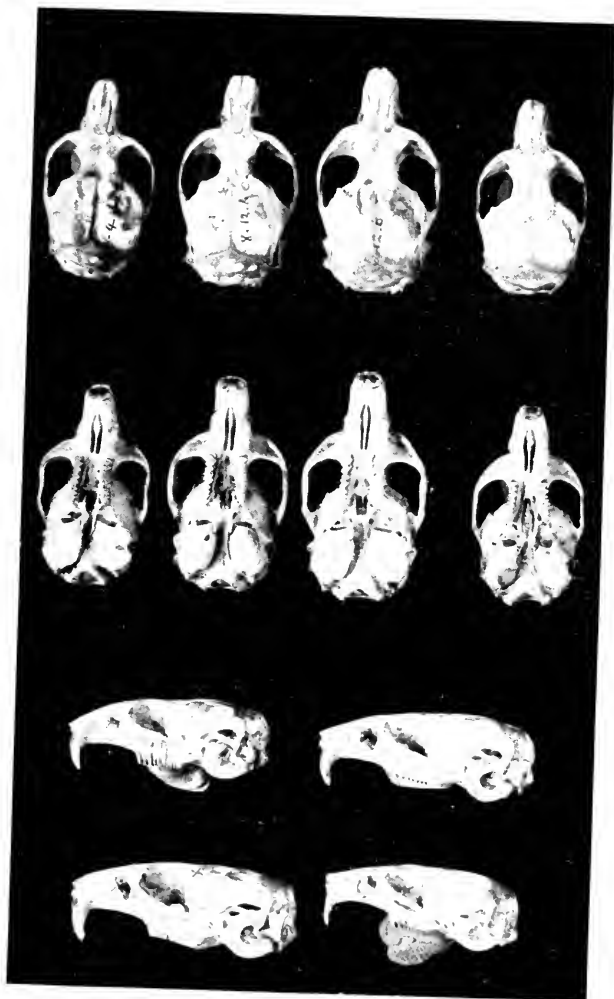
EXPLANATION OF PLATE XI.

Skulls of *Evotomys*.

From left to right :—

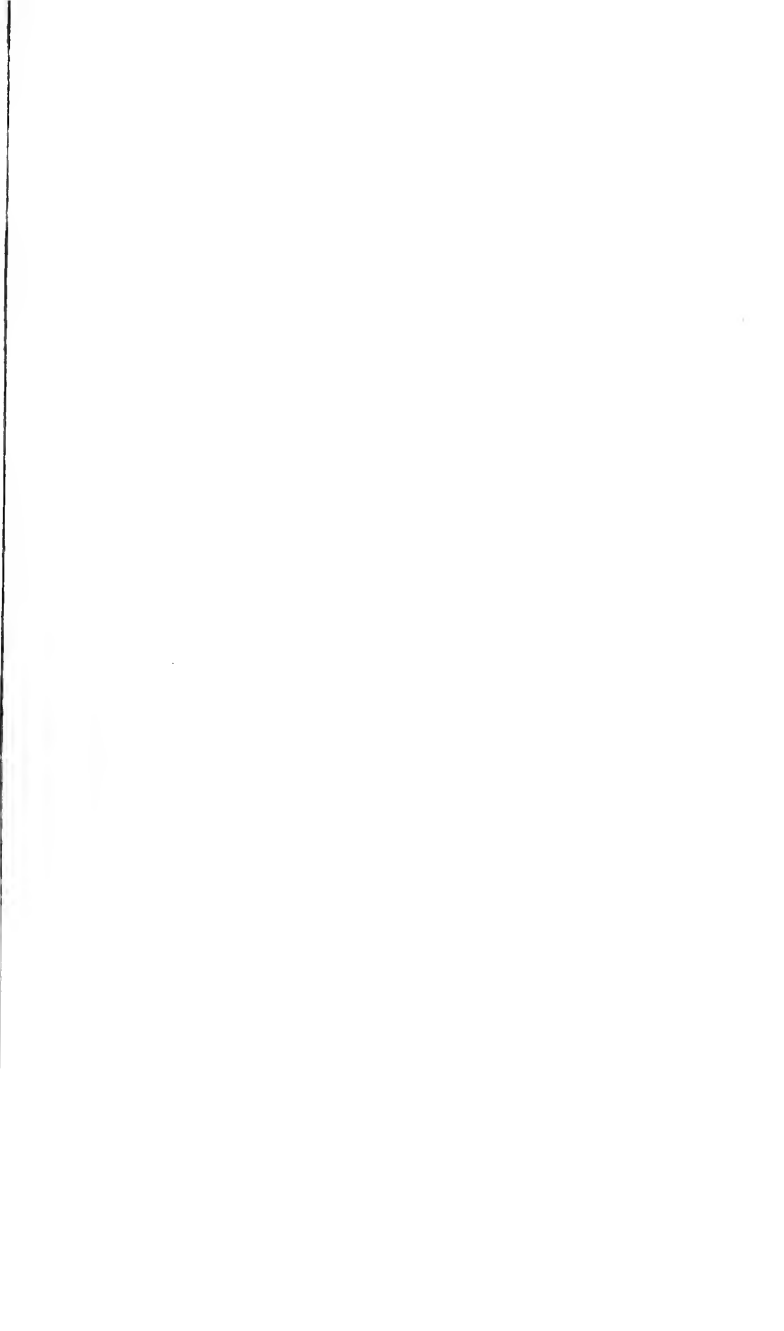
1. *E. rufocanus smithii*, young female (6.1.4.344). Condyllo-basal length 23·5 mm.
2. *E. r. smithii*, young male (Type of "*Crascomys viigatæ*"). Condyllo-basal length 25·4 mm.
3. *E. r. regulus*, subadult male (Type). Condyllo-basal length 26·6 mm.
4. *E. wosnessenskii*, old female. Condyllo-basal length 23·2 mm.





