The specific Status of the Narrow-Skulled Vole (Subgenus *Stenocranius* Kashchenko) in North America[1]

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During Würm time it is probable that an extensive land connection, produced when the Bering-Chukchi Platform was exposed by eustatic regression of the sea, existed between unglaciated areas in northeastern Eurasia and northwestern North America. The vast region so formed was evidently inhabited only by organisms adapted to life in an arctic environment. As the continental glaciers retreated at the end of Würm time, the connection between the two present continents was eliminated by rising sea levels, and the plants and animals dispersed from the amphiberingian region both eastward and westward at higher latitudes. Since 1937 when Hultén recognized the biogeographic significance of the Amphiberingian Refugium, its important implications have been increasingly apparent in connection with the distribution of recent mammals.

In 1942, Klaus Zimmermann determined that the geographic range of the northern vole, *Microtus oeconomus* Pallas, extends to the east beyond the Bering Strait, and he predicted that other, presumably palaearctic, species of small mammals would be found also to occur in North America. The soundness of Zimmermann's predictions has been substantiated in recent years by the clarification of the distributional status of other species.

It is the purpose of this paper to present data to show that another rodent, the narrow-skulled vole, *Microtus (Stenocranius) gregalis* Pallas, occurs also in North America. The geographic distribution of this vole in North America is similar to that of other mammalian species (e. g., *Microtus oeconomus; Clethrionomys rutilus* Pallas) which are believed to have dispersed from the amphiberingian region during post-glacial time (Rausch, 1963). Although thought by Ognev (1950) to occur in Alaska, the study of a small amount of material by Rausch (1953) brought out apparent differences in certain cranial characteristics between the Eurasian and North American forms of narrow-skulled voles. From later work it has been found that these characters are quite variable, and the name *M. gregalis* consequently has been applied (Rausch, 1963) to the North American vole previously designated *M. miurus* Osgood. A comparison of the Eurasian and North American forms of *M. gregalis* is presented here.

Materials and Methods

A study has been made primarily of skins and skulls or skulls alone from 119 specimens of *Microtus gregalis* from Eurasia and 149 specimens from North America. The data analyzed for statistical purposes were obtained from those skulls considered to be adult by reason of size and conformation. The number of Eurasian specimens utilized was reduced by elimination of immature and damaged skulls and those for which sex was not recorded. Only from North American voles were complete skeletons available. The techniques applied for the study of chromosomes are described below.

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[1] This paper ist respectfully dedicated to Professor Dr. Klaus Zimmermann on the occasion of his 70th birthday.

Although all the specimens studied cannot be listed, the series of Eurasian voles can largely be duplicated by examination of material that is available in the collections mentioned below (however, it was not possible to measure the skulls in the University of Moscow Museum). Excepting the series of *oreas,* in the United States National Museum, all of the North American specimens utilized are in my possession.

Acknowledgements

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Systematics

The subgenus *Stenocranius* was established by Kashchenko (1901) for Eurasian voles having the following characteristics (p. 167): skull long and narrow, with interorbital width less than 3 mm (usually 2.3 to 2.7 mm); greatest length of skull in adult individuals about 10 times the interorbital width, about twice the zygomatic width, and about 2$^1/_2$ times the width of the skull at the back („at the posterior upper edge of the ear appertures“); tail short, about $^1/_5$ to $^1/_4$ the length of the body. The interorbital width subsequently has been found in some cases to exceed 3 mm, but even so, as Ognev (1950) pointed out, the elongated, relatively narrow skull is readily distinguishable from skulls of voles belonging to the subgenus *Microtus.*

The subgenus *Stenocranius* is represented in Eurasia by the single species, *Microtus gregalis. M. g. major* Ognev was recognized as a distinct species by Vinogradov and Argyropulo as late as 1941 (see Ognev, 1950), although it was listed as a subspecies of *M. gregalis* by Bobrinskii et al. (1944). Fourteen Eurasian subspecies were recognized by Ognev (1950), following study of the extensive collections at his disposal. Additional subspecies were considered to be valid by Ellerman and Morrison-Scott (1951). Ognev discussed the uncertainty of status of some of these forms; Prof. W. G. Heptner (personal communication) is of the opinion that too many Eurasian subspecies have been named. With these thoughts in mind, it is probable that future critical studies will reduce the number of races considered to be valid ones. The subspecies recognized by Ognev are listed below, with type localities. Certain synonyms are included in order to clarify the status of some of the subspecies given by Ellerman and Morrison-Scott; for complete synonymy, see Ognev (1950).

Microtus g. gregalis Pallas. Type locality: Chulym River region, east of Tomsk.

M. g. dukelskiae Ognev. Type locality: Village of Vostochnoe, on the upper Enisei River, 35 km southeast of Minusinsk.

M. g. eversmanni Poliakov (syn. *M. ravidulus* Miller). Type locality: Uimon (? = Uimen'), on the Katun' River, Altai.

M. g. castaneus Kashkarov. Type locality: Chichkan and Dzhargart Gorge, Talaskii Alatau, Tian'-Shan' Mountains.

M. g. montosus Argyropulo. Type locality: Sary-Tash, Alaisk Valley, Turkestan.

M. g. raddei Poliakov (syn. *M. g. angustus* Thomas). Type locality: Vicinity of Lake Tarei-Nor (Barun-Torei), near the Mongolian border (southeastern Transbaikalia).

M. g. dolguschini Afanas'ev. Type locality: Lower Ili River, vicinity of Ak-Kul', Turkestan.

M. g. major Ognev. Type locality: Near Lake Nëi-Te (? = Nei-To), Iamal Peninsula.

M. g. tundrae Ognev. Type locality: Tundra Station, 40 km south of Arkhangel'sk.

M. g. nordenskiöldii Poliakov. Type locality: Taimyr Peninsula.

M. g. buturlini Ognev (syn. *M. g. unguiculatus* Koliushev). Type locality: Russkoe Ust'e, delta of the Indigirka River.

M. g. brevicauda Kashchenko. Type locality: Left bank of the Aldan River, Iakutia.

M. g. zachvatkini Heptner. Type locality: Perovska Bay, northeast shore of the Aral Sea.

M. g. tarbagataicus Ognev. Type locality: Podgornoe, Urdzharsk district, Tarbagatai Mountains.

The approximate distribution of *M. gregalis* in Eurasia (based mainly upon records published by OGNEV [1950, cf. Map. XI]), with type localities of subspecies designated, is shown in Fig. 1 (localities determined from Atlas SSSR, Moscow, 1955). No attempt has been made here to define accurately the ranges of individual subspecies.

