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Palaearctic Shrews of the Subgenus Otisorex: Biotopic Preference, Population Number, Taxonomic Revision and Distribution History

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Based on a study of morphometric measurements of 67 shrews captured in the northern Far East of the USSR and of relevant literature, the presence in the Palaearctic was established of only one shrew species of the subgenus *Otisorex*, namely *Sorex cinereus* Kerr, 1792. In the far northeast Palaearctic this species is represented by three subspecies: in Chukotka by *S. c. portenkoi* Stroganov, 1956; in Kamchatka by *S. c. camtschatica* Yudin, 1972; and on Paramushir Island by *S. c. leucogaster* Kuroda, 1933. *S. cinereus* is a common and quite numerous species in the far northeast Palaearctic. Optimal biotopes for this shrew are damp deciduous forest valleys with high grasses. In Chukotka this species is most numerous in the tussocks of tundra valleys. *S. c. portenkoi* and *S. c. leucogaster* are very alike morphologically, which is explained by their similar origin. *S. c. camtschatica* differs sharply from the first two phylogenetically and morphologically. The impermissibility of the species *S. beringianus* Yudin, 1967 is demonstrated. It is assumed that there were two separate invasions of *S. cinereus* into the Palaearctic from the Nearctic. Derivatives of the first invasion are *S. c. portenkoi* and *S. c. leucogaster*, of the second *S. c. camtschatica*.

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I. INTRODUCTION

In the far northeast Palaearctic, the first species of the subgenus *Otisorex*, *Sorex cinereus* Kerr, 1792 was discovered by Stroganov (1956). On the basis of his examination of a collection of shrews taken by Portenko in 1932 in the Anadyr River valley, by Larinov in 1952 in the vicinity of Yakutsk and by Yudin in 1954 in the coastal estuary of the Anadyr, Stroganov (1956) described a new subspecies of this species, *i.e.*, *S. cinereus portenkoi*. Shrews from near Yakutsk (6 specimens) and one shrew caught by Telegin in the lowlands of the Yenisei River were identified by Stroganov (1957) as a separate subspecies, *S. cinereus caecutienoides*. Subsequently, Yudin (1972) re-examined the available specimens of *S. cinereus* and determined that

certain shrews trapped in the vicinity of Yakutsk and in the lowlands of the Yenisey were *S. caecutiens* Laxmann, 1780.

During the last decade (1964—1974), *S. cinereus* has been captured in significant quantities in various parts of the northern regions of the Far East. In this period Yudin took 15 specimens of this species on Chukotka, 14 on Kamchatka and 76 in the upper reaches of the Omolon River (Yudin, 1973). Dolgov & Krivosheyev (1973) found three specimens of this species on the Chukotka peninsula. Voronov (1966) caught a small shrew on September 15, 1960 on Paramushir Island (the northern island of the Kurile chain). It is evidently *S. cinereus*, since the skull measurements coincided with the data given by Stroganov (1957) for this species. The craniometric measurements were not given in the paper by Voronov (1966), and in later works (Voronov, 1972, 1974) he does not mention the presence of *S. cinereus* on Paramushir Island. Skull measurements of this shrew were taken by Reimers, who confirmed that it belongs to *S. cinereus* (Reimers *et al.*, 1968).

Comparing the external morphological measurements of seven and the cranial characters of six specimens of *S. cinereus* taken on Kamchatka with analogous data for eleven specimens from the Anadyr valley, Yudin (1972) designated the Kamchatka population of *S. cinereus* as a separate subspecies, *S. c. camtschatica*, to which he relegated the specimens of *S. cinereus* trapped in the Omolon River valley (Yudin, 1973).

In 1967, on the basis of a study of four shrews captured in 1966 on Paramushir Island and the skull of one shrew taken by Voronov in 1966 nearby, Yudin (1967) described *S. beringianus* Yudin, 1967, a new species for Palaearctic fauna. Because of the absence of the postmandibular canal, this species was assigned to the subgenus *Otisorex*.

On this basis, the subgenus *Otisorex* in the far northeast Palaearctic was considered to be represented by two species, *S. beringianus* Yudin, 1967 and *S. cinereus* Kerr, 1792. The latter, in turn, was assumed to be represented by two subspecies, *S. cinereus portenkoi* Stroganov, 1956 and *S. cinereus camtschatica* Yudin, 1972.