Skulls of *Erotomys*.



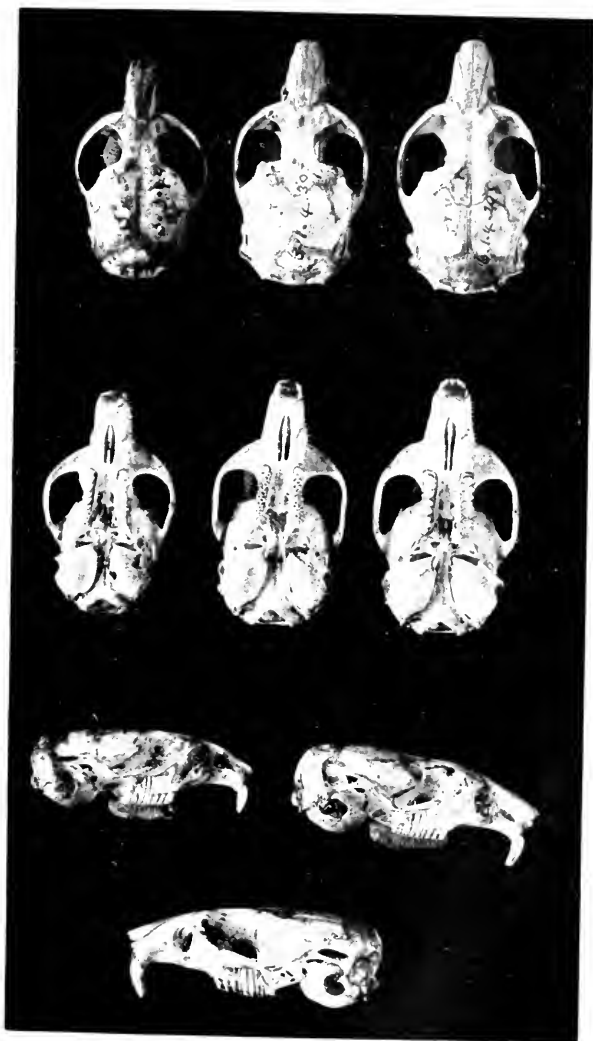


EXPLANATION OF PLATE XII.

Skulls of *Evotomys rafocanus smithii*.

From left to right:—

1. Young male (Type). Condyllo-basal length 23·7 mm.
2. Subadult male (Type of "*Crascomys andersoni*"). Condyllo-basal length 25·7 mm.
3. Adult (Type of "*Crascomys bedfordiæ*"). Condyllo-basal length 26·9 mm.



Skulls of *Ereotomys rufocanus smithi*.





EXPLANATION OF PLATE XIII.

*Mimomys*.