The Eurasian subspecies of *M. gregalis* comprise two major groups whose ranges for the most part are widely separate: one, including *tundrae, major, nordenskiöldii,* and *buturlini,* inhabits the tundra zone from the region of the Onezhsk Peninsula in the west to the Anadyr region of northeastern Siberia; excepting *brevicauda,* the remaining forms are found across central Asia below lat. 60° N. According to OGNEV, *brevicauda* ranges from the middle course of the Viliui River in the north to possibly as far south as the upper Amur River. It closely resembles *buturlini* of the northern group, with which it probably intergrades, and again according to OGNEV (1950, p. 497), specimens from the taiga zone north of Nerchinsk, at the foot of the Iablonov Range (east of Lake Baikal), show evidence of intergradation with *raddei.* This somewhat hypothetical distribution of *brevicauda* is indicated in Fig. 1; it may actually connect the northern and southern groups.

Although the systematic status of some of the Eurasian subspecies is uncertain, clearly the northern subspecies comprise a homogeneous group. Of these, *tundrae* was considered by OGNEV to be a well characterized form, but he stated (p. 493) that *major, nordenskiöldii,* and *buturlini* may be identical.

Most members of the southern group also appear to be similar; *zachvatkini,* however, known from the semi-desert north of the Aral Sea, is evidently indistinguishable from *major.* Their present distribution suggests that the former represents a southward extension of *major* down the Ural Mountains. This in actuality does not occur, since *major* is clearly restricted distributionally to the northernmost part of the Ural (Prof. HEPTNER, personal communication). The situation is further complicated by the presence of *gregalis* in the southern Ural; according to SHVARTS (SCHWARTZ) et al. (1960), the northern limits of the range of the latter, an inhabitant of the forest-steppe zone, are somewhat south of Sverdlovsk, while *major* is found only as far south as the vicinity of Salekhard, near the mouth of the Ob' River. Consequently, the two forms are separated by a distance of more than 1000 km.

It appears that *gregalis* and *major* represent well differentiated populations at two extremes of a Rassenkreis. Cross-breeding experiments have produced hybrids that possessed intermediate characteristics and were fertile in the F_1 and subsequent generations (SHVARTS et al., 1960).

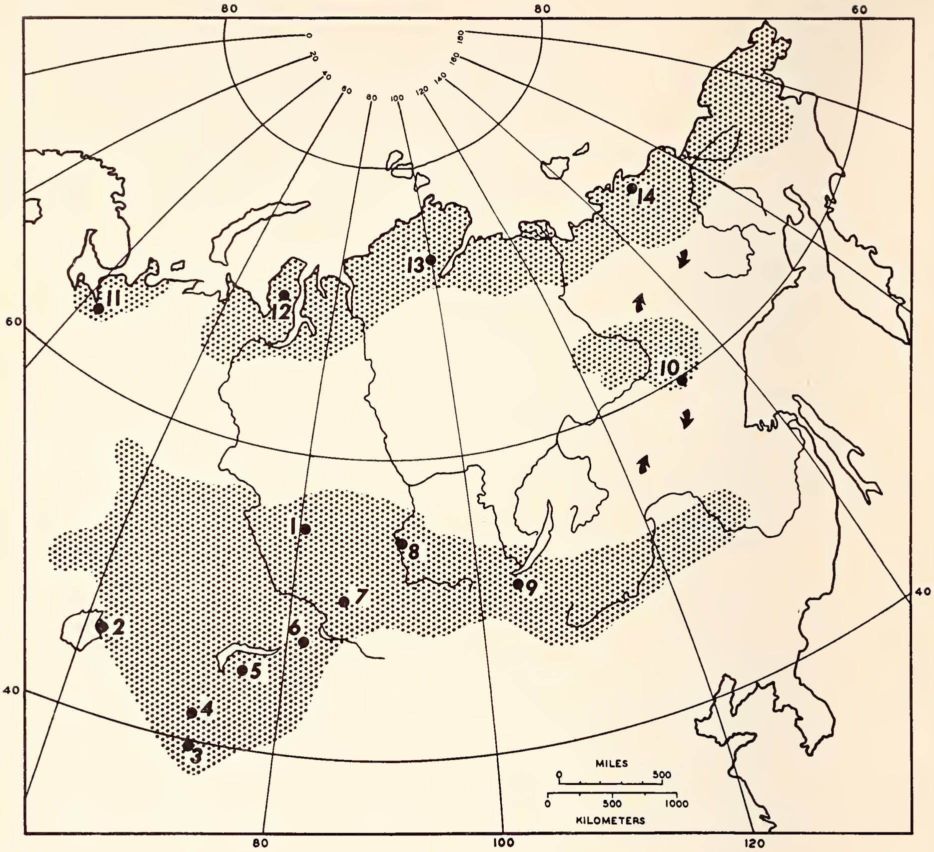

Fig. 1. Approximate distribution of *M. gregalis* in Eurasia. The subspecies for which type localities are shown by number are: 1 - *gregalis;* 2 - *zachvatkini;* 3 - *montosus;* 4 - *castaneus;* 5 - *dolguschini;* 6 - *tarbagataicus;* 7 - *eversmanni;* 8 - *dukelskiae;* 9 - *raddei;* 10 - *brevicauda;* 11 - *tundrae;* 12 - *major;* 13 - *nordenskiöldii;* 14 - *buturlini.* The arrows indicate possible connection by *brevicauda* of the northern and southern groups of subspecies.

Of the 14 subspecies Ognev recognized, I have been able to study in detail material representing 6: *gregalis, eversmanni, raddei, major, buturlini,* and *brevicauda.* Other forms were very briefly examined at the Zoological Museum in Moscow.

In North America as well, the subgenus *Stenocranius* is represented by one species. This vole was designated *Microtus miurus* Osgood by Hall and Cockrum (1952), pending studies to determine the extent of its relationship to the Eurasian species. The 5 forms recognized by Hall and Cockrum are listed here as subspecies of *M. gregalis.* Type localities are included.

M. g. miurus Osgood. Type locality: Head of Bear Creek, south of Hope, upper Kenai Peninsula, Alaska.

M. g. oreas Osgood. Type locality: Toklat River, northeast of Mt. McKinley, Alaska Range, Alaska.

M. g. muriei Nelson. Type locality: Kutuk River, central Brooks Range, northern Alaska.

M. g. andersoni Rand. Type locality: Near headwaters of Little Keel River, upper Canol Road, Northwest Territories, Canada.

