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Problems of the Morphology and Zoogeography of Representatives of the Genus *Lemmus* Link 1795 from the Palaearctic

Проблемы морфологии и зоогеографии представителей рода *Lemmus* Link 1795 из Палеарктики

Zagadnienia morfologii i zoogeografii przedstawicieli rodzaju *Lemmus* Link 1795 z Palearktyki

(with 4 tables)

I. INTRODUCTION

The lemming — one of the commonest rodents of the Palaearctic — has a very extensive range of occurrence (Miller, 1896; 1912; Hinton, 1926; Pohle, 1932; Ellermann, 1940; Ognev, 1950; Ellermann & Morrison-Scott, 1951; Van den Brink, 1956; Darlington, 1957).

In Europe the form described as *Lemmus lemmus* (Linnaeus, 1758) — Norway lemming, occurs in the mountains of Scandinavia and on the Kola peninsula, and to the east of the White Sea, the Siberian Lemming. The synonym of this form is *Lemmus obensis* Brants, 1827 (Ellermann,

1949; Ellermann & Morrison-Scott, 1951). Pallas (1758) described this form as *Mus lemmus* var. *obensis*, while Middendorf (1853) described it as *Myodes obensis*.

The range of occurrence of lemmings is subject to considerable variations and depends on the mass appearances of these animals. Many research workers have examined this problem, and literature on this subject is very extensive (Elton, 1942; Grass, 1947; Kalela, 1941; 1949; Lack, 1954). I have not dealt with this problem in my present work from either theoretical or descriptive aspect, my interest being concentrated only on the influence by mass appearance of this mammal on the qualitative composition — the age and size of the material captured. Thompson (1955) gives certain data on this problem, to which I shall return in the next part of this work.

The problem of the systematics and morphology of lemmings is an extremely interesting one. These animals occur over a large region under conditions peculiar to the Arctic tundra, with its very characteristic vegetation, in areas extending along the coast of the Arctic Ocean to the mountains of Scandinavia. The climatic conditions there are everywhere similar (only the Scandinavian mountains to a certain extent forming an exception).

The extent of our knowledge of the biology of lemmings differs considerably in respect of the populations living in different areas within their whole range. We know relatively most about the Norway lemming, since there are many works on this animal by the eminent Norwegian zoologist, R. Collett (1876; 1877; 1895; 1907; 1911—12; and also Crotch-Duppa, 1878; Sommerville, 1891; Elton, 1942; Isakov, 1939; Kalela, 1941; 1949; Rendahl, 1942; Wildhagen, 1953).

The Siberian lemming is less well-known, both as regards the ranges of its occurrence in the south and its biology. Among the more important works on its morphology the following may be mentioned: works by Vinogradov, 1925 and Ognev, 1950. The poorer store of knowledge we possess on the Siberian lemming is due to the enormous area of its occurrence, parts of which have never yet been subjected to research work.

There is a lack of works describing the morphology of lemmings, and in literature on this animal we encounter only scanty and incomplete data on its craniometric and body measurements, based on small amounts of material (Lilljeborg, 1874; Collett, 1911—1912; Miller, 1912; Vinagrodov, 1925; Hinton, 1926; Bergström, 1948; Ognev, 1950). My work is aimed at providing a list of suitable measurements which may prove of value in further research on this interesting rodent.

Lemmings were known as early as the Pleistocene (Simpson, 1945). They formerly occurred widely over almost the entire area of Europe, their range retreating to the north with the recession of glaciation, and in fact in the Scandinavian mountains in which lemmings now occur as their most southerly station, these animals constitute a post-glacial relict of a certain kind.

The question of the numbers of species and subspecies of lemming described is an open one. Many of the species described from north-east Asia are nowadays considered at most as subspecies. According to Ellermann & Morrison-Scott (1951), two species appear in the Palaearctic area:

Lemmus lemmus (Linnaeus, 1758)

Lemmus sibiricus (Kerr, 1792).

Vinogradov (1925) gives the following subspecies of Siberian lemming from the Soviet Arctic regions:

Lemmus obensis obensis (Brants, 1827) — from the White Sea to the River Lena, the Vaigach and Novaya Zemlya Islands.

Lemmus obensis bungei (Vinogradov, 1924) — the lower course of the Lena river;

Lemmus obensis novosibiricus Vinogradov, 1924 — New Siberian Islands;

Lemmus obensis chrysogaster Allen, 1903 — Eastern Siberia,

Lemmus paulus Allen, 1914 — further to the east from the Kolyma river;

Lemmus flavescens Vinogradov, 1925 — Kamchatka;

Lemmus amurensis Vinogradov, 1924 — relict form, not connected with the distribution of another species.

In more recent works on lemmings (Ellermann & Morrison-Scott, 1951) it is accepted that these are all subspecific forms only of *L. sibiricus* (Kerr, 1792), and indeed there is no adult specimen in collections of the *„flavescens"* form, the *„amurensis"* form is described on the basis of one very young specimen only, and only the form *„paulus"* is described by Vinogradov (1925) on the basis of six specimens. All these forms, in the author's opinion, are similar to *Lemmus minusculus* Osgood, 1904 and *Lemmus trimucronatus* (Richardson, 1825) from Alaska and Canada. Ognev (1950) also, in comparing *Lemmus obensis chrysogaster* Allen, 1903 with *Lemmus alascensis* Merriam, 1900 from Alaska, reaches the conclusion that they are representatives of one species. He assumes that there is a possibility of a separate subspecies occurring on Kamchatka, but does not rule out the possibility that the forms *„chrysogaster"*, *„flavescens"* and *„paulus"* are identical with the form *„alascensis"*.

In the present work I have, like Ellermann, treated individuals from areas to the east of Kolyma, identified as separate species, as representatives of the species *Lemmus sibiricus* (Kerr, 1792).

The systematics problem of Palaearctic lemmings will be further discussed in this work. I accepted as my starting point the existence of two groups — two species — the Norway and the Siberian lemmings. The description of their morphology and the systematic problems connected with it form the subject of the present work.

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II. MATERIAL AND METHODS

This work is based on material consisting of 186 skulls of Norway lemmings and 139 skulls of Siberian lemmings. The descent and sex of almost all the specimens were known. The specimens were taken from the Zoological Museum of Oslo University, the Zoological Museum of Bergen University, the Zoological Museum at Trondheim, the Museum in Tromsö, The Royal Museum of Natural History in Stockholm, the Zoological Museum of the Lomonosov University in Moscow and the Museum of the Zoological Institute of the Soviet Academy of Sciences in Leningrad.