- 1, 1a. *Mimomys pliocænicus*. Left  $m_1$ , Norwich Crag; outer and inner views of tooth represented by Fig. 99, 3.
2. *M. savini*. Right  $m_1$  outer view; same specimen as that shown in Fig. 101, 5.
3. *M. savini*. Left  $m_1$  outer view; same specimen as that shown in Fig. 101, 13.
4. *M. intermedius*. Left  $m_1$  very young, outer view; same specimen as in Fig. 99, 10.
5. *M. intermedius*. Right  $m_1$  very young, outer view; same specimen as in Fig. 99, 8.
6. *M. intermedius*. Right  $m_1$  young, outer view; same specimen as in Fig. 99, 9.
7. *M. savini*. Left  $m_1$  young, outer view; same specimen as in Fig. 99, 15.
8. *M. savini*. Left  $m_1$  adult, outer view; same specimen as in Fig. 101, 3.
9. *M. savini*. Left  $m_1$  very young, outer view; same specimen as in Fig. 99, 13.
10. *M. savini*. Right  $m_1$  adult, outer view; same specimen as in Fig. 101, 14.
- 11, 11a. *M. cantianus*. Inner and outer views of type specimen, a right  $m_1$ , shown in Fig. 99, 21.





Fig. 1.

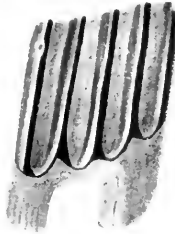


Fig. 1a.

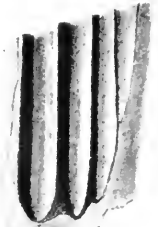


Fig. 2.



Fig. 3.



Fig. 4.



Fig. 5.



Fig. 6.

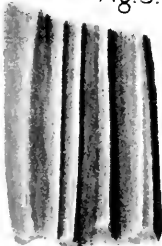


Fig. 7.



Fig. 8.



Fig. 9.



Fig. 10.