M. g. cantator Anderson. Type locality: Near Tepee Lake, north slope of St. Elias Range, Yukon Territory, Canada. The approximate distribution of this vole in North America, with type localities of the subspecies designated, is shown in Fig. 2. As in Eurasia, the distribution of the narrow-skulled vole is not wholly known in North America, so that its range cannot yet be delineated in detail. The distribution maps published by Hall and Cockrum (1953) and by Hall and Kelson (1959) are too generalized to convey an appreciation of the ecologically restricted occurrence of this rodent.

The skins and skulls of all but one of the North American subspecies were studied. The type material of *andersoni* was examined at the National Museum of Canada, but I was unable to make detailed comparisons. This form is known from only 4 specimens. The examples of *cantator*, known previously from only 4 or possibly 5 specimens, were collected near Nabesna, in the Wrangell Mountains of southern Alaska. The other subspecies of narrow-skulled vole were represented by series taken at or near the type localities.

Comparison of Eurasian and North American Narrow-Skulled Voles

External characteristics. The small quantity of material would not permit an ideal comparison, that should take into account changes in pelage related to age and to season. In the sample examined, color was found to be quite variable among adults of both the Eurasian and North American forms from any given locality, although all

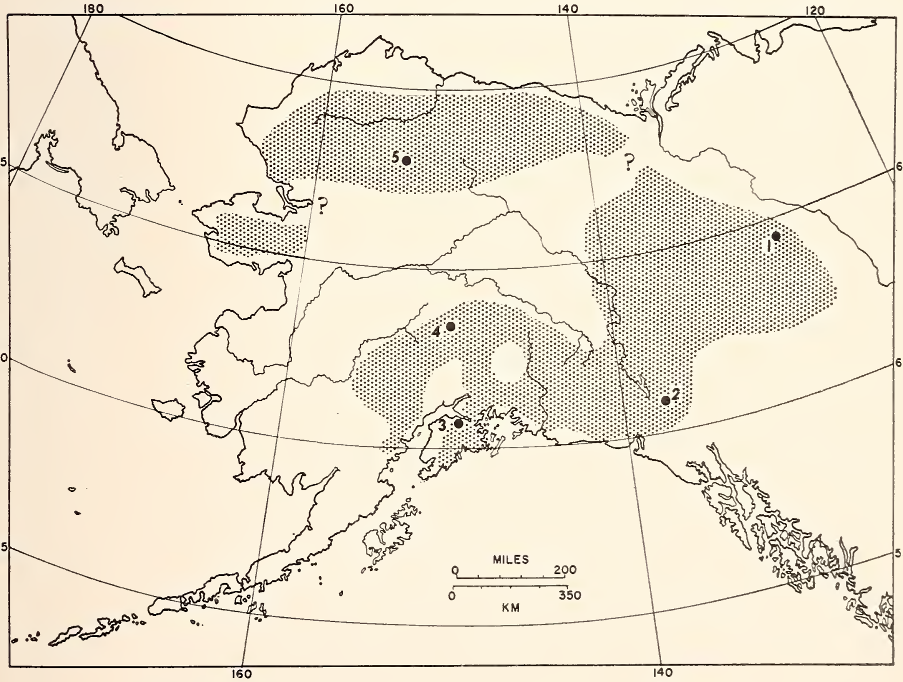

Fig. 2. Approximate distribution of *M. gregalis* in North America. The subspecies for which type localities are shown by number are: 1 - *andersoni;* 2 - *cantator;* 3 - *miurus;* 4 - *oreas;* 5 - *muriei.*

of the narrow-skulled voles have the same general pattern: darker dorsal color, lighter, often contrasting sides, pale ear patches, and grey to buffy underparts. This pattern is most strongly developed in the North American animals and least developed in some of the members of the southern group of Eurasian subspecies. The North American voles are most similar to those occurring in northeastern Siberia *(major, buturlini,* and *brevicauda).* Differences in color are greater among the Eurasian forms than between the North American and northeastern Siberian animals.

Of the North American subspecies, best known is the north-Alaskan *muriei,* for which the characteristics of the molt and the sequence of pelages have been described in detail by Bee and Hall (1956). According to these authors, these voles progressively become more brown from east to west, with the brownest specimens occurring on the Seward Peninsula. In laboratory-reared animals from stock originating at Lake Schrader in northeastern Alaska, the pelage acquired a more ochraceous color than I have observed in wild individuals; this was possibly influenced by their unnatural diet.

The oldest individuals of *muriei* available, taken in July and August in the vicinity of Lake Schrader, are grizzled-grey dorsally, shading to buff (near Olive Buff; capitalized names of colors according to Ridgway, 1912) on the flanks, rump, and tail. The guard hairs are very dark, with the cover hairs either buffy or buffy with darker tips. Ventrally, the color is grey washed with buffy, becoming ochraceous around the base of the tail. The feet are pale buffy to grey dorsally; the well defined ear patches are quite buffy. Smaller breeding adults, probably a year younger, from the same area are less grey. Specimens collected farther south during the summer, in the vicinity of Arctic Village, and farther west, in the region of Anaktuvuk Pass, have a more brownish tinge, with more intensely ochraceous sides and rump. Specimens in winter pelage, taken at Anaktuvuk Pass in mid-October, are greyer and the colors in general are less intense.

Rand (1945) described *andersoni* as being largely grey with the overall pattern about as in *muriei.* Rand's specimens were collected in early September, and perhaps were in at least partial winter pelage. Only one was an adult. It is possible that this form intergrades with *muriei* in the mountains west of the Mackenzie River (see Fig. 2).

The Yukon subspecies *cantator* was described from immature animals collected on 15 August (Anderson, 1946). Two adults were later taken at the head of Kluane Lake (Banfield, 1960). My series from the Wrangell Mountains indicates that this is the darkest of the North American forms. In summer pelage, the combination of hair colors imparts a dark, brownish shade dorsally, with a tendency toward a darker median streak over the head and neck. There is an admixture of buffy cover hairs dorsally; the sides and ear patches are paler but not ochraceous. The long hairs of the dorsal surface of the tail are sometimes nearly white; the underparts of the body are buffy-grey. The area of the face around the vibrissae is comparatively dark.

The subspecies *oreas,* from the Alaska Range, is more ochraceous overall, with contrasting sides and rump. The ear patches, dorsal surface of the feet and tail, and the underparts are more ochraceous than in any of the other North American forms. This subspecies evidently intergrades with *cantator* in eastern Alaska. A single specimen taken about 8 km northeast of Paxson, south of the Alaska Range, was referred to *cantator* by Baker (1951). However, animals trapped on the Denali Highway about 25 km west of Paxson appear to be intermediate between *cantator* and *oreas.*

Specimens of *miurus* from Palmer Creek, near the type locality, taken during middle to late August, have the usual pattern, with brighter sides and rump, well defined ear patches, and pale, slightly buffy underparts. In color, this form, which is generally buffy rather than ochraceous, appears to be more or less intermediate between *cantator* and *oreas.* Animals collected in late August by Dr. F. H. Fay on the north fork of Indian Creek, about 100 km farther south, are similar to those from

Palmer Creek. Subadults from Indian Creek are darker and somewhat more ochraceous than the adults.