A certain deficiency, which is inevitable when working on museum material, was the impossibility, in the majority of cases, of investigating large series of specimens caught at one time in one place. This to a certain extent adversely affects the results obtained, and makes comparison difficult.

I measured the skulls of all specimens by means of a nonius with accuracy of 0.1 mm, taking the following measurements:

1. Condylobasal length — distance from the frontal indentation in the intermaxillary bone (between incisors) to the furthest point on the occipital projection.

2. Basic length of skull — distance from the frontal indentation in the inter-maxillary bone to the lower indentation in the foramen magnum.

3. Diastema — distance from the posterior edge of incisor cavity to the first upper molar.

4. Breadth of occipital — (maximum) — measured at the crista of the occipital bone.

5. Zygomatic breadth of skull — measured on the sutures of the arches.

6. Interorbital constriction.

7. Height of skull per bullae measured so that the lower arm of the nonius rested on the most convex point of the bullae, and the upper arm on the anterior part of the interparietal bone, perpendicularly to the horizontal axis of the skull.

8. Height of palate — one point of the nonius rested on the posterior edge of the anterior palatal cavity, and the other on the boundary between the nasal and frontal bones.

9. Height of braincase — measured from the edge of the base of the occipital and sphenoidal bones to the anterior edge of the interparietal bone.

10. Length of molars in upper jaw.

11. Length of molars in lower jaw.

I chose these particular measurements as they are the ones most frequently encountered in craniometric works, and give a good picture of the shape of the skull.

The question of age is of considerable significance. As I mentioned above, some of the lemming forms were described on the basis of very young individuals, and on this account old specimens caught in other areas may be regarded as completely different forms, if we do not remember that great changes have taken place in the skulls of lemmings, as the case with other *Microtinae*, during the course of their development. In the first place the skull has greatly increased in length and breadth (H i n t o n, 1926; R a u s c h, 1953), bone ridges have been strongly formed, the minimum breadth of the frons has decreased as the result of the formation of a bony ridge between the eye-sockets, beginning at the base of the nasal bone.

I found that as a result of the above, the palatal height in old specimens had undergone a relatively great increase. The height of the braincase, however, measured on the sphenoidal bone (inter b u l l a e) similarly to many other rodents (H i n t o n, 1926; W a s i l e w s k i, 1952) increases with age to an inconsiderable degree only, but the mutual relation changes between these two values of measurement of skull height. With young specimens the palatal height is always lower (absolute values) than the height of the braincase. In old individuals the reverse relation is found, as a result of the formation of the bone ridge. The palatal height is greater, or equal, to the height of the brain case. This is a very significant age feature, making it possible to define the age of lemmings completely accurately. In my opinion it would be interesting to check whether similar dependences occur in other rodents.

Division of the material into age groups is of great importance in all comparative investigations. V i n o g r a d o v (1925) distinguished six groups in lemmings (adult, sub-adult, from I do IV and juveniles), on the basis of the degree of formation of the bony ridge on the skull. This is undoubtedly a very accurate division, especially when a large number of specimens is available, but when somewhat small series only are compared, this detailed division makes comparison difficult, since we than have only a few indivi-

duals in each age group. In my work I have divided the material into young and sexually mature individuals only, since it seems evident that the criterion of sexual maturity is the most certain index here. Among the specimens which I caught at Valdres (the valley in the Central Norway mountains) and those which I prepared from material fixed in alcohol, I never encountered a pregnant female having a condylobasal length of less than 25 mm. As variation in length of skull is to a large extent determined by age (S p a r k e r, 1948), the division according to condylobasal length of skull may be accepted as a criterion. I therefore classed individuals with a condylobasal length of less than 25 mm. as young. This agrees with data given by V i n o g r a d o v, who obtained these results on the basis of degree of formation of the bony ridge on the skull.

It should, however, be remembered that lemmings attain sexual maturity in different periods in different years. During a peak period of population numbers this takes place far earlier than in other years, and this may to a certain extent affect the size of mature individuals during, or immediately after, a population peak. Certain data bearing witness to this are supplied in the works by T h o m p s o n (1955) from Alaska, who found that the migratory individuals are smaller than the settled ones.

When carrying out comparative research work it is of great importance to know whether we are dealing with migratory or settled specimens. Therefore, when we have a series of specimens from one place, and these specimens are decidedly larger or smaller than those from another area, these differences should not necessarily be attributed to subspecific differentiation, as they may be caused by biological factors, e.g. a different phase of the population cycle. In my opinion the specimens from the islands in the Arctic Ocean come from stationary populations, and that this is the reason for their greater size.

Sometimes it may happen that a research worker in process of making a collection of specimens from, for instance, an arctic island, endeavours to catch the biggest and finest specimens. This, of course, affects the result obtained later on — all averages are naturally greater. If, however, we take into consideration the extremes of variation, we can see that they fluctuate within the same limits as in other areas. In addition, the distribution of individuals in the different classes of length is different in such

a case. This is illustrated by diagram 1, drawn up for Norway and Siberian lemmings, and lemmings from the New Siberian Islands. While the curve for Norway lemmings has a characteristic lay-out, in the case of Siberian lemmings we see two „peaks" of the curve. There are no individuals of average size. This is also the case with lemmings from the New-Siberian Inslands, where there are large specimens only. This is evidence of the fact that species from these areas were usually selected, the largest specimens being captured as being most suitable for museum purposes. This applies chiefly to material from places difficult of access. In the collections from Scandinavia, the material is more uniform and equal, the majority being individuals of average size. There are few of the largest specimens.

The Scandinavian material comes chiefly from periods when the greatest numbers of lemmings occurred — from their population peaks, and in the museum collections which I was able to use there were practically no specimens from districts in which these animals usually live, i.e. mountainous areas over 1000 m. above sea level. I was therefore unable to discover whether the largest specimens caught during migration were, in fact, the biggest, that is, the animals usually encountered high up in the mountains. The majority of the specimens were average individuals, or young ones, that is, the animals which form the bulk of the migrating population. I imagine that the upper limit of size of Norway lemmings is similar to the limit of Siberian specimens, which in general were caught in different conditions from those in the Scandinavian collections. The Siberian individuals appear to be chiefly stationary specimens.

There are no accurate data on the length of life of lemmings. In the case of *Dicrostonyx groenlandicus* (T r a i l l 1823) this is, according to M a n n i n g (1954), 667 days for females and 748 days for males. These data, however, apply to artificially reared specimens.