II. MATERIALS AND METHODS

Sixty seven specimens of *S. cinereus* were collected in 1971 and 1973, including 14 specimens in Chukotka, 32 specimens in Kamchatka and 21 specimens on Paramushir Island (Fig. 1). They were all trapped in 50 m polythene fences with five separate cones (Okhotina & Kostenko, 1974), which were set up on cleared and packed-down strips of land. The cones were dug into the ground at 10 m intervals (the first and fifth placed 5 m from the ends of the fence; the upper edges of the cones were 8—10 cm below the surface of the ground). The lower edge of the polythene was dug in to a depth of 8—10 cm down the center line of the cleared strip (Fig. 2). The polythene was held upright by stakes and

passed through the center of the cones, so that animals running along the fence on either side fell into the cones, which were half filled with water to drown, thus prevent the shrews from eating each other. In determining the relative population number, expressed in per cent, one unit was adopted as the number of shrews caught in one fence during 20 days, *i.e.* 100 cone-days. The *glans penis* of adult males and the upper unicuspid teeth of all specimens were measured with an ocular rule under 8 power binoculars. The shade of fur color was determined on the Ridgway scale (1912). The significance of differences between average values was checked as necessary by the Student *t* test for comparison of averages

Fig. 1. Trapping location of *Sorex cinereus* in the North of the Far East USSR. Numbers indicate the number of shrews caught at given place, 4, 6, 4 — *S. c. portenkoi*, 1, 31 — *S. c. camtschatica*; 21 — *S. c. leucogaster*.

of independent groups. Criteria of subspecies differences were taken from Mayr (1969).

Fourteen linear measurements accurate to 0.1 mm were made on the skulls, defined as follows: 1 — condylobasal length, 2 — greatest length of skull (from posterior bulge of occipital condyles to the anterior tip of the premaxilla, with I^1), 3 — length of braincase (from anterior tip of the joint process of the scale bone to the posterior bulge of the occipital condyles), 4 — length of rostrum (from the anterior tip of the maxillary to the anterior border of the *for. anteorbitalia*),

5 — maxillary tooth row length, 6 — upper unicuspid row length, 7 — breadth of braincase (the outer greatest distance across the braincase), 8 — interorbital constriction, 9 — foreorbital constriction (constriction between *foramina anteorbitalia*), 10 — breadth of distal part of rostrum (constriction between exterior sides of rostrum in region of the first upper unicuspid tooth), 11 — depth of braincase (from tips of tympanic bullas to the highest part of cranium), 12 — length of mandible, 13 — height of *proc. coronoideus*, 14 — length of *proc. angularis*.

In comparing craniometric characters of Palaearctic subspecies of *S. cinereus* (Table 3), only those characters were included which showed statistically significant differences.

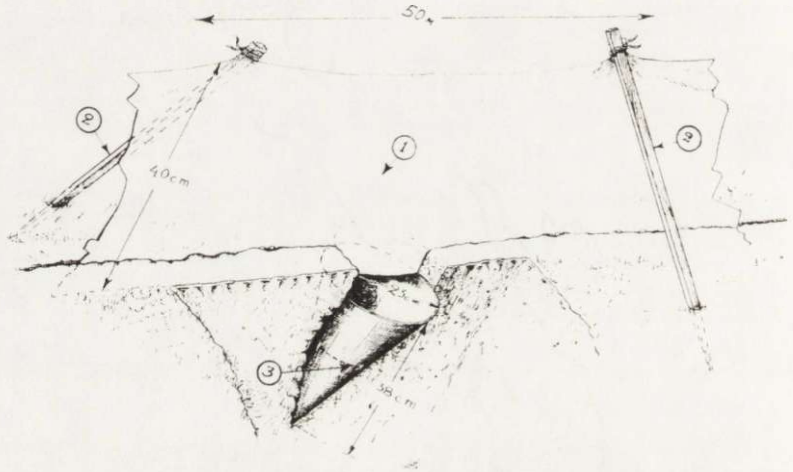

Fig. 2. Diagram showing placement of cones in polythene trapping fences.
1. Polythene fencing, 2. Stakes holding polythene vertical, 3. Water line in cone.

III. RESULTS AND DISCUSSION

1. Biotopic Preference and Relative Population Number of *S. cinereus* in the Northeast Palaearctic

In Chukotka *S. cinereus* was trapped in three areas: in the valley of the main branch of the Amguema River, on the coast of Krest Bay; in the vicinity of the village Egvekinot, and on the north coast of the Gulf of Anadyr near Nunlingran village.