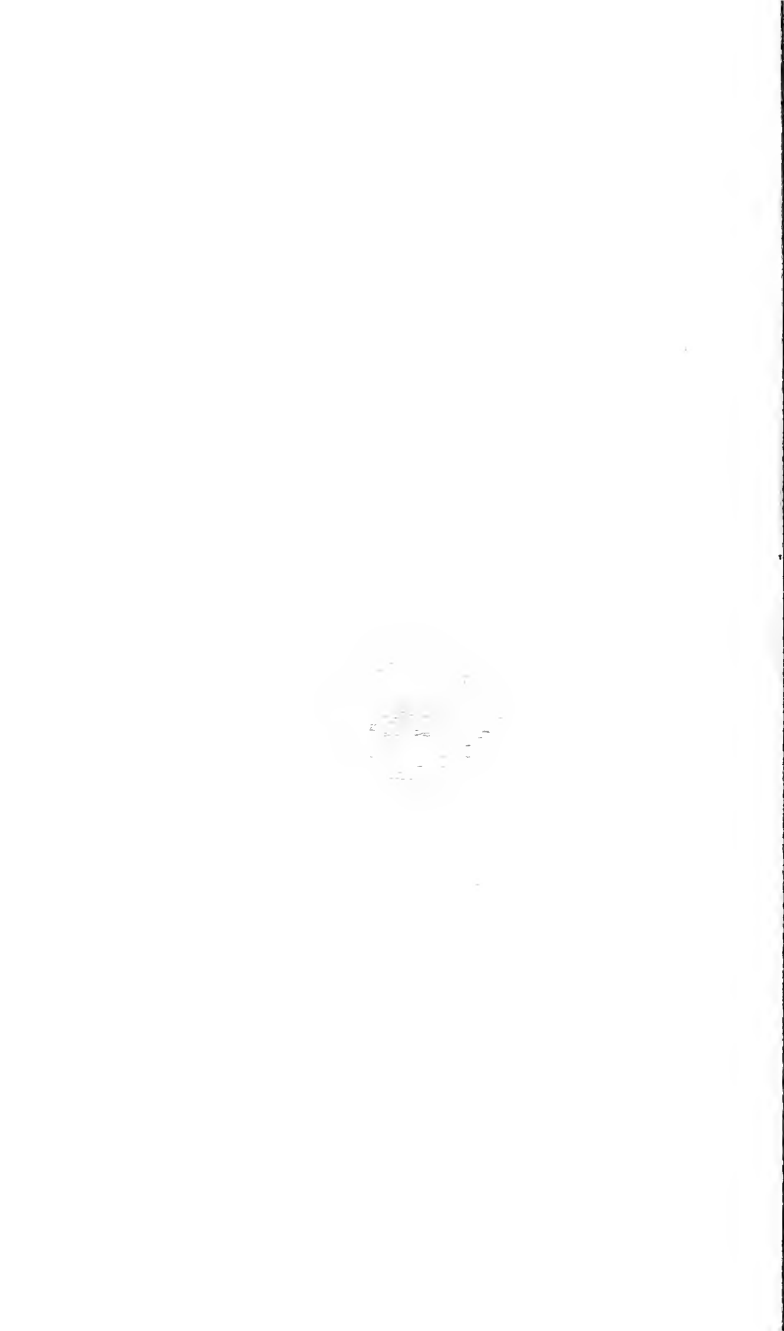


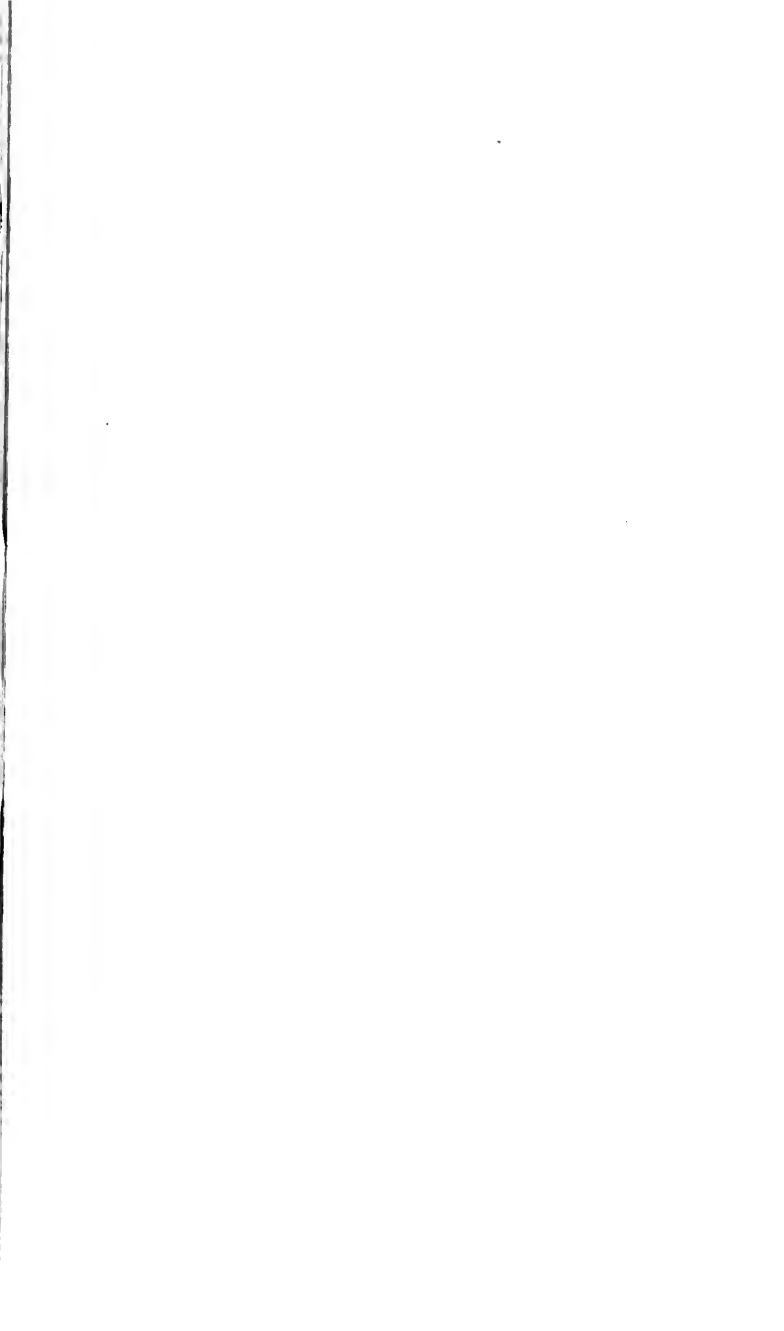
Fig. 11.



Fig. 11a.

*Mimomys.*  
Lateral views of  $m_1$ .





EXPLANATION OF PLATE XIV.