As regards the skull measurements of young lemmings, it may be stated, on the basis of several specimens which were still blind, and which form part of the collection in the Museum in Oslo, that immediately after birth the condylobasal length of skull of lemmins is 18—19 mm. The first young specimens which have become independent, have a measurement of about 22 mm. The animals are by then, of course, covered with hair. Growth takes place very

rapidly. Especially rapid growth may be observed in the case of *Dicrostonyx* between the 15th and 21st day. Females of this species mature within 25—30 days (H a n s e n, 1957).

I do not, unfortunately, possess corresponding data for Siberian lemmings, but it may be assumed that they do not differ greatly from the data given above.

III. SEXUAL DIMORPHISM OF THE NORWAY LEMMING

The presence of sexual dimorphism in the skull structure, a frequent phenomenon in various rodents, may have a significant effect on the results obtained. In order to establish this as a fact,

Table 1.
Sexual dimorphism in the Norway lemming

Measurement	Males			Females		
	min.	avg.	max.	min.	avg.	max.
Condylobasal length	25.2	28.60	32.3	25.9	28.41	31.6
Basal length	23.6	27.12	30.7	24.5	27.03	29.9
Diastema	7.9	9.42	11.0	8.0	9.33	10.4
Occipital breadth	12.1	13.78	15.9	12.2	13.83	15.1
Zygomatic breadth	16.2	18.80	21.2	17.0	18.83	21.2
Interorbital constriction	3.1	3.79	4.1	3.2	3.73	4.1
Height of skull per bullae	8.7	9.37	10.2	8.8	9.44	10.1
Palatal depth	7.1	8.17	9.2	7.3	8.06	8.7
Depth of brain-case	7.2	7.96	9.0	7.2	7.93	9.0
Maxillary tooth-row	6.3	7.29	8.2	6.8	7.43	8.3
Mandibular tooth-row	6.2	7.15	8.4	6.6	7.24	8.2
Number of individuals	44			39		

it is essential to have a suitably large series of specimens coming from the same place and caught at the same time. I had such a series available only for the Norway lemming from the Hordaland area in north-west Norway. These specimens are in the collection of the Zoological Museum of Bergen University. All 83 specimens were caught within one area in the second half of October 1953, and this number is amply sufficient for the purpose of determining whether sexual dimorphism, reflected in the skull dimensions, exists in the case of the Norway lemming.

The results of craniometric measurements are given in Table 1.

As will be seen from the above data, the differences between males and females, both in the averages and in the limits of variation, are minimum and, practically speaking, are of no importance. There are no statistically significant differences between averages. As this applies to all measurements, it may be stated that the Norway lemming does not exhibit sexual dimorphism in its skull dimensions, and it is therefore possible to treat both sexes jointly in succeeding comparisons. This conclusion agrees with that of Collett (1907), who observed that females may be of the same dimensions as males.

There were, unfortunately, no such series in the Siberian lemming material, which would make it possible to determine whether clearly distinguishable sexual dimorphism exists. However, in view of the great similarity of the Norway lemming to the Siberian, I presume that the same is true of the Siberian lemming. In succeeding comparisons I shall, therefore, consider both sexes together. This is, of course, a certain simplification, but I do not consider that it can have any fundamental effect on the results.

IV. GEOGRAPHICAL VARIATIONS OF THE NORWAY LEMMING

In Scandinavia the lemmings live in the mountains, at heights of 1000 m. above sea level, and it is only in the years of population peaks that they descend to the valleys, and during exceptionally numerous population peaks reach as far south as Oslo (Collett, 1895; Crotch-Duppa, 1878; Elton, 1942; Hagen, 1953; 1956; Wildhagen, 1949; 1952). The course of such population cycles is fairly regular in character and population peaks move from the south to the north (Hagen, 1956). This regularity consists in the fact that if in a given year a population peak takes place in, let us say, central Norway, it may be assumed that a similar mass appearance took place in the southern part of the country the previous year. The intensivity of such population peaks varies from very localised peaks to enormous „plagues". Sometimes, when climatic conditions are favourable, a high population level may be maintained for two years in one place. This non-typical phenomenon occurred in 1959 in southern Norway, where a population peak was maintained from 1958 (author's observations).

It must be remembered that the material used in this work does not form one uniform whole, but comes from different places, was caught in different years (some of the specimens were caught 100 years ago), and often completely fortuitously. An exception to this is the material in the Zoological Museum in Bergen University, where the collection of lemmings was made comparatively recently and according to plan. On this account I have explained any possible deviations from averages as being more due to deficiencies in capture methods than to the existence of real differences. Certainly a greater amount of material collected from the same areas, but within a stated period, would be more uniform.

I have divided the material dealt with in this work in the following way: southern part — specimens from south-east Norway and the mountains of central Sweden, western and central part — specimens from the Hardangerfjord (Hordaland province), the Dovre mountains, the Sör and Nord Trondelag provinces, — the northern part, the provinces of Nordland, Tromsö, Finmark and the Kola peninsula.

This is a somewhat schematic division, but I was chiefly concerned in my work with differentiating between certain regions, the material from which I could compare in order to establish any possible differences exhibited in the skull dimensions.

A comparison of the whole material is given in Table 2. From this it will be seen that the material as a whole is similar. Certain deviations in the averages of material from the western and central parts may definitely be explained by the fact that it is the most uniform, since the majority of the material comes from one place and from one period of population peak. The majority of the specimens are average and young animals, which of course affects the result of the calculated average. If, however, we take into consideration the range of variations, it is clear that they are in almost exact agreement with the corresponding data for specimens from the remaining areas. In addition, the differences between averages are not statistically significant.

On these grounds it may be stated that the Scandinavian lemmings do not exhibit the existence of geographical variation, expressed in the skull dimensions, which might be taken as evidence of the non--uniformity of this material. From the aspect of their biology and ecology, considerable uniformity can also be

found. They inhabit almost identical biotopes, their biology is the same, the population cycle follows the same course and they possess a certain continuity throughout the whole of Scandinavia (H a g e n, 1956), they are a coincident phenomenon. Only the lighting conditions differ in the polar summer in the Arctic, but in the Scandinavian Mountains we also encounter the phenomenon of „midnight sun" in the summer, so that from this aspect also there are no great differences.

In this work I have laid most emphasis on craniometry, as a factor by means of which it is easiest to grasp the existence of differences qualifying as either subspecific or even specific. I did not succeed in establishing such differences in the Norway lemmings. These differences are also statistically indiscernible.