In the Amguema River valley, *S. cinereus* was found in dry sedge tussocks of the tundra. On the nearby slopes of the valley, overgrown with sedge and grasses and thickets, *S. cinereus* was not found. Only specimens of *S. arcticus* K e r r, 1792 were captured there.

Altogether in the Amguema main river valley, 14 shrews were taken, of which 4 were *S. cinereus* (28.6%) of the total shrews caught) and 10 were *S. arcticus* (71.4%). The relative population number for *S. cinereus* was 6.2.

In the vicinity of Egvekinot, *S. cinereus* was found in two biotopes: 1) among the sedge tussocks of the coastal tundra of Krest Bay; and 2) on the steep mountain slopes of the southern coast of the Bay at a height of 350—400 meters above sea level in an area of sedge-moss mountain tundra.

Six specimens of *S. cinereus* were captured in the vicinity of Krest Bay. The relative population numbers for this species in coastal and mountain tundra were 7.7 and 1.4, respectively. No other shrew species was found in this part of Chukotka.

Near Nunlingran village, *S. cinereus* was hunted in two biotopes on the canopied slopes of the mountains, in dry sedge tussocks and in sedge-moss tundra.

In this part of Chukotka only eleven shrews of three species were found: four *S. cinereus* (36.4%), four *S. minutissimus* Zimmermann, 1780 (36.4%) and three *S. caecutiens* (27.2%). The relative population numbers for *S. cinereus* were 9.5 and 3.3, respectively, in dry sedge tussock tundra and in sedge-moss tundra.

Thus, among four species of shrews inhabiting Chukotka, *S. cinereus* in 1971 was the dominant one with 45.2% of the total number of shrews captured, with a relative population number of 5.6. A clear biotopic preference for this species was not determined because of the small number of specimens taken. The other three species comprised 32.2% for *S. arcticus*, 12.9% for *S. minutissimus* and 9.7% for *S. caecutiens*.

In Kamchatka, shrews were caught in two places, in the high mountains of the Middle Ridge in the vicinity of Esso village and on the western coast of the southern part of the peninsula in the main branch river valley of the Yuzhnaya Bystraya.

Near Esso village, the trapping fences were set up in the woods of the Gornaya Bystraya River valley, on the lower and upper parts skirting the mountains, over-grown with woods, and on the high plateau covered with sedge tussock tundra with clumps of shrub *Salix* sp. In this area of Kamchatka, 75 shrews were captured, belonging to four species: 65 specimens of *S. caecutiens* (86.7% of the total catch), 8 *S. isodon* Turov, 1924 (10.7%), one *S. minutissimus* (1.3%) and one *S. cinereus* (1.3%). The sole specimen of *S. cinereus* (♀ subad.) was caught near the river bank, on the border of the valley's birch-larch forest growing on the first bank of the terrace and in fields full of various grasses. The relative population number of *S. cinereus* comprised 1.5.

In the middle section of the Yuzhnaya Bystraya River valley, traps were set up in three biotopes: 1) in valleys of damp willow woods with thick high-growing grasses; 2) in the lower parts of the slopes shirting the valley, with thin birches and various grasses; and 3) in the middle section of the slopes, overgrown with birch woods.

In this part of Kamchatka, 274 shrews were captured, representing five species: 186 specimens of *S. caecutiens* (67.9%), 46 *S. isodon* (16.8%), 31 *S. cinereus* (11.3%), 10 *S. minutissimus* (3.6%) and one *S. daphaendon* Thomas, 1907 (0.4%). Of the 31 specimens of *S. cinereus*, 25 (80.7% of the total of this species) were caught in the moist willow woods along the banks in high grass, five of them (16.1%) in the lower areas skirting the slopes and one (3.2%) in the birch woods of the middle slope. The relative population numbers of *S. cinereus* in the above-mentioned biotopes were calculated at 32.0, 10.0 and 3.3, respectively.

The dominant species of all the five shrew species caught in 1973 in Kamchatka was *S. caecutiens* (71.8% of the total catch). *S. isodon* was taken in considerably fewer numbers (15.5%), and *S. cinereus* amounted to 9.2%. *S. minutissimus* was trapped infrequently (3.2%) and *S. daphaenodon* rarely (0.3%).

It is evident from the above data that in Kamchatka *S. cinereus* is not a numerous, though a relatively common species. The preferred biotopes of this species in the given region were damp valley larch forests with high-growing grasses. In mountainous sections, *S. cinereus* is rarely met, even in coastal valley forests.