*Mimomys intermedius* Newton.

Upper Freshwater Bed, West Runton.

Fig. 1. Palate (*Savin Collection*).

Figs. 2 and 3. Outer and inner views of fragmentary right ramus. The outer view shows the insertion places of the two divisions of the *masseter medialis* muscle particularly well.



Fig. 1.



Fig. 2.

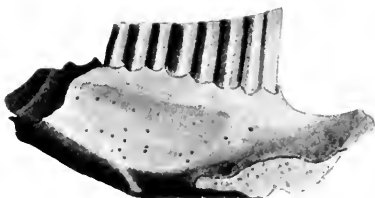
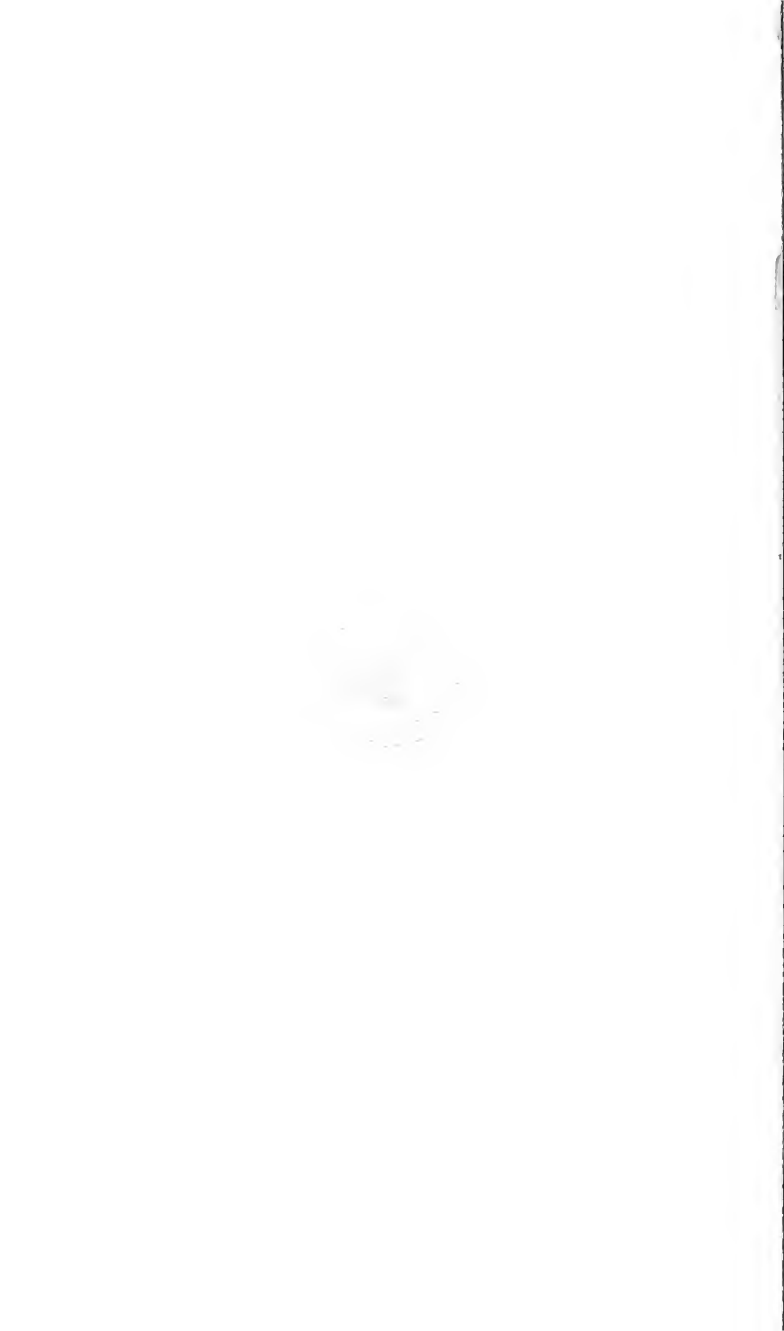
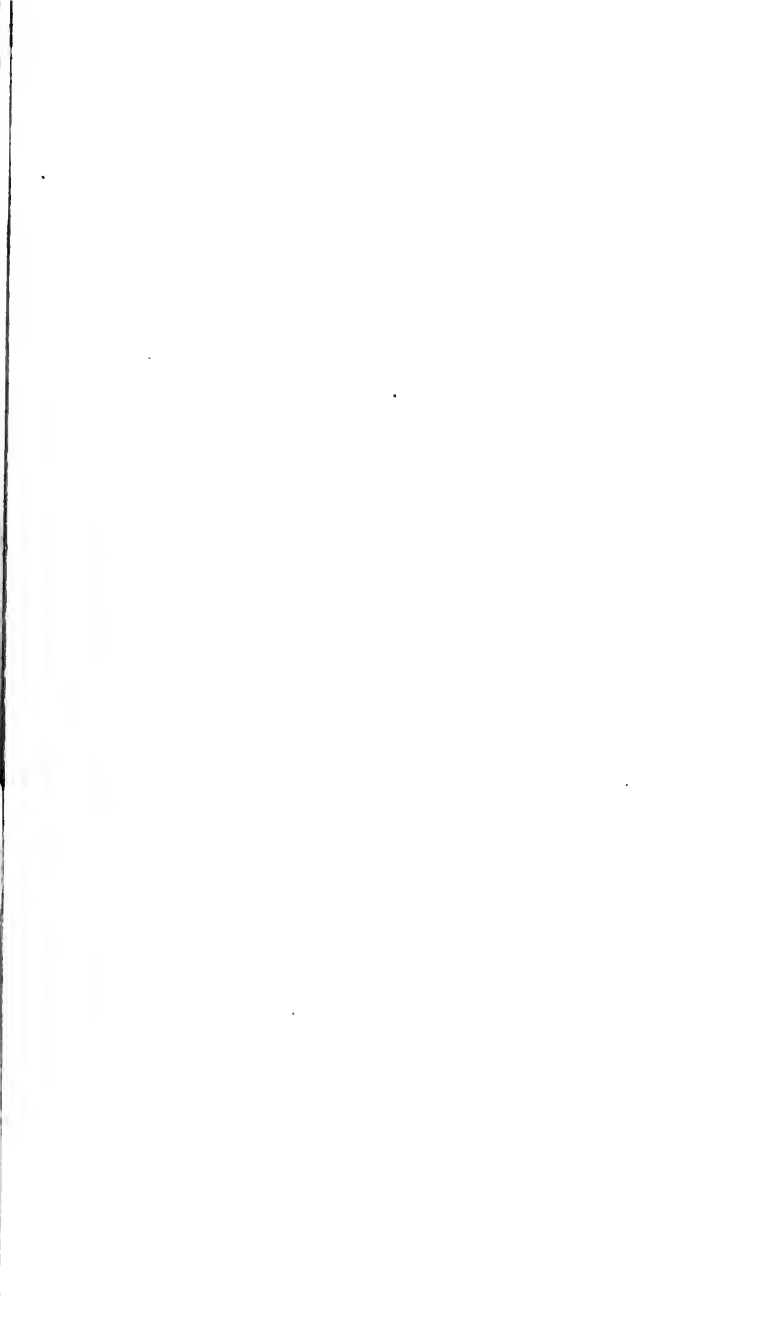