Table 2.
Geographical variations in the Norway lemming

Measurement	Southern part		Central part		Northern part	
	min. – max.	avg.	min. – max.	avg.	min. – max.	avg.
Condylobasal length	25.2 – 33.2	29.47	25.2 – 33.4	28.68	26.0 – 33.7	29.96
Basal length	24.0 – 31.5	27.71	23.6 – 30.7	27.19	24.6 – 31.9	28.44
Diastema	8.3 – 11.6	9.81	7.9 – 11.0	9.42	8.2 – 11.6	9.99
Occipital breadth	12.2 – 15.8	14.23	12.1 – 15.9	13.87	13.3 – 16.8	14.64
Zygomatic breadth	16.6 – 23.2	19.55	16.2 – 21.5	18.91	15.8 – 22.9	19.86
Interorbital constriction	3.1 – 4.2	3.84	3.1 – 4.1	3.76	3.3 – 4.3	3.81
Height of skull per bullae	8.6 – 10.4	9.50	8.7 – 10.2	9.42	8.7 – 10.5	9.83
Palatal depth	7.3 – 9.5	8.19	7.1 – 9.2	8.18	7.1 – 10.1	8.60
Depth of brain-case	7.2 – 8.8	7.96	7.2 – 9.0	7.97	7.3 – 9.6	8.26
Maxillary tooth-row	6.6 – 8.6	7.78	6.3 – 8.3	7.38	6.2 – 8.4	7.44
Mandibular tooth-row	6.5 – 8.7	7.56	6.2 – 8.4	7.21	5.8 – 8.4	7.51
No. of animals	55		91		53	

Usually, however, differences in the colour of the coat are taken into account, but this cannot be done in the case of the Norway lemming, since there is such an enormous individual variation that classification on the basis of this feature is, practically speaking, completely unacceptable. On this account the criterion of colour cannot be applied to the case of the Norway lemming. For other lemmings, e. g. from the New Siberian Islands, the question of colour is very important, since similarly to the Collared lemming

(Dicrostonyx groenlandicus) they change their colouring in the winter, and their seasonal dimorphism of coat colour is their most characteristic feature.

It may be stated that the Norway lemming is very uniform throughout the whole area of its occurrence, and from the systematic standpoint, constitutes a subspecies, one of the very characteristic Scandinavian geographical strains. I shall, however, return to this question in the later part of this work

V. GEOGRAPHICAL VARIATIONS OF THE SIBERIAN LEMMING

The Siberian lemming occurs within the region formed by the Soviet Arctic zone, from the White Sea to Kamchatka, and possibly even further in the territory of Alaska and Canada. I had, unfortunately, no material from the two latter regions. The whole vast area of the Arctic tundra may be divided into several smaller zoogeographical units (P l e s k e, 1884; B r a u n e r, 1888; K u z n e c o v, 1950). Many authors are of the opinion that the boundary between the Euro-Siberian and Eastern Siberian zoogegraphical sub-provinces lies in the vicinity of the River Yenisey. The majority of the divisions so far made are based chiefly on the distribution of birds, and do not correspond to the zoogeography of tundra mammals. One of the most recent theories on the zoogeographical division of the Palaearctic, put forward by K u z n e c o v (1950), based chiefly on the distribution of mammal settlements, is as follows:

Zone	Region
Norwegian - Murmańsk	—
Northern Siberian	
	a. Bolshezemelski — Yamal — Gydan, from Kanin peninsula to Gydan peninsula
	b. Novaya Zemlya
	c. Taimyr
	d. Khatanga — Lena
	e. New — Siberian
	f. Yana — Indygir
Kolyma — Anadyr	—

As the material on the Siberian lemming available for my work came chiefly from several places in the Soviet arctic zone, the

division which I have used in the table of craniometric dimensions differs slightly from that used by Kuznecov. When comparing material composed of Siberian lemmings, I had series of specimens from the following regions:

a. Archangel district and the northern Urals
b. Novaya Zemlya and Vaigach
c. Yamal peninsula
d. Taimyr peninsula
e. New-Siberian Islands
f. areas to the east of the Khatanga river.

These last areas contain certain fauna elements similar to American ones. According to Vinogradov, the forms from these areas described as *Lemmus paulus* and *Lemmus flavescens* are similar to the Alaskan and Canadian forms. I included these specimens in my comparisons.

A list of the craniometric measurements of Siberian lemmings is given in Table 3.

From this table the difference between the forms from the New--Siberian Islands, which are decidedly bigger than the remainder, will at once be clear. Lemmings from this area, described under the name of *Lemmus obensis novosibiricus* (Vinogradov, 1924) also differ distinctly in colour from the remainder. They are far lighter in colour than specimens from the continent, and change their colour as winter approaches. Since they are also somewhat isolated from the mainland (by about 100 to 300 km.) and the connection with the mainland by ice in the winter constitutes in practice an insuperable barrier to these small rodents, I consider that complete agreement is possible with the view that this is a well-developed geographical strain of Siberian lemming.

If, on the other hand, we compare specimens from the two regions furthest to the west and east of the range of the Siberian lemming, we notice a very interesting phenomenon — these specimens do not in any way differ from each other, and the averages and limits of variation are almost identical (condylobasal length of western specimens 25.4 — 33.8, of eastern specimens 25.1 — 34.1, respective averages 29.40 and 29.86). The differences between the averages are statistically nonsignificant. The case is similar in regard to lemmings from Yamal situated more of less in the centre of the area of occurrence of the Siberian lemming,