Narrow-skulled voles have never been recorded in the Chugach Mountain Range, but *miurus* may occur there. The voles of the Talkeetna Mountains in south-central Alaska appear to be referable to *miurus*. Ten specimens have been collected in the vicinity of Willow Pass about 90 km north of the town of Anchorage, but only two skins were preserved. These animals resemble *miurus* in color and in cranial characteristics.

The Eurasian subspecies tend to be more brown in color than those in North America. A specimen of *buturlini*, collected July 5 on the lower Kolyma River (lat. 70^0 N.), is indistinguishable in dorsal color from some specimens of *muriei*. However, examples of *buturlini* in the University of Moscow Museum appeared to be browner. Two specimens of *major*, taken in early August on the Paiuta River, Iamal Peninsula, are brownish dorsally (described by OGNEV as Buffy Brown), but are indistinguishable from some specimens of *muriei*. The guard hairs in *major* are dark brown rather than blackish, while the ventral color is pale and only slightly buffy. Ten specimens from Baidaratskaya Gulf, collected during August, differ somewhat from the animals from the Paiuta River in that they have more buffy sides and rump; they closely resemble the North American forms. One specimen from the northern Ural, collected in June, has a distinctly buffy color ventrally and is also more ochraceous above than the other specimens of *major*. Some individuals have a rather well defined median streak over the head and neck. The early description of the color of *major* by OGNEV (1925) does not agree with his more recent statements (1950) nor with my observations.

The subspecies *brevicauda* appears in color to be intermediate between *major* and the North American forms. Some specimens from the Viliui River region of Iakutia are indistinguishable from *muriei*, but in general *brevicauda* is somewhat less buffy, tending toward brown dorsally. The guard hairs are dark brown, while a median streak is present on the head. The ear patches, sides, and rump are buffy ochraceous, the underparts grey with a buffy tinge, and the tail is darker and less yellowish dorsally than is the case in *muriei*. In the sample studied, *brevicauda* in having a heavily furred tail resembles the northern forms of both continents.

Progressing from east to west, the Eurasian subspecies belonging to the southern group become darker. However, the range in color is not great when the size of the geographic area involved is taken into consideration. The easternmost representative of the southern group, *raddei*, was represented by two specimens from Lake Tasei, Chita district, taken in late July, two specimens from the same area collected in late June, and 5 specimens from Mongolia. The latter, collected during June and July in the region of Urga (= Ulan Bator) and Sain-Noian-Khan, are a part of the series referred to *M. angustus* Thomas by ALLEN (1924). These voles are hardly distinguishable from Alaskan specimens either in general color or in pattern. The Mongolian specimens are somewhat more grey than those from Transbaikalia, and are also grey ventrally while the latter are buffy.

The subspecies *eversmanni*, from the Altai, was represented by specimens considered by HOLLISTER (1913) under the names *M. eversmannii* (Poliakov) and *M. tianschanicus* Büchner. Four skins were from animals taken in late July-early August at Topucha, on the headwaters of the Katun' River, and 15 were from the Chuia River area, near the Chogan-Burgazi Pass, farther south. The former tend toward reddish-brown to brown dorsally, with dark guard hairs that contrast strongly with the predominantly brown cover hairs. These specimens are pale buffy-grey ventrally. The overall pattern is typical, though rather weakly defined. Those from Chogan-Burgazi Pass, collected in July, tend to be more buffy above. Ventrally they range

Table 1 Summary of cranial measure

Species	Sex	N	Condylobasal Length			Zygomatic Width			Lambdoidial Width	
			Range	M	σ	Range	M	σ	Range	M
gregalis	♀	8	24.2—26.0	25.0	.6062	11.7—13.6	12.5	.5905	9.8—10.5	10.1
eversmanni	♂	6	24.0—26.8	25.2	.9101	13.2—15.2	14.1	.6975	10.5—12.8	11.5
	♀	3	25.0—25.2	25.1	—	12.9—13.0	12.9	—	10.0—10.4	10.3
raddei	♂	7	23.7—26.4	25.6	.8896	11.2—14.4	13.3	1.0563	9.9—11.9	11.1
	♀	8	24.0—27.2	24.9	.9387	11.5—14.6	12.8	.8594	10.1—11.7	10.5
major	♂	6	25.1—27.7	26.5	.8812	13.4—15.5	14.3	.7000	11.2—12.7	11.7
	♀	5	24.1—26.9	25.7	1.0070	11.6—13.9	12.9	.7899	10.4—11.5	10.8
muriei	♂	38	24.1—29.6	26.5	1.3111	10.8—16.1	13.0	1.1546	10.3—12.6	11.4
	♀	26	24.3—28.2	26.0	1.0775	11.2—14.3	12.6	.8677	10.4—12.2	11.1
oreas	♂	14	24.8—28.0	26.3	.9696	11.7—15.5	13.5	1.1832	10.1—12.5	11.4
	♀	13	24.6—27.9	25.9	.9889	10.1—15.1	12.7	1.2075	10.1—12.3	11.0
miurus	♂	10	23.6—27.4	25.2	1.1874	12.6—15.9	13.6	1.0030	10.2—12.2	11.1
	♀	7	23.8—26.7	24.3	.9617	12.2—14.6	12.9	.7355	10.5—12.8	11.0
cantator	♂	4	22.8—24.0	23.5	—	11.1—11.6	11.3	—	10.1—10.9	10.6
	♀	4	24.1—25.3	24.8	—	11.5—13.1	12.5	—	10.5—11.0	10.8

from grey to pale buffy-grey. Except for a few specimens having ear patches and slightly buffy sides, the „typical" pattern is difficult to distinguish.