Fig. 3.

*Mimomys intermedius* Newton.





## EXPLANATION OF PLATE XV.

### *Mimomys majori* Hinton.

Lateral views of teeth represented in Figs. 99, 104 and 105.

1. *Mimomys majori*. Right  $m_1$ , very young, outer view; crown view, Fig. 99, 17 and 104b.
2. *M. majori*. Left  $m_1$  adult, outer view ; crown view, Fig. 105, 7.
3. *M. majori*. Right  $m_1$  young, outer view ; crown view, Fig. 105, 6.
4. *M. majori*. Right  $m_1$  youngish, outer view ; crown view, Fig. 105, 8.
5. *M. majori*. Right  $m_1$  young, outer view ; crown view, Fig. 105, 13.
6. *M. majori*. Right  $m_1$  young, outer view ; crown view, Fig. 105, 3.
7. *M. majori*. Right  $m_1$  adult, outer view ; crown view, Fig. 105, 11.
8. *M. majori*. Left  $m_1$  young, outer view ; crown view, Fig. 105, 13.
9. *M. majori*. Left  $m_1$  young, outer view ; crown view, Fig. 105, 4.
10. *M. majori*. Right  $m_1$  young adult, outer view ; crown view, Fig. 105, 12.
11. *M. majori*. Right  $m_1$  young, outer view ; crown view, Fig. 105, 9.
12. *M. majori*. Left  $m_1$  young, outer view ; crown view, Fig. 105, 1.