Table 3.
Geographical variations in the Siberian lemming

Measurements	Northern Ural	Novaya Zemlya, Vaigach	Yamal	Taimyr	New Siberian Islands	Eastern Siberia
Condylobasal length	25.4 - 33.8 /29.40/	27.7 - 34.7 /31.09/	25.5 - 32.5 /29.13/	27.4 - 35.4 /31.46/	27.1 - 36.7 /32.33/	25.1 - 34.1 /29.86/
Basal length	24.1 - 31.8 /27.86/	26.3 - 32.9 /29.30/	23.9 - 30.6 /27.31/	25.4 - 33.2 /29.49/	26.9 - 34.8 /30.98/	24.1 - 31.9 /28.39/
Diastema	8.2 - 11.7 /9.65/	8.8 - 11.8 /10.31/	8.0 - 10.8 /9.47/	8.3 - 12.0 /10.25/	7.8 - 12.5 /10.51/	8.1 - 11.3 /9.53/
Occipital breadth	13.9 - 16.3 /15.07/	13.9 - 17.3 /15.73/	13.2 - 16.3 /14.75/	13.7 - 18.6 /16.36/	14.8 - 19.1 /16.65/	13.2 - 16.8 /14.89/
Zygomatic breadth	17.1 - 23.4 /20.17/	18.7 - 23.4 /20.88/	17.3 - 22.9 /19.91/	17.8 - 23.9 /20.92/	15.5 - 24.6 /20.96/	15.7 - 23.2 /20.81/
Interorbital constriction	3.4 - 4.2 /3.80/	3.5 - 4.4 /3.86/	3.4 - 4.1 /3.71/	3.8 - 4.6 /4.21/	3.5 - 4.5 /4.09/	3.3 - 4.2 /3.83/
Height of skull p. bullae	9.3 - 10.4 /9.77/	9.4 - 10.9 /10.30/	8.9 - 10.8 /9.85/	9.4 - 11.8 /10.90/	10.1 - 12.3 /10.94/	8.7 - 11.4 /10.08/
Palatal depth	7.8 - 9.9 /8.59/	7.8 - 10.2 9.21/	6.9 - 10.2 /8.59/	7.8 - 10.8 /9.06/	7.8 - 11.0 /9.30/	6.9 - 9.9 /8.56/
Depth of brain-case	7.3 - 8.8 /8.15/	7.8 - 9.4 /8.49/	7.3 - 8.9 /8.18/	7.5 - 9.9 /8.97/	8.2 - 10.2 /8.97/	7.2 - 9.2 /8.34/
Maxillary tooth-row	6.8 - 9.2 /7.65/	7.0 - 8.8 /8.04/	6.7 - 8.3 /7.66/	7.4 - 9.3 /8.21/	6.5 - 9.3 /8.39/	6.3 - 9.1 /7.88/
Mandibular tooth-row	6.4 - 8.2 /7.30/	6.5 - 8.5 /7.70/	6.2 - 8.4 /7.54/	6.9 - 8.8 /7.94/	6.4 - 9.2 /8.16/	6.5 - 8.7 /7.71/
No. of animals	18	16	25	29	22	29

and yet in the opinion of certain research workers, they are supposed to belong to at least different subspecies, if not species.

From the facts given above it will be seen that no geographical variation can be observed in the Siberian lemming from the west to the east. The reasons for this may differ — probably one of them is the relatively great uniformity in the habitat conditions acting on these animals, as all the specimens compared come from areas more to the south of 70° N, where these conditions are similar.

According to views held up to the present, the following subspecies occur in this area — *L. obensis obensis* Brants, 1827, *L. obensis bungei* Vinogradov, 1924, *L. obensis chrysogaster* Allen, 1903, and the *„paulus"* and *„flavescens"* forms. I inspected and measured the forms so labelled in the collections. They do not differ in any respect from specimens from the Archangel and Yamal districts. It is possible that such differences would become evident in larger series of material, but in none of the museum collections known, to me is there such a series, nor, as far as I know, are there any in other museums. It must be noted that these forms were described from single or young specimens, which are, of course, smaller than adults. I do not consider that slight variations, (when as I have explained in the case of the Norway lemming, great individual variation exists) can be accepted as a basis for differentiating new forms. The case is different with the lemmings from the New-Siberian Islands, as the animals differ greatly not only as to dimensions, but also as to the very characteristic colouring of their coats, not encountered on the mainland.

With the Siberian lemming it is clearly evident that the forms furthest to the north are slightly bigger than the remainder. As I pointed out previously in the case of lemmings from the New-Siberian Islands, we can observe a similar phenomenon among the lemmings of Taimyr and the Novaya Zemlya and Vaigach islands. There are no statistically significant differences between the averages for these two places, neither are there when compared with the averages for specimens from the New-Siberian Islands. On the other hand differences exist between the averages for northern specimens and those from the Northern Urals, Yamal and Eastern Siberia, although not so great as in the case of comparison with specimens from the New-Siberian Islands. I do not think, however, that it is possible, in the case of the larger specimens

from Novaya Zemlya, Vaigach and Taimyr, to speak of a systematic separateness, or that they are separate geographical strains. In the first place, these areas are not at all isolated from the others (Taimyr), or the distance between the continent and the island is very small (Vaigach, which forms a kind of platform to Novaya Zemlya, divided from it by the narrow Kara straits which freeze over completely). Penetration of continental forms to the north, and reversely, from the north to the south, is quite possible, and takes place during migrations. As the fundamental principle — geographical isolation — is not therefore maintained — I am of the opinion that we may accept the fact that this is at most a northern variety of the continental subspecies.

It seems to me that on the basis of these data we may state that the Siberian lemming occurs throughout the whole of its range basically in two subspecies — a smaller, darker-coloured continental form, and a larger, lighter-coloured specimen exhibiting seasonal variation in colour, from the New-Siberian Islands.

The continental subspecies has created a larger variety on the northern limits of its range, which occurs on Taimyr, on Vaigach Islands and Novaya Zemlya islands. There are, however, no grounds for treating this variety as a separate systematic unit.

The question of the Eastern Siberian forms requires further investigation, based, however, on greater quantities of material, as far as possible uniform. It is impossible to establish, on the basis of the material available to me, whether fundamental differences do exist here. The absence of such differences may perhaps be due to the small amount of comparative material available.

It would be interesting to compare Siberian specimens with material from Alaska and Canada. The few comparative examples which I saw would seem to be very similar to Palaearctic specimens, both as to size and colour. This is, however, only my impression, as I had no larger amount of material available suitable for purposes of comparison, but only single specimens.

VI. THE SUBSPECIFIC SYSTEMATICS OF PALAEARCTIC LEMMINGS

On the basis of material examined, I have assumed that the Norway lemming occurs only as the nominal form — *Lemmus lemmus lemmus* (L i n n a e u s, 1758), and the Siberian lemming

in two forms — *Lemmus sibiricus sibiricus* (K e r r, 1792) and *Lemmus sibiricus novosibiricus* (V i n o g r a d o v, 1924).

Table 4.

Comparison of skull measurements of three subspecies of lemming, and averages and ranges of variation for the whole species *L. lemmus* (L).