On Paramushir Island in the vicinity of Severo-Kurilsk, shrews were trapped in three biotopes: 1) on mountain slopes with sedge and grass cover; 2) along river banks lined with *Salix* sp. among grasses and *Filipendula kamtschatica*; 3) along waterfalls overgrown with *Alnus kamtschatica* with sparse grass cover.

In 1973 on Paramushir Island, 159 shrews of three species were captured. *S. isodon* was dominant with 111 specimens (68.9%); *S. caecutiens* with 27 specimens (17.0%) and *S. cinereus* with 21 (13.2%) were taken in about equal numbers.

In the first biotope there were 4 specimens of *S. cinereus* (19.0% of shrews of this species); in the second there were 11 (52.4%) and in the third, six (28.6%). The relative population numbers of this species in these biotopes comprised 6.2, 14.5 and 7.5, respectively. The preferred biotope was willow banks with thick grass cover.

It is interesting to note that on nearby Skumshu Island, separated from Paramushir by four kilometers of swift-flowing strait, there were only two shrew species, *S. caecutiens* which comprised 88.2% (of the total catch of 34) and *S. minutissimus* (11.8%).

A survey of the biotopic preference of *S. cinereus* in the far northeast Palaearctic as a whole shows that this species prefers valley terrain. Optimal biotopes, where relative population numbers were highest, were damp riverside deciduous forests with high grasses. *S. cinereus* was found much less often on mountain slopes above the valleys. Similar biotopic attachment of this species was also mentioned by Yudin (1973).

In Chukotka, among the four shrew species found in 1971, *S. cinereus* was the dominant one. In Kamchatka this species was fairly common, in 1973 placing third among a total of five species captured. On Paramushir Island, *S. cinereus* may be considered a common species. Therefore, the statements of Stroganov (1957), Yudin (1973), Dolgov & Krivosheyev (1973) and Voronov (1974) that *S. cinereus* in Chukotka, Kamchatka and on Paramushir Island is one of the rarest and scarcest species, are not accurate. Evidently the above-mentioned zoologists carried out their shrew trapping in years of depressed population of *S. cinereus*.

Confirmation of our data that this species is neither rare nor scarce is found in the numbers caught by Yudin in the Omolon River valley in 1969, where *S. cinereus*, among seven species inhabiting this region of the Far East, was in third place with 7.2% of 1049 captured shrews (Yudin, 1973).

2. Taxonomic Status of *Sorex beringianus* Yudin, 1967

According to Yudin, the basic diagnostic features of *Sorex beringianus* Yudin, 1967 were the unique size and relationship of the upper unicuspid teeth (the third unicuspid smaller than the fourth, the very small fifth tooth being one fifth the size of the fourth) and the shape of the *glans penis*: cylindrical, short (3.8—3.9 mm), thick (1.1—1.4 mm), the tip crowned with a massive circular wreath.

It should be mentioned that in 1930 Kishida, on the basis of his inspection of shrews from the collection of Dr. Yamashina, collected in 1928 in the northern Kurile Island, stated that Paramushir Island was inhabited by five shrew species. Two of these Kishida designated as *Sorex leucogaster* (nom. nudum) and *S. jamashinai* (nom. nudum). Later Kuroda (1933) found that these designations concerned the same species in differing summer and winter pelage. Kuroda used the name »*Sorex leucogaster* Kishida«, though from the text of his article it was clear that Kishida was in no way responsible for the description of the given species. It was Kuroda who set forth several morphological characters and a short description of the pelage of these shrews and thus, in fact, he is the author of this species, *S. leucogaster* Kuroda, 1933.

In any case, from the moment of publication of Kuroda's paper (1933), the name *S. leucogaster* became acceptable. This name satisfies all the criteria of validity. The name *S. leucogaster* Kishida, 1930 is now *nomen nudum*.

Yudin (1967) does not cite works of Kishida (1930), Kuroda (1933) and Voronov (1966).

Comparison of the morphological characters presented by Kuroda for *S. leucogaster* and by Yudin for *S. beringianus* with analogous characters for our *S. cinereus* captured on Paramushir Island, showed a lack of statistically reliable differences (Table 1). An exception was the length of hind foot, the size of which according to Yudin's data was smaller than shrews examined by Kuroda and us ($P<0.01$). Evidently Yudin measured the length of the hind foot on preserved specimens. The differences in the length of the rostrum and *proc. angularis* in Yudin's data and ours are apparently due to some subjective difference in the method of measurement of these characters and in the larger number of our catch.