The nominate form of the narrow-skulled vole is the darkest of all in color. The 4 specimens studied in detail were all collected in late May. Two skins from Bassandaika and Mariinsk Station, in the vicinity of Tomsk, are especially dark, possibly being in fresh summer pelage; the dorsal streak in one is nearly black and extends almost full length of the body. The sides are paler, with no tendency toward the buffiness seen in most of the other forms examined. The ventral pelage is grey to buffy-grey, the feet are pale above, and the dorsal surface of the tail is dark brown. Ear patches are weakly defined but visible. The two other specimens, also

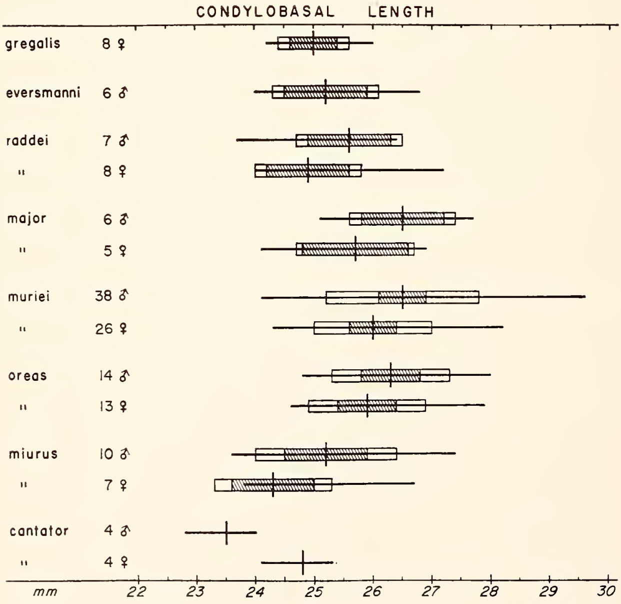

Fig. 3. Comparison of condylobasal lengths of various subspecies of *M. gregalis.* Solid black line represents range; vertical line represents mean; hollow rectangle represents 1 standard deviation on each side of mean; shaded rectangle represents 2 standard errors on each side of mean. ($SE_{\bar{M}} = \frac{\sigma}{\sqrt{N}}$)

ments (in mm) of adult voles *Table 1*

	Length Nasals			Length Maxillary Tooth Row			Length Incisive Foramen			Interorbital Width		
σ	Range	$\bar{M}$	σ	Range	$\bar{M}$	σ	Range	$\bar{M}$	σ	Range	$\bar{M}$	σ
.2572	6.3—7.1	6.7	.2523	5.4—6.2	5.8	.3019	4.0—5.0	4.4	.3371	2.2—2.7	2.5	.1581
.7106	6.6—7.3	7.0	.2580	5.8—6.4	5.8	.3627	4.3—5.0	4.8	.2414	2.4—4.0	3.2	.5612
—	6.4—6.9	6.7	—	5.7—5.7	5.7	—	4.4—4.6	4.5	—	2.6—2.6	2.6	—
.6425	6.1—7.3	6.9	.3605	5.4—6.5	5.8	.3138	3.1—4.9	4.2	.5502	2.5—3.0	2.8	.1509
.5098	6.1—7.0	6.4	.3297	5.3—6.6	5.8	.3807	4.1—4.7	4.4	.2029	2.5—2.9	2.7	.1322
.5032	6.4—7.8	7.3	.5865	5.4—6.2	5.9	.2675	4.1—4.8	4.5	.2158	2.7—3.2	3.0	.1732
.3714	6.1—7.0	6.7	.3405	5.5—6.5	5.8	.3898	4.0—4.8	4.6	.2898	2.8—3.3	3.0	.1897
.5319	5.6—8.1	6.8	.6565	5.6—6.7	6.1	.2701	3.5—5.1	4.4	.3535	2.8—3.6	3.2	.2186
.4483	5.9—7.5	6.7	.4135	5.4—6.6	6.0	.2785	3.9—4.8	4.4	.2651	2.9—3.6	3.2	.1740
.6253	6.1—7.8	6.9	.4701	5.4—6.3	5.9	.2738	4.4—5.5	5.0	.3240	2.8—3.5	3.2	.1963
.5857	6.1—7.8	6.9	.5329	5.5—6.5	5.9	.3255	4.5—5.4	4.8	.2863	3.1—3.6	3.2	.1414
.5621	6.2—7.3	6.6	.3066	5.2—6.3	5.6	.3240	4.0—4.7	4.2	.2213	3.3—3.6	3.5	.1183
.8148	6.0—6.7	6.3	.4472	5.4—6.1	5.6	.2236	3.8—4.7	4.3	.3193	3.3—3.6	3.5	.1183
—	5.6—6.1	5.8	—	5.1—5.5	5.3	—	3.8—4.3	4.1	—	3.1—3.3	3.1	—
—	6.0—6.6	6.3	—	5.3—5.7	5.6	—	4.3—4.3	4.3	—	3.1—3.4	3.2	—

from the Tomsk region, are probably still in winter pelage, for they are somewhat lighter in color with the dorsal streak poorly marked. According to Ognev, animals from the Karaganda region of Kazakhstan, at the southern limits of the range of *gregalis,* are paler than those to the north.

Cranial characteristics. Cranial measurements and other numerical data for adult voles representing 8 subspecies have been summarized in Table 1. Some cranial dimensions are compared in Figures 3–5. In the samples analyzed, the differences in cranial proportions among these subspecies are not great but in most cases are significant.

The differences among subspecies on either continent are as great as or greater than between the northern Eurasian and northern North American forms, exemplified by *major* and *muriei,* respectively. The latter, nearly equal in size, differ somewhat in proportions. It appears that *muriei* is the largest of the subspecies of *M. gregalis,* since the mean cranial dimensions reported by Bee and Hall (1956, p. 139) exceed those presented here.

The specimens of *eversmanni* exhibited unusually great variation in the interorbital width (see Fig. 4). Among 25 specimens designated *M. tianschanicus (= M. g. eversmanni)* in the British Museum, from the Tian'-Shan' Mountains, mainly from the vicinity of Dzharkent (= Panfilov), this dimension ranged from 2.6 to 4 mm (av. 3.2 mm). Although the zygomatic width in *eversmanni* is proportionally greater than in any of the other forms examined, the interorbital width as reported does not exceed the usual limits for *M. gregalis.* In fact, Büchner (1889, p. 110) was impressed by the smallness of this dimension. In Ognev's (1950) material, interorbital width in *eversmanni* ranged from 2.5 to 3.1 mm. Hollister (1913) observed unusual variation in the size of the skull in adult voles, but reported interorbital widths ranging only from 2.1 to 2.6 mm. The reasons for this discrepancy are not clear at the present time, since it was not possible to recheck the material in the British Museum.