Measurement	L. lemmus lemmus	L. lemmus sibiricus	L. lemmus novosibiricus	L. lemmus /total/
Condylobasal length	25.2 - 33.7 /29.18/	25.1 - 35.4 /29.73/	27.1 - 36.7 /32.33/	25.1 - 36.7 /29.73/
Basal length	23.6 - 31.9 /27.60/	23.9 - 33.2 /28.91/	26.9 - 34.8 /30.78/	23.6 - 34.8 /28.26/
Diastema	7.9 - 11.6 /9.68/	8.0 - 12.0 /9.86/	7.8 - 12.5 /10.51/	7.8 - 12.5 /9.80/
Occipital breadth	12.1 - 16.8 /14.13/	13.2 - 18.6 /15.42/	14.8 - 19.1 /16.65/	12.1 - 19.1 /14.73/
Zygomatic breadth	15.8 - 23.2 /19.33/	15.7 - 23.9 /20.31/	15.5 - 24.6 /20.96/	15.5 - 24.6 /19.74/
Interorbital constriction	3.1 - 4.3 /3.79/	3.3 - 4.6 /3.93/	3.5 - 4.5 /4.09/	3.1 - 4.6 /3.85/
Height of skull p. bullae	8.6 - 10.5 /8.91/	8.7 - 11.8 /10.26/	10.1 - 12.3 /10.94/	8.6 - 12.3 /9.44/
Palatal depth	7.1 - 10.1 /8.30/	6.9 - 10.8 /8.80/	7.8 - 11.0 /9.30/	6.9 - 11.0 /8.55/
Depth of brain-case	7.2 - 9.6 /8.03/	7.2 - 9.9 /8.50/	8.2 - 10.2 /8.97/	7.2 - 10.2 /8.26/
Maxillary tooth-row	6.2 - 8.6 /7.57/	6.3 - 9.3 /7.92/	6.5 - 9.3 /8.39/	6.2 - 9.3 /7.75/
Mandibular tooth-row	5.8 - 8.7 /7.36/	6.2 - 8.8 /7.48/	6.4 - 9.2 /8.16/	5.8 - 9.2 /7.53/
No. of animals	186	117	22	325

Tables 2 and 3 reveal the great similarity between the measurements of Norway and Siberian lemmings, especially of the continental form. There are no statistically significant differences between the averages for specimens from the Northern Urals, Yamal and Eastern Siberia and the three groups of Norway lemmings. This is evidence of the great similarity between these specimens, coming from such widely-separated areas as southern Norway and Kamchatka. Comparison of averages and ranges of variation for the Norway and Siberian lemming, and the lemming

from the New-Siberian Islands, and of the whole material, is given in Table 4. It appears that the ranges of variation almost correspond (certain deviations occur in the island form), and differences between averages are also slight. There are statistically significant differences between them, but these differences are far greater

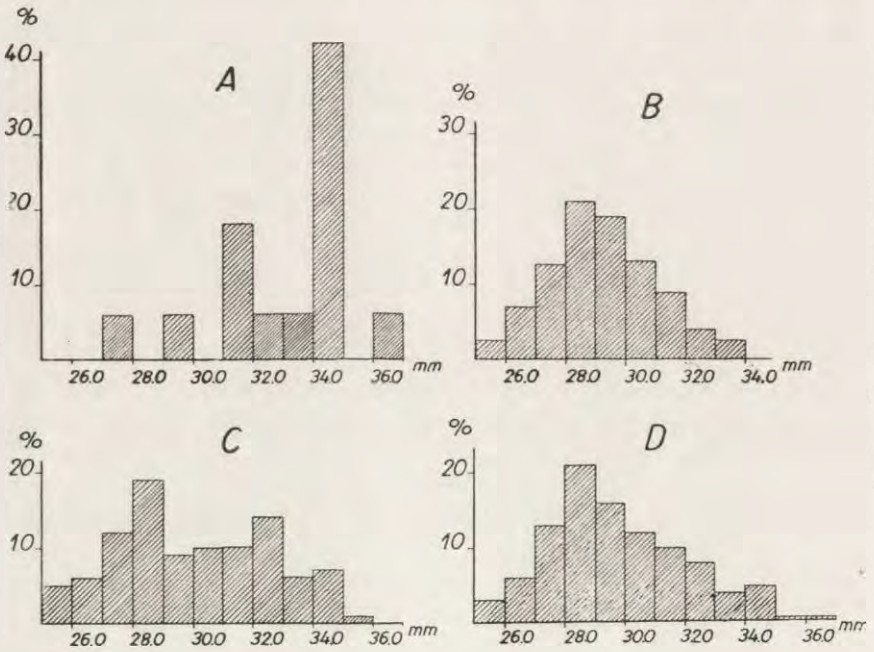

Fig. 1. Percentages of individuals in different classes of condylobasal length. A — Lemmings from the New-Siberian Islands, B — Norway lemming, C — Siberian lemming, D — whole material.

when comparing the island form with the continental and Norway, then when comparing Siberian lemmings with Norway ones. The most important question is, however, the lack of morphological differences in skull structure between the various individuals. It is surely impossible to distinguish the skull of Norway lemmings from that of Siberian lemmings. In principle it is on the grounds of their origin only that we can allocate specimens to this or that „species".

The only differences making it possible to differentiate between the two „species" are differences in colour. The Norway lemming

is variegated in colour, the Siberian is greyer and more uniform altogether lighter in colour. On the grounds of colour only, we should distinguish three „species", especially as the differences existing in the skull measurements clearly mark the island form as a separate one. From this aspect the Norway lemming is far more similar to the Siberian, than the latter is to the form from the New-Siberian Islands, which has so far been considered as a subspecies of the Siberian lemming. In general, however, the majority, of zoologists consider that differences in colour only are not sufficient to constitute grounds for determining specific difference.

It is nevertheless clear that there are three forms which should be treated as equal systematic units, on the basis of results of morphological investigations. On the other hand, these lemmings occupy the same ecological niche, play the same part in the biocenosis of the tundra, have the same enemies, the same character of migrations and the same population cycle (E l t o n, 1942).

The fact is well-known that differences occur between representatives of this same species coming from different places. The northern forms are, in general, larger than representatives of the same species from the south (C r o s s & D y m o n d, 1929). In the case of Palaearctic lemmings of the genus *Lemmus,* these differences are clearly visible. Their range is intersected by the White Sea, which forms a natural boundary between the Norway and Siberian forms. In the same way the Laptev Sea and East Siberian sea separate the form peculiar to the New-Siberian Islands from the continental subspecies. The latter possesses a larger variant on the northern confines of its range (Novaya Zemlya, Taimyr). The Norway lemmings do not exhibit such differences. The mountain lemming in Scandinavia does not form a continuous population (E l t o n, 1942), but in normal years lives in the massif of the mountains, separated by valleys. During the glacial epoch the lemmings descended, pushed by glaciation as far as the British Isles and Portugal. The same occurred in Siberia, where the result was the relict form, the Amur lemming. Basically the lemming is an animal endemic to the arctic zone of the Palaearctic. In areas further to the south they are in general post-glacial relict

animals, such as we have in the case of the Norway and Amur lemmings.