There is no difference in the structure of the *glans penis* of *S. beringianus* and of the *S. cinereus* specimens captured on Paramushir Island and in Kamchatka and Chukotka. All the adult males of *S. cinereus* trapped by us in the three areas listed had short, thick cylindrical *glans penis*, the tips of which had a circular crown. Their overall length was 4.2—4.9 mm ($\bar{x}=4.65$), thickness at the base 1.0—1.2 mm ($\bar{x}=1.12$) and before the crown at the tip, 0.9—1.1 mm ($\bar{x}=0.98$). The height of the crown was 1.0—1.2 mm ($\bar{x}=1.12$); the width was 0.4 mm. The slightly larger *glans penis* of adult males *of S. cinereus* from Paramushir Island, in comparison with the similar size of that organ in *S. beringianus* (Yudin, 1967) is explained by the fact that our measurements of the *glans penis* were taken from freshly captured animals.

On the other hand, the structures of the *glans penis* of *S. cinereus* described by Yudin (1969, 1971, 1973) for Nearctic forms and animals from Kamchatka, are different from our data. This fact was also mentioned by Dolgov & Krivosheyev (1973); they explained it by assuming that Yudin had described and made drawings of this organ from imperfectly preserved material. At the same time, Dolgov & Krivosheyev (1973) commented on the clearly identical structure of the *glans penis* of adult males of *S. beringianus* and *S. cinereus* from Chukotka and Alaska and, for this reason they considered the question of the taxonomic status of *S. beringianus* to be pending.

The measurement of the upper unicuspid teeth of all our *S. cinereus* showed that 21.4% of the specimens of this species trapped in Chukotka had a third unicuspid smaller than the fourth; in Kamchatka this same relationship between the third and fourth unicuspids was noted in 25.8

Table 1

Comparison of morphometric measurements of shrews from Paramushir island.

Measurement g, mm	*S. leucogaster* Kuroda, 1933 n=4	*S. beringianus* Yudin, 1967 n=4—5	*S. cinereus* Author's data n=21
Body weight	—	3.6—4.52	3.3—6.1 [1]
			4.0 ± 0.18
			0.81 (20.25)
Head and body length	52.0—62.0	46.0—56.0	49.2—65.3
	56.5 ± 1.47	52.2 ± 2.25	56.9 ± 0.75
	2.94 (5.20)	4.50 (8.62)	3.35 (5.89)
Tail length	41.0—42.0	40.0—41.0	38.2—46.4
	41.5 ± 0.28	40.4 ± 0.24	42.1 ± 0.88
	0.57 (1.37)	0.48 (1.19)	4.05 (9.62)
Hind foot length	11.5—12.0	11.0—11.2	10.2—12.9
	11.9 ± 0.12	11.1 ± 0.06	11.7 ± 0.03
	0.25 (2.10)	0.12 (1.08)	0.56 (4.79)
Condylobasal length	—	15.0—15.8	15.1—15.9
		15.5 ± 0.14	15.5 ± 0.05
		0.31 (2.00)	0.23 (1.48)
Greatest length of skull, with I	16.0—16.8	—	15.5—16.5
	16.2 ± 0.20		16.1 ± 0.08
	0.39 (2.41)		0.34 (2.11)
Length of braincase	—	8.6—9.0	8.1—9.3
		8.8 ± 0.07	8.7 ± 0.06
		0.15 (1.70)	0.29 (3.33)
Length of rostrum	—	3.9—4.1	4.0—4.4
		4.0 ± 0.03	4.3 ± 0.02
		0.07 (1.75)	0.09 (2.09)
Maxillary tooth row length	6.5—7.0	6.5—6.7	6.1—6.8
	6.6 ± 0.08	6.6 ± 0.05	6.5 ± 0.05
	0.17 (2.57)	0.11 (1.66)	0.23 (3.54)
Upper unicuspid row length	—	2.0—2.1	1.9—2.3
		2.0 ± 0.02	2.1 ± 0.02
		0.04 (2.00)	0.09 (4.28)
Breadth of braincase	7.0—7.9	7.2—7.9	7.3—7.9
	7.4 ± 0.20	7.6 ± 0.13	7.6 ± 0.03
	0.40 (5.40)	0.29 (3.81)	0.13 (1.71)
Interorbital constriction	3.0—3.0	2.6—3.0	2.9—3.1
		2.8 ± 0.08	3.0 ± 0.02
		0.18 (6.43)	0.07 (2.33)
Foreorbital constriction	—	2.0—2.2	2.0—2.1
		2.1 ± 0.03	2.1 ± 0.01
		0.07 (3.33)	0.02 (0.95)
Breadth of distal part of rostrum	—	1.2—1.4	1.2—1.4
		1.3 ± 0.04	1.3 ± 0.01
		0.08 (6.15)	0.05 (3.85)
Depth of braincase	—	4.4—5.0	4.4—5.0
		4.7 ± 0.11	4.8 ± 0.04
		0.24 (5.11)	0.19 (3.96)
Height of *proc. coronoideus*	—	3.0—3.1	3.0—3.3
		3.1 ± 0.02	3.1 ± 0.02
		0.05 (1.61)	0.07 (2.26)
Length of *proc. angularis*	—	1.9—2.0	1.6—1.9
		2.0 ± 0.02	1.7 ± 0.02
		0.05 (2.50)	0.08 (4.71)