Of the specimens of *cantator* considered to be adult, the females evidently were

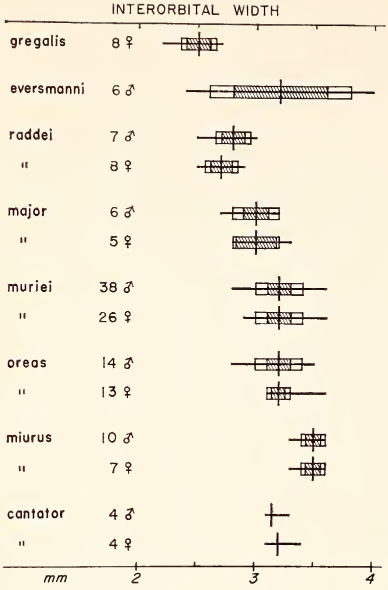

Fig. 4. Comparison of interorbital widths of various subspecies of *M. gregalis.* Range, mean, standard deviation, and standard error are indicated as in Figure 3.

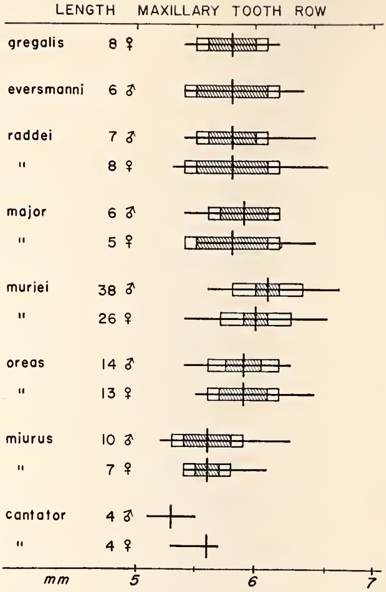

Fig. 5. Comparison of lengths of maxillary tooth row in various subspecies of *M. gregalis.* Range, mean, standard deviation, and standard error are indicated as in Figure 3.

older than the males (Fig. 3). This form appears to be similar to *miurus* in size of the skull.

Certain characteristics of the palate and dentition require further discussion. In the Eurasian voles, the posterior, sloping portion of the median ridge of the palate is usually strongly developed, forming a median keel that continues posteriad and finally terminates in bilateral ridges that tend to form the postero-medial edges of the lateral pits of the palatine. In the case of the North American animals, the posterior ridge of the palate usually terminates rather abruptly, forming a broad shelf rather than a keel. In an earlier study, I concluded that the differences in the structure of the palate were sufficiently great to distinguish the North American voles from those of Eurasia (Rausch, 1953), but subsequent examination of more material has disclosed that the supposed differences are not constant. Not only do the two types of palates occur in both Eurasian and North American voles, but intermediate types also are seen in animals from both continents (Fig. 6). It is true, however, that one type predominates in voles of each continent.

Microtus gregalis is characterized by comparatively small and delicately formed teeth. In the various subspecies, the length of the maxillary tooth rows is directly proportional to condylobasal length. The dentition of the narrow-skulled voles exhibits a degree of variability comparable to that seen in other species of *Microtus.* The teeth of the Eurasian and North American animals are quite similar with the exception of P_4 (nomenclature according to Kellogg, 1922), which usually has 5 closed triangles in the Eurasian animals and 6 in those in North America. The anterior portion of P_4 is usually not so well developed in the Eurasian voles; the secondary protoconulid may be small or even absent, and only rarely does it form a completely closed triangle. In the North American voles, P_4 usually narrows posterior to the paraconid and the secondary paraconid, resulting more or less in the isolation of the secondary protoconulid. The latter usually forms a closed triangle, thus making a total of 6 in P_4.

However, the numbers of triangles in P_4 are not constant for either the North American or the Eurasian voles. The latter may have as many as 6 completely closed triangles and the North American animals may have as few as 5. Intermediate stages are commonly seen, making exact classification of type difficult. For example, in a series of 10 animals from the Talkeetna Mountains, in south-central Alaska, the secondary protoconulid formed completely closed triangles in 3, and partially closed triangles in 2; the secondary protoconulid was not distinct in the remaining 5, which consequently possessed only 5 closed triangles.

There appears to be a greater tendency for the formation of 6 closed triangles in P_4 in the voles belonging to the northern group of Eurasian subspecies. It may be found that this character forms a gradient in Eurasia and that the northeastern Siberian and North American voles are most similar in this detail. The subspecies belonging to the southern group of voles in Eurasia seem nearly always to have only 5 closed triangles. Some variants of P_4 have been illustrated by OGNEV (1950, p. 477).

Other characteristics. The post-cranial skeletons of the Eurasian and North American voles were not compared. In both, the tail comprises about 1/5 to 1/4 of the length of the body, depending upon the subspecies; the North American voles typically have 13 caudal vertebrae.

The form of the os penis in *M. gregalis,* as depicted by OGNEV (1950, p. 461) is similar to that of the North American voles. OGNEV's figure indicates that the lateral processes may be ossified, but this was not observed by ANDERSON (1960), either in Alaskan animals or in a single specimen from "eastern Europe". I observed at least partially ossified lateral processes in the os penis of a specimen of *miurus;* following staining with alizarin red S, the ossified portions measured .5 mm long by about .08 mm in diameter. The form of the os penis exhibits considerable individual variation, and the degree of ossification depends partly upon age. Consequently, the description of this structure should be based upon a large series of specimens. There is at present no reason to suppose that any significant differences exist between voles of the two continents in the form or in pattern of ossification of the os penis.

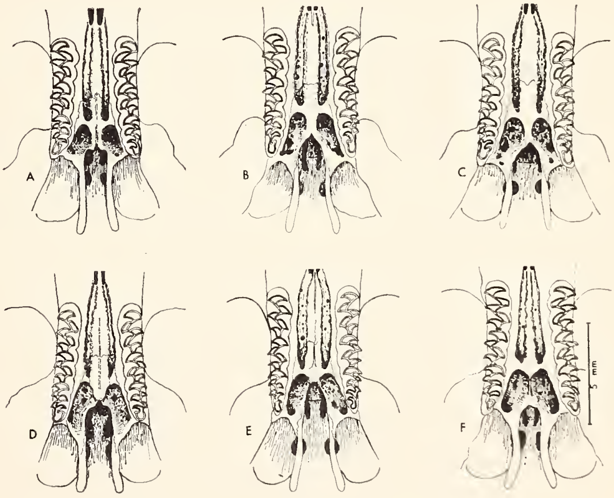

Fig. 6. Variation in structure of the palate in North American and Eurasian examples of *M. gregalis.* A - *gregalis* ♀ from Tomsk region; B - *muriei* ♀ from Anaktuvuk Pass, Brooks Range; C - *miurus* ♂ from Palmer Creek, Kenai Peninsula; D - *miurus* ♂ from Palmer Creek, Kenai Peninsula; E - *muriei* ♂, captive stock, Schrader Lake origin, Brooks Range; F - *buturlini,* sex?, from lower Kolyma River.