The history and origin of tundra fauna is very little investigated. One of its most typical features, however, is that the majority of tundra species (in this case the lemming) possesses an enormous range. Tundra fauna is relatively young. It is an interesting fact that the mammal fauna of the Western Siberian tundras is similar to that of the Eastern Siberian tundras. Hitherto *Microtus gregalis* (P a l l a s, 1769) has been given as an example. My observations indicate that there are no fundamental differences between the lemmings of the eastern and western tundras, which is a further example illustrating the question under discussion. It constitutes confirmation of the assumption that at first (the beginning of the Pleistocene or earlier) tundra fauna began to form somewhere to the north of Eastern Siberia, where probably during the Tertiary climatic conditions prevailed far more severe than in Western Siberia, and even more so than in Europe (K u z n e ç o v, 1950). Therefore the lemmings which moved as far as Scandinavia during the glaciation period preserved, through living in similar conditions, a type of structure and skull size very similar to that of the Eastern Siberian animals. Living in isolation, however, they developed certain features (colour) distinguishing them from the Eastern Siberian forms. A similar phenomenon occurs in a second isolated form — the lemming from the New-Siberian Islands.

In the light of the facts given above it seems to me to be pointless to maintain the systematic division into species of a group so uniform from every aspect. This division dates from the XVIII — XIX centuries, when new species were described from newly-investigated territories, while the present-day taxonomic criteria were not, of course, applied and, most important, no comparison was made of large series of material of the greatest possible uniformity. Certain species were described on the basis of a single, and even of young, specimens.

I, therefore, consider that all Palaearctic lemmings of the genus *Lemmus* should be regarded as one species. On account of priority, the specific name *Lemmus lemmus* should be retained for the nominal form established by L i n n a e u s in 1758, who was the first to describe the Norway lemming from Scandinavia (a spot not exactly identified in the mountains of Swedish Lapland).

Since it appears from the material analysed in this work that there are only three basic Palaearctic forms of lemmings of the genus *Lemmus* — the Norway, the Siberian and the form from the New-Siberian Islands (I consider the large Siberian forms as a variety only), on this account I am of the opinion that they should be accepted as distinct geographical strains — subspecies. These forms, in the light of the facts given above, are distinctly differing taxonomic units of equal rank.

The subspecific systematics of the Palaearctic lemmings of the genus *Lemmus* would therefore be as follows:

Genus: *Lemmus* L i n k, 1795.

Species: *Lemmus lemmus* (L i n n a e u s, 1758), (synonyms *L. sibiricus* (K e r r, 1792) and *L. obensis* B r a n t s, 1825).

Subspecies:

1. *Lemmus lemmus lemmus* (L i n n a e u s, 1758). Mountains of Scandinavia and Kola peninsula).

2. *Lemmus lemmus sibiricus* (K e r r, 1792),
(from the straits of the White Sea to Kamchatka, possibly this subspecies, or another of its forms occurs in Alaska and Canada. It occurs on the Vaigach and Novaya Zemlya Islands. Eastern and southern limit of occurrence not exactly known).

3. *Lemmus lemmus novosibiricus* (V i n o g r a d o v, 1924)
(New-Siberian and Lyakhov Islands).

The subspecies and forms hitherto described under the names of *obensis, bungei, chrysogaster, paulus* and *flavescens* are synonyms of the subspecies *Lemmus lemmus sibiricus* (K e r r, 1792).

At the present time it is not possible to give an opinion on the Amur lemming form, on account of the lack of comparative material. O g n e v (1948) states that only four specimens of the Amur lemming are known. It may only be assumed that as a relict form it might be considered as a separate subspecies.

The limits of occurrence of *L. l. sibiricus* (southern and eastern) also remain an open question and require exact determination. It is highly probable that its range extends to include areas of Alaska and Canada, but this would also necessitate further research work.

The views put forward in this work on the subspecific systematics of Palaearctic lemmings are the result of morphological analysis of museum material. Only checking by means of cross-breeding artificially reared individuals of different subspecies, however,

would make it possible to determine with complete certainty what the biological connection is between groups differing as to morphological features.

VII. CONCLUSIONS AND SUMMARY

On tne basis of an analysis of lemmings from the Palaearctic zone of the genus *Lemmus* Link, 1795, (325 skulls), the author reached the conclusion that only one species of lemming occurs in this area — *Lemmus lemmus* (Linnaeus, 1758). Over the whole range of its occurrence this species occurs in three subspecies:

Lemmus lemmus lemmus (Linnaeus, 1758)
Lemmus lemmus sibiricus (Kerr, 1792)
Lemmus lemmus novosibiricus (Vinogradov, 1924)

The forms so far described as *Lemmus sibiricus* (Kerr, 1792), *Lemmus obensis* Brants, 1825, *Lemmus paulus* Allen, 1914, *Lemmus flavescens* Brants, 1825, *Lemmus obensis chrysogaster* Allen, 1903, *Lemmus obensis bungei* Vinogradov, 1924, *Lemmus obensis obensis* Brants, 1827 are only synonyms. The form *Lemmus amurensis* Vinogradov, 1924 is probably only a subspecies of the species *Lemmus lemmus* (Linnaeus, 1758).

In this work the great similarity of the Eastern Siberian form to the Western form has been demonstrated. There are no statistically significant differences between them. This may be evidence of the origin of the Palaearctic lemming fauna from North-east Siberia.

Two varieties occur in lemmings of the Siberian subspecies — the northern variety being the bigger. This applies to specimens from the Vaigach and Novaya Zemlya Islands, and also Taimyr.

Sexual dimorphism in skull size was not observed in lemmings Males and females are equal in size.

The author described the method of defining the age of lemmings on the basis of the mutual relation of palatal length to the heigth of the brain case measured inter bullae.

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РЕЗЮМЕ

В настоящей работе автор рассматривает проблемы морфологии леммингов рода Lemmus Link. 1795. Эти грызуны встречаются на очень широком ареале в условиях арктической тундры. До сих пор имелось немного данных по морфологии этих зверей, а подвидовая систематика сибирских форм основывалась на малочисленных материалах.