The groove which forms the external vestige of the reduced fourth outer fold is a prominent feature in figs. 1, 3, 6, 11 and 12 of this plate ; it can be seen also in figs. 4, 5, and 8.





Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.

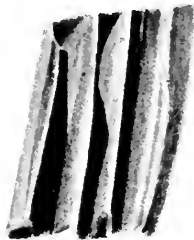


Fig. 5.



Fig. 6.



Fig. 7.



Fig. 8.



Fig. 9.

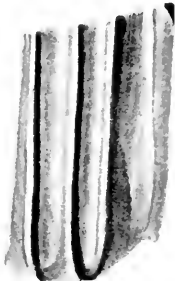


Fig. 10.

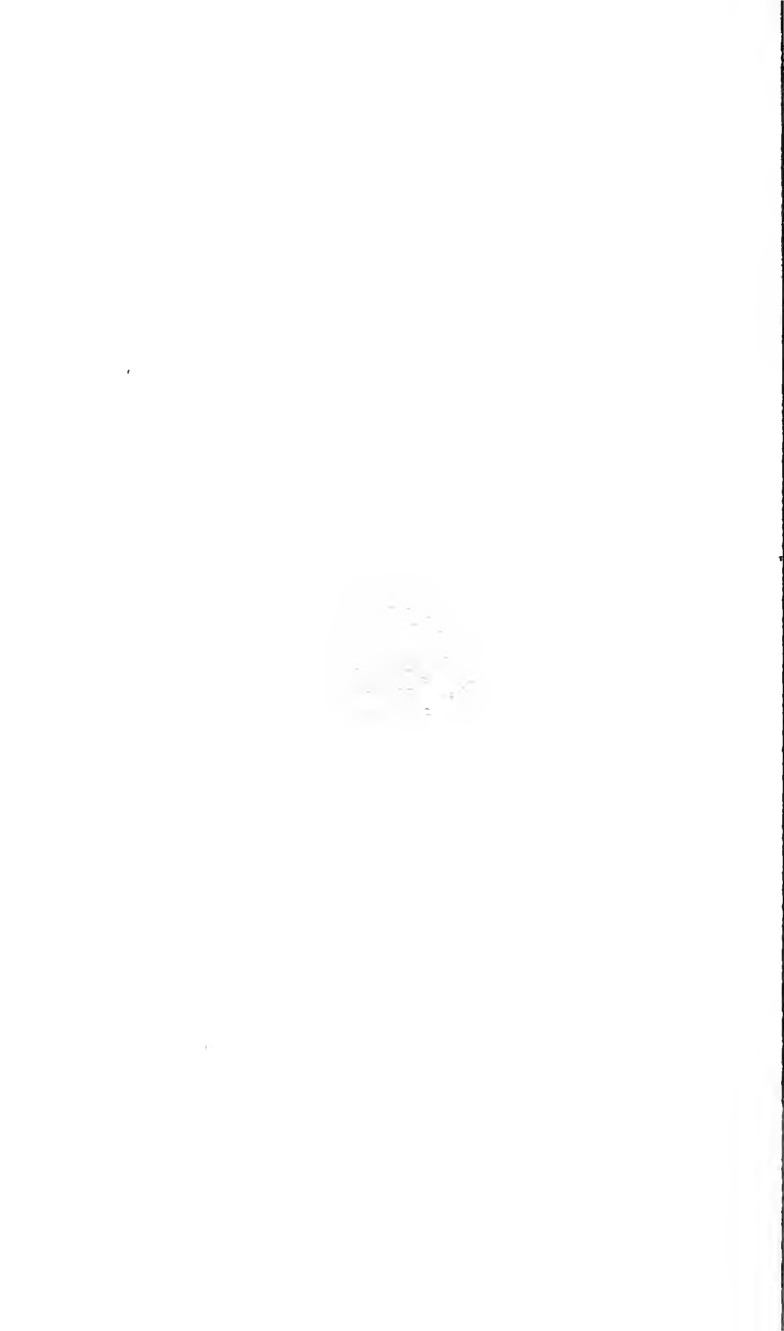


Fig. 11.



Fig. 12.

*Mimomys majori* Hinton.  
Outer views of  $m_1$ .







147  
15