[1] First line — min.—max.; second line — avg. ± S.E.; third line — S.D. (C.v.)

per cent of the specimens and on Paramushir Island in 60.0 per cent. Moreover, Hall & Kelson (1959) showed that in many specimens of *S. cinereus ohionensis* Bole and Moulthrop, the third unicuspid tooth is much smaller than the fourth. The very small size of the fifth unicuspid in relation to the fourth is one of the diagnostic features of *S. cinereus* (Stroganov, 1956, 1957; Yudin, 1971).

Hence, the size and relationships of the upper unicuspid teeth and especially the structure of the *glans penis* are the diagnostic features which show that *S. beringianus* and *S. cinereus* are one and the same species, but they are specimens of an independent subspecies. This is confirmed by the karyoanalysis performed in 1975 by Ivanitskaya (personal communication, February, 1976) which showed the chromosomes of shrews from Paramushir Island and *S. cinereus* from Canada (Meylan, 1968) to be identical in number and morphology.

In agreement with the International Code of Zoological Nomenclature (Article 23 and 50 b), the name of this subspecies should be accepted as *Sorex cinereus leucogaster* Kuroda, 1933. Its synonyms are *S. leucogaster* Kuroda, 1933 (=*S. leucogaster* Kishida, 1930 nom. nud.) and *S. beringianus* Yudin, 1967.

3. Subspecies Forms of *S. cinereus* of the Palaearctic

In order to clarify the taxonomic status of the subspecies of *S. cinereus* in the Palaearctic, identical morphological measurements were compared, as well as the pelage of specimens from Chukotka, Kamchatka and Paramushir Island.

It became clear that in adult specimens of *S. cinereus*, the identical craniometrical characters compared had statistically valid differences, which showed a coefficient of subspecies variation of not less than 1.5 (Mayr, 1969). The young of any given year showed statistically valid differences more often than did adults, but their coefficient of subspecies variation was rarely equal to 1.28. For this reason, in determining the presence or absence of differences among the three mentioned populations of *S. cinereus*, only adult specimens were used.

Shrews from Kamchatka were distinguished by larger body measurements, longer tails and hind feet. The latter were very dark below and framed with fringes of light colored stiff hair 0.8—0.9 mm long, extending even to the toes. This was also noted by Yudin (1973). Specimens from Paramushir Island and Chukotka did not have such coat color and stiff fringes on the feet.

Specimens of *S. cinereus* from Chukotka and Paramushir Island had a very similar habitus. The size of the tail was an exception, shrews from

Paramushir Island having a longer one. This is reflected in the hind foot-to-tail ratio and tail-to-body ratios (expressed in per cent), the coefficients of subspecies variation of which are 3.19 and 1.96, respectively (Table 2).

It should be noted that shrews from Chukotka and Paramushir Island had a tricolor pelage pattern and a sharp demarcation line dividing the dark back from the underparts.

Members of the Chukotka population had a dark brown back (Clove Brown, Ridgway, pl. XL) with sharp demarcation from the lighter side stripes, which were brownish yellow (Wood Brown, pl. XL) in the young and yellowish brown (between Wood Brown and Buffy Brown, pl. XL) in specimens that had lived through the winter. In the young the color of the side stripes gradually shaded into light gray (Pale Smoke Gray, pl. XLVI) underparts and in adults to a mousy gray (Light Grayish Olive, pl. XLVI). The pelage of the members of the Paramushir population was duller and more uniform in both young and adult forms. Although there was some variation in the color of the back, between Chaetura Drab and Fuscous (pl. XVII), in the young and Clove Brown in overwintered animals, the side stripes of Wood Brown and the underparts of Light Grayish Olive were the same for shrews of various ages.