Chromosomes. MATTHEY and ZIMMERMANN (1961) recommended that changes in the systematic status of *Microtus* species be supported by cytogenetic studies. These could not be made in the present case because of the lack of living Eurasian voles; however, the chromosomes of one of the North American subspecies have been studied with the hope that similar work in Eurasia will later make possible the desired comparisons. I am indebted to Mrs. R. V. RAUSCH for the information presented below.

Four male voles *(muriei)* captured at Anaktuvuk Pass in October, 1962, provided the material studied; the one female obtained died before it could be examined. The methods applied have been described by NADLER and BLOCK (1962), except, as advised by Dr. NADLER (personal communication), the expelled bone marrow was placed directly into 1 per cent sodium citrate solution and incubated, after which the tissue was fixed and stained (Orcein, Synthetic, Chroma Ges.). Permanent preparations were made by the freezing method (CONGER and FAIRCHILD, 1953), using Permount (Fisher Co.) as the mounting medium. Earlier attempts to obtain suitable preparations by means of the *in vitro* culture of leukocytes were unsuccessful because of the degree of agglutination caused by the phytohemagglutin added to stimulate mitosis.

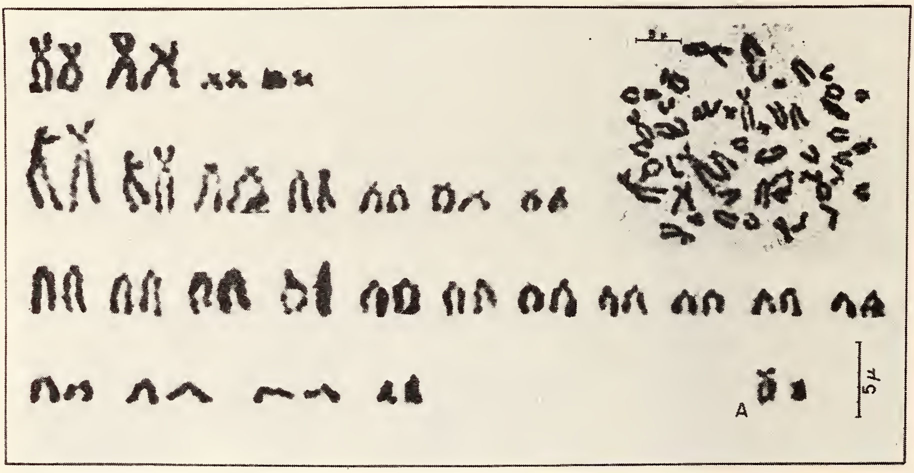

Fig. 7. A karyogram of *M. g. muriei.* Inset shows disposition of chromosomes in typical preparation. Heterochromosomes are designated by A. (Photographed on Kodalith Ortho film, Kodak Co.).

This vole has a modal chromosome number (diploid) of 54 (see Fig. 7). For 80 cells from the four animals, the numbers of chromosomes near 54 were as follows: 51 in 6 cells; 51 ?+1 in 6; 52 in 10; 52 ?+1 in 2; 53 in 9; 53 ?+1 in 4; 54 in 28; 55 in 4. For cells having 54 chromosomes, comparisons were made directly with corresponding photomicrographs, making it possible to match the pairs and to identify the heterochromosomes (since no female animals were studied and no testicular preparations were made, further identification of the heterochromosomes was not possible). A karyogram for this species is shown in Fig. 7. All of the chromosomes of this vole appear to be acrocentric or submetacentric; it is possible that one of the smallest is metacentric.

The chromosomes have not previously been studied in any voles of the subgenus *Stenocranius* and therefore no comparisons with other species have been attempted here. The diploid number of 54 is known for such diverse species as *Microtus californicus* (PEALE) and *M. ochrogaster* (WAGNER).

Discussion

Fossil evidence indicates that the geographic distribution of *M. gregalis* was much more extensive during late Pleistocene time than it is at present. Remains of *M. anglicus* Hinton (= *M. gregalis;* see Zeuner, 1958, p. 381) are known from upper Pleistocene deposits as far west as England (Hinton, 1926); in northeastern Siberia, *M. gregalis* has been identified from upper Pleistocene deposits (Riss glaciation) in the Aldan River basin and from deposits of Würm age in the Primorsk lowlands and on Bol'shoi Liakhov Island (Vangengeim, 1961).

The Pleistocene remains of *M. gregalis* in Europe have been associated with faunal assemblages characteristic of arctic tundra (Hinton, 1926; Zimmermann, 1942; Kowalski, 1959); included also were the collared lemming, *Dicrostonyx torquatus* Pallas, and *Lemmus sp.* (the skulls of *L. lemmus* Linnaeus and *L. sibiricus* Kerr are indistinguishable; see Sidorowicz, 1960), whose distributional history appears to have been much the same as that of *M. gregalis.* Three of these species *(M. gregalis, D. torquatus,* and *L. sibiricus)* are similarly distributed at present, occurring in the tundra zone of Eurasia eastward from the general region of the Onezhsk and Kanin Peninsulas (Ognev, 1948, Maps X and XI). *L. lemmus* is found in the northern part of the Scandinavian Peninsula, where it possibly survived the Würm glaciations in northern refugia (Lindroth, 1958).

The pattern of present distribution of *M. gregalis* in Eurasia suggests that the tundra-inhabiting forms survived the upper Pleistocene glaciations in glacier-free refugia, while the southern group of subspecies, whose members have become adapted to existence in a variety of habitats including semi-desert, dry steppe, taiga, and alpine tundra, may represent populations that existed beyond the southern limits of glaciation.[2] This ecological diversification, accompanied by morphological divergence, is indicative of relatively long separation of the northern and southern groups of subspecies. Since the eastern Siberian *brevicauda* seems to belong with the northern group, southward extension of its range and some degree of differentiation may have taken place during post-glacial time.

It is believed that only the uplands were glaciated in northeastern Siberia east of the Lena River (Farrand, 1961). Probably, *M. gregalis* and other tundra-inhabiting mammals were widely distributed in these regions as well as in the Amphiberingian Refugium during late Pleistocene time. The mammals inhabiting the Amphiberingian Refugium must have dispersed into acceptable habitat following the retreat of the glaciers. The North American subspecies of *M. gregalis* more or less surround the unglaciated region that comprised the eastern part of the Refugium, and the comparatively small extent of their geographic range also suggests post-Pleistocene dispersal (Rausch, 1963). Fossil remains of *M. gregalis* in North America are known only from Pleistocene deposits within the limits of the former Refugium (Fairbanks area). This material, identified as *M. miurus,* was collected and studied by Dr. Charles A. Repenning and his co-workers, of the United States Geological Survey, who kindly permitted this reference to their unpublished record.