Эта работа опирается на материале 325 черепов леммингов из различных мест распространения, хранящихся в Зоологических Музеях в Норвегии, Швеции и СССР.

Основным заложением работы было констатирование существования двух групп леммингов — сибирской и норвежской. В пределах каждой группы сравнивалось серии черепов из различных районов с целью подтверждения явления географической изменчивости. В исследуемом материале самцы и самки обсуждалось совместно, так как анализ краниометрических измерений серии черепов из срединной Норвегии не уяснил существования полового диморфизма выражающегося в различиях структуры черепа.

По мере возраста у леммингов происходят большие изменения в строении и пропорциях черепа. Череп прежде всего растет в длину и ширину и оформляются сильно костные гребни.

Констатировано, что благодаря тому у старших особей небная высота подвергается относительно большому увеличению. Зато высота мозговой коробки измеряема на клиновидной кости (между b u l l a e) увеличивается с возрастом лишь в очень незначительной степени. Изменяется затем реляция этих двух величин измерений высоты черепа. У молодых особей нёбная высота всегда ниже (абсолютная величина) высоты мозговой коробки, у особей старших это отношение обратное, вследствие создавания костного гребня. Нёбная высота больше, или равная высоте мозговой коробки. Это очень существенный признак, позволяющий безошибочно определить возраст жизни у леммингов.

В этой работе материал разбит на молодые и половозрелые особи. Так как изменчивость длины черепа по большей части определена возрастом, поэтому за критерий раздела принято кондилобазальную длину черепа. Особи с Кб. выше 25 мм являются как правило половозрелыми.

Обсуждалось в работе влияние метода и времени отлова на возрастный состав отловленого материала. Особи из стационарных популяций являются большими от мигрирующих особей. Это видно при сравнивании материалов скандинавских и сибирских.

Анализ материала скандинавских леммингов не выказывает географической изменчивости. Материал весьма однородный и составляет явственно один подвид.

Среди сибирских леммингов видно две группы — особи из Новосибирских островов, которые явственно больше, и меньшие континентальные экземпляры. Лемминги из Новосибирских островов отличаются кроме того более светлой окраской, которая обнаруживает сезонную изменчивость.

Автор полагает, что данные в этом случае, различия, можно принять как подвидовые тем более, что они являются большими помежду островной формой и континентальной (сибирской), чем между формой сибирской и норвежской. Зато сибирские лемминги происходящие из двух концов ареала не обнаруживают никаких различий, а по выраженным до сих рор мнениям они должны принадлежать к двум отдельным подвидам. Географическая изменчивость не замечается у сибирского лемминга в направлении из запада на восток. Автор объясняет это однородностью условий среды влияющих на этих зверей. Особи из мест более выдвинутых к северу являются явственно большими. Это относится к экземплярам из Новой Земли, Вайгача и Таймыра. Однако автор полагает, что эти экземпляры составляют только большую северную разновидность континентального подвида и что нет оснований для установления их в отдельную систематическую единицу.

Сравнивая три живущие в Палеарктике подвиды леммингов можно заметить большое сходство между ними. Почти невозможным становится, отличить череп норвежского лемминга от черепа сибирского лемминга. Три существующие формы леммингов отличаются только окраской, однако отчётливо видно, что это три равносильные систематические единицы. Их биология и экология указывают на их биологическую однородность.

Сходства между отдельными формами палеарктических леммингов бросают интересный свет на происхождение фауны тундры. Новым примером является то, что фауна Западно - сибирской тундры близка Восточно - сибирской. Это подтверждает мнение, что в начале (в начале Плеистоцена, или раньше) фауна тундры формировалась где-то на Северовостоке Сибири, где вероятно в третичном периоде были более суровые условия. Поэтому лемминги, которые во время оледенения мигрировали в Скандинавию и живя в подобных условиях сохранили очень похожий тип строения и величины черепа к восточно - сибирским формам. Одним различием является у них окраска. На основании этих данных, автор полагает, что все палеарктические лемминги рода Lemmus следует считать одним видом.

Учитывая приоритет следует оставить видовое название *Lemmus lemmus* (Linnaeus, 1785) номинантной формы, установленное Линнеем в 1758. Этот вид встречается во всем ареале в трех подвидах — норвежским — *Lemmus lemmus lemmus* (Linnaeus, 1758), сибирском *Lemmus Lemmus sibiricus* (Kerr, 1792) и из Ново-сибирских Островов — *Lemmus lemmus novosibiricus* (Vinogradov, 1924), которые являются равносильными систематическими единицами. Границы ареала подвида, сибирско - южная и восточная требуют точного установления. Весьма возможно, что его распространение продолжается на территорию Аляски и Канады.

Представленные в этой работе мнения на подвидовую систематику палеарктических леммингов являются морфологическим анализом музейных материалов. Однако только при скрещивании и разведении особей различных видов будет возможным установить бесспорно какая биологическая связь является между группами отличающимися морфологическими признаками.

STRESZCZENIE

Na podstawie analizy 325 okazów lemingów z rodzaju *Lemmus* Link, 1795, autor doszedł do wniosku, że na terenie Palearktyki występuje tylko jeden gatunek leminga — *Lemmus lemmus* Linnaeus, 1758. Na obszarze swego areału geograficznego gatunek ten występuje w trzech podgatunkach:

1. *Lemmus lemmus lemmus* (Linnaeus, 1758),
2. *Lemmus lemmus sibiricus* (Kerr, 1792),
3. *Lemmus lemmus novosibiricus* (Vinogradov, 1924).

Forma *Lemmus amurensis* Vinogradov, 1924 jest prawdopodobnie tylko podgatunkiem gatunku *L. lemmus* (Linnaeus, 1758). Pozostałe formy opisywane pod różnymi nazwami należy uważać za synonimy *Lemmus lemmus* (Linnaeus, 1758).

W pracy tej zostało wykazane bardzo duże podobieństwo lemingów wschodniosyberyjskich do form zachodnich. Może to świadczyć o pochodzeniu fauny lemingów Palearktyki z północno-wschodniej Syberii.

U lemingów podgatunku syberyjskiego występują dwie odmiany, z których północna jest większa. Dotyczy to okazów z wysp Wajgacz i Nowa Ziemia oraz Tajmyr.

Autor nie stwierdził u lemingów norweskich różnic o charakterze dymorfizmu płciowego. Samce i samice są równe co do wielkości.

Autor opisał metodę określania wieku lemingów na podstawie wzajemnego stosunku wysokości podniebiennej czaszki do wysokości puszki mózgowej, mierzonej między b u l l a e.

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