In *S. cinereus* specimens from Kamchatka, the sharp sidelines were absent, and in only three young ones (9.4% of the total number) were they faintly visible in the hind parts. Pelage was bicolored: the dark brown (Fuscous, pl. XLVI) of the dorsal fur became lighter on the sides and shaded into Smoke Gray (pl. XLVI) of the underparts in the young and brownish gray (between Hair Brown and Deep Grayish Olive, pl. XLVI) in shrews that had wintered.

The tail of all specimens was distinctly bi-colored: the dark brown (Fuscous) above and light gray (Pale Smoke Gray) below.

Specimens of *S. cinereus* from Chukotka and Kamchatka differ significantly in body measurements and their indices (Table 2). All the differences are greater than is acceptable for subspecies variations. Specimens from Kamchatka and Paramushir Island had the same body length and the same indices of hind foot-to-tail length and tail index (without statistically valid variation); the coefficients of subspecies variation were: body weight — 1.28, length of tail — 1.44, hind foot — 8.76 and hind foot-to-body index — 1.46. Specimens from Chukotka and Paramushir Island showed coefficients of subspecies variation in four morphological measurements: body weight — 1.65, tail length — 2.29, hind foot-to-tail ratio — 3.19 and tail-to-body ratio — 1.96. The other coefficients of variation were lower than 1.28.

A camparison of craniological features (Table 3) revealed the largest

cranial variation between members of the Paramushir and Kamchatka populations: in the 11 cranial features compared, eight (66.6%) showed subspecies variations (condylobasal length, maxillary tooth row length, upper unicuspid row length, breadth and depth of braincase, height of *proc. coronoideus*, length of mandible and *proc. angularis*). In members of the Kamchatka and Chukotka populations, comparison of 11 craniometric measurements showed that only five (45.4%) differed on a subspecies level (condylobasal length, rostrum length, interorbital and foreorbital constrictions and breadth of braincase). Comparison of the craniological features of Chukotka and Paramushir population of *S. cinereus* did not reveal even statistically valid variations.

Analysis of the comparative data of specimens of the three populations of *S. cinereus* showed that in cranial features and pelage, members of the Chukotka and Paramushir populations are very similar, which is undoubtedly explained by their common genetic character. However, differences on a subspecies level in four morphological features and long insular isolation afford a basis for distinguishing the Paramushir population of *S. cinereus* as a separate subspecies, which, as was shown above, should be accepted as *S. c. leucogaster* K u r o d a, 1933.

The Kamchatka population of *S. cinereus* is undoubtedly an independent subspecies, which decidedly differs from the first two in having a larger skull, body, tail and hind foot and in its unique stiff fringes and bicolored pelage.

Unfortunately, it does not appear to be possible without further examination of these collections to ascertain the real subspecies of the *S. cinereus* specimens caught by Yudin in the Omolon River valey and relegated by him (Y u d i n, 1973) to a new subspecies, *S. c. camtschatica* Y u d i n. The morphological data of all specimens of the Omolon and Kamchatka populations cited in Yudin's work as evidence of their identicity have not been processed statistically. Only observed ranges and averages for a number of characters were given; therefore, the comparison of the morphological characters of specimens of these two populations is impermissible. Moreover, in this work measurements of young and adult specimens were combined, which significantly degrades these data.

4. Distribution History

The significant divergence in morphological characters in *S. cinereus* of Kamchatka in comparison with the Chukotka and Paramushir populations may be explained by their different phylogenetic origin and also by the different periods of penetration into the Palaearctic of *S. cinereus*.

The first invasion of *S. cinereus* into the Palaearctic evidently took place in early or middle Pleistocene, when one of the first Beringian land bridges existed (Sher, 1971; Král & Ivanitskaya, 1973). This form settled over Chukotka, the Koryak mountain range and Kamchatka. In a period of marine recession, during the time of the second phase of late Pleistocene glaciation, when the islands of the Paramushir chain (Paramushir, Sumshu and Atlasova) were one land mass with Southern Kamchatka (Melekestsev, Yegorova & Lupikina, 1974), this form, *S. cinereus*, occupied the territory of present Paramushir Island. Morphological data and pelage both show it to be evidently close to the subspecies *S. c. hollisteri* Jackson inhabiting Alaska (Jackson, 1928).