The North American populations of *M. gregalis* are quite similar ecologically. They occur in arctic or alpine tundra, or in subalpine situations, in which case they usually inhabit areas grown to shrubs such as *Salix* spp., *Alnus, Spiraea,* and others, often with a dense ground-cover of mosses. Colonies of *cantator* have been found within spruce forest *(Picea glauca)* near timber line in the Wrangell Mountains, where they were especially numerous in a burned-over area grown densely to willow *(Salix)*

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[2] In a publication received after completion of this paper, Shvarts (1963; see literature) has also discussed the relationships and distribution of the narrow-skulled voles.

with spruce trees interspersed. Observations on the ecology of these voles have bee reported by Quay (1951), Rausch (1951, 1953), and Bee and Hall (1956). The habi of drying leafy vegetation as winter food is characteristic of at least 3 of the North American forms *(muriei, oreas,* and *cantator),* but has not been recorded for either *andersoni,* which is poorly known, or *miurus.* This activity does not appear to be typical of the Eurasian voles, although observations reported by Ognev (1950, p. 468) for voles in Kuraisk Steppe, western Altai, suggest that hay piles are sometimes made. It is possible that I have overlooked other pertinent observations recorded in the Russian literature.

More than 300 specimens of *M. gregalis* have been examined in Alaska for helminth parasites (Rausch, 1952); however, since the helminths in microtine rodents generally do not exhibit host specificity below the generic level (Rausch, 1957), comparatively little information of zoogeographic importance has been obtained. One of the cestodes, *Paranoplocephala omphalodes* (Hermann, 1783), is a holarctic species having a wide distribution in Eurasia. On the North American mainland, it is known only from the holarctic *M. gregalis* and *M. oeconomus;* evidently it has not extended its range beyond that occupied by these voles, although nearctic species of *Microtus* presumably are susceptible to infection.

Addendum

After this manuscript had been completed, Dr. George P. Holland, Canada Department of Agriculture, Ottawa, kindly provided a list of fleas collected from *M. gregalis* in North America. Four species, none of which is specific for this vole, have been recorded: *Peromyscopsylla ostsibirica longiloba* (Jordan), *Amalaraeus penicilliger dissimilis* Jordan, *Megabothris calcarifer gregsoni* Holland, and *M. groenlandicus* (Wahlgren). All but the last are holarctic species, believed by Holland to be survivors from the amphiberingian fauna (Holland, 1963: Faunal affinities of the fleas [Siphonaptera] of Alaska with an annotated list of species; Pacific Basin Biogeography, Bishop Museum Press).

A tick, *Ixodes angustus* Neumann, has been recorded from this vole as well as from other species of small mammals in Alaska.

Summary

On morphological and zoogeographical grounds, discussed in the present paper, it is concluded that the narrow-skulled vole in North America, previously designated *Microtus (Stenocranius) miurus* Osgood, is conspecific with the Eurasian *M. (Stenocranius) gregalis* Pallas. Fourteen subspecies in Eurasia and 5 in North America are now recognized, but it is probable that the number in Eurasia will be reduced through future investigation. The Eurasian subspecies of this vole comprise two major groups, of which one occupies the tundra zone and the other occurs across central Asia below lat. 60^0 N.; their geographic ranges are largely separate but evidently become confluent in northeastern Siberia. The members of the northern group of Eurasian subspecies and the North American forms are closely related; the present distribution of the latter indicates post-glacial dispersal from the Amphiberingian Refugium. It is believed that the tundra-inhabiting voles in Eurasia likewise survived the Pleistocene glaciations in northern refugia, while the members of the southern group of subspecies probably represent populations that survived south of the limits of the continental glaciers. The ranges of the two Eurasian groups probably have become confluent during post-glacial time in northeastern Siberia as a result of the southward spread of the northern forms. At least, the subspecies having the intervening range closely resembles members of the northern group. Some of the ecological and ethological characteristics of these voles are briefly discussed. The chromosome number of one of the North American subspecies of narrow-skulled vole was determined to be 54; this is the first time that the chromosomes of a member of the subgenus *Stenocranius* have been investigated. A karyogram has been included.

Zusammenfassung

Auf morphologischen und tiergeographischen Grundlagen, die in dieser Arbeit besprochen wurden, ist festgestellt worden, daß die schmalschädlige Wühlmaus in Nordamerika, früher *Microtus (Stenocranius) miurus* Osgood bezeichnet, mit der palaearktischen Art *M. (Stenocranius) gregalis* Pallas identisch ist. Zur Zeit gelten 14 Unterarten in Eurasien und 5 in Nordamerika als unterscheidbar; vermutlich aber wird die Zahl der palaearktischen Unterarten durch eingehendere Untersuchungen künftig vermindert werden. Auf Grund ihrer Verbreitung bilden die palaearktischen Unterarten zwei beinahe vollständig getrennte Gruppen. Die Wühlmäuse der nördlichen Gruppe bewohnen die Tundrazone, während die Vertreter der zweiten Gruppe über Mittelasien südlicher als 60° N. B. verbreitet sind. Die Verbreitungsgebiete der zwei Gruppen verbinden sich anscheinend. Die nordamerikanischen schmalschädligen Wühlmäuse sind mit den in der Tundrazone vorkommenden palaearktischen Formen nahe verwandt; sie haben sich wahrscheinlich während der Postglazialzeit aus dem Amphiberingschen Refugium verbreitet. Möglicherweise überlebten die tundrabewohnenden Wühlmäuse Eurasiens die Eiszeit ebenfalls in vereinzelten Refugien in Nordostsibirien, während die Formen der südlichen Gruppe sie jenseits der Grenzen des Festlandsgletschers überlebten. Wahrscheinlich wurden die zwei Verbreitungsgebiete dieser Art in Eurasien erst während der Postglazialzeit durch das Vordringen der nordischen Formen verbunden, da eine nähere Verwandtschaft zwischen den nördlichen und der dazwischenliegenden Unterart besteht. Einige ökologische und ethologische Eigentümlichkeiten dieser Wühlmäuse werden kurz besprochen. Es wurde festgestellt, daß eine der nordamerikanischen Unterarten der schmalschädligen Wühlmaus 54 Chromosomen hat; sie ist der einzige Vertreter der Untergattung *Stenocranius*, dessen Chromosomen untersucht worden sind.

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