In the Gydansk stage of the Sartan glaciation (Main Wisconsion) during eustatic recession of the world's ocean beds to −115 m (Kind, 1974), a second invasion of *S. cinereus* took place from North America to Kamchatka, along the Pacific parts of the Bering land bridge. This form became distributed all over Kamchatka. It was prevented from spreading to the north by great glaciers, which in this period covered the Koryak mountain range and the Anadyr mountains (Hopkins, 1972). Paramushir Island was again separated from Kamchatka at that time (Melekestsev *et al.*, 1974). Morphologically and in pelage color, this form apparently was similar to *S. c. streatori* Merriam, which occurs along the northwest coast of Canada and the southern parts of Alaska (Jackson, 1928). Later, evidently in the Holocene, this subspecies, circumventing the Koryak range, penetrated to the west up to the southern part of the Anadyr mountain range (the Olomon River valley, 156—162° EL).

The hypothesis of Yudin (1973) that the second invasion of *S. cinereus* from North America into Asia took place across the Aleutian Islands is mistaken. Although in the period of the recession of the world ocean during the Illinois and Wisconsion glaciation periods, the far eastern islands of the Aleutian chain were one land mass with the Pacific parts of Beringia and North America (Hopkins, 1972), the central and western islands of this chain, beginning with the island Unalaska, were never connected with each other, let alone with the Asian continent (Hoffmann & Peterson, 1967; Yurtsev, 1974). The Komandor Islands are the above-water peaks of the far western part of the Aleutian underwater mountain range, the slopes of which in the northeast fall into the depression of the Bering Sea and in the southwest into the Kurile-Kamchatka trough (Erlikh & Melekestsev, 1974).

Indirect evidence of the absence in the Quaternary of a land connection between the central and western Aleutian Islands and Asia and North

America is the absence of shrews, in particular on the Komandor Islands. Shrews were found on the smaller island of St. Matthew (in the Pribilovs), which in the last glaciation was united with Beringia (Hopkins, 1972).

Also mistaken are the statements of Král & Ivanitskaya (1973) concerning a minimum of three invasions of *S. cinereus* into the Palaearctic across the Bering land bridge and the formation from the forms of the first two invasions of the modern species of shrews, *S. gracillimus* Thomas, 1907 and *S. beringianus*. Although *S. cinereus* and *S. gracillimus* are similar in their habitus, the structure of the *glans penis* of these species, which belong to different subgenera, has undoubted specific variation. Moreover, *S. gracillimus* is endemic to East Asia and only in the optimum of the middle Holocene made its way along the coasts of the Sea of Okhotsk to the north to about 57° NL, which is the northern boundary of its present distribution (Krivosheyev, 1973).

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PALEARKTYCZNE RYJÓWKI PODRODZAJU *OTISOREX*: PREFERENCJA BIOTOPOWA, LICZEBNOŚĆ POPULACJI, REWIZJA TAKSONOMICZNA I HISTORIA ROZMIESZCZENIA

Streszczenie

W oparciu o pomiary morfometryczne 67 ryjówek schwytanych w skrajnie północno-wschodniej części ZSRR (Tabela 1—3) i odpowiednią literaturę, ustalono obecność tylko jednego gatunku ryjówki z podrodzaju *Otisorex*, a mianowicie *Sorex cinereus* Kerr, 1972. W skrajnie północno-wschodniej Palearktyce gatunek ten jest reprezentowany przez trzy podgatunki: na Czukotce przez *S. c. portenkoi* Stroganov, 1956; Na Kamczatce *S. c. camtschatica* Yudin, 1972; na wyspie Paramuszir przez *S. c. leucogaster* Kuroda, 1933. *S. cinereus* jest pospolitym i raczej licznym gatunkiem w skrajnie północno-wschodniej Palearktyce. Optymalnymi biotopami dla tej ryjówki są wilgotne lasy liściaste z wysokimi trawami. Na Czukotce gatunek ten jest najliczniejszy w kępach traw tundry. *S. c. portenkoi* i *S. c. leucogaster* są bardzo podobne morfologicznie, co tłumaczy się ich podobnym pochodzeniem. *S. c. camtschatica* różni się wyraźnie od dwu pierwszych filogenetycznie i morfologicznie.

Wykazano brak możliwości wyróżnienia gatunku *S. beringianus* Yudin, 1967 (Tabela 1). Przypuszcza się, że były dwie oddzielne inwazje *S. cinereus* do Palearktyki i Nearktyki. *S. c. portenkoi* i *S. c. leucogaster* pochodzą z pierwszej inwazji, *S. c. camtschatica* z drugiej.