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Relationships within the Holarctic Sorex arcticus — Sorex tundrensis Species Complex

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Systematics of Holarctic *Sorex arcticus* — *Sorex tundrensis* species complex has been in dispute; the current literature places North American and Eurasian populations in *S. arcticus*, separated by *S. tundrensis* in the Yukon and in Alaska. Results of morphometric analysis of the three populations indicate that the Eurasian shrews more closely resemble *tundrensis* than *arcticus*, and they are referred to that taxon. The fundamental number of autosomes in *arcticus* (NFa=34) also differs from that of the Eurasian populations of *tundrensis* (NF=52, 56; NFa=48, 52)); unfortunately North American *tundrensis* have not been karyotyped. A map of the distribution of the Eurasian subspecies is presented: chromosome analysis of specimens assigned to *S. t. sibiriensis* indicate that there are probably two distinct species in this area, but nomenclatural changes are considered premature, pending further study.

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1. INTRODUCTION

The species complex of long-tailed shrews which includes *Sorex araneus*, *S. arcticus* and *S. tundrensis* is one of only two with Holarctic distributions (Figs. 1, 2), the other being the *Sorex cinereus* complex (Van Zyll de Jong, 1982). *Sorex araneus* Linnaeus, 1758, is the common shrew of Eurasia, occurring throughout Western Europe from the Arctic coast to the mountains of the Mediterranean zone and ranging east through Eurasia to the Yenisei River and Lake Baikal (Corbet, 1978) The widespread North American species, *S. arcticus* Kerr, 1792, first described from Hudson Bay, occupies the northern transcontinental coniferous forest from Nova Scotia and Quebec discontinuously westward to the north central Yukon. Eurasian shrews that have been assigned to *S. arcticus* occupy Siberian taiga and tundra from the Ural Mountains east to Chukotka, and south to the Altai Mountains, northern Mongolia, and the Ussuri region (Corbet, 1978). *S. tundrensis* Merriam, 1900, was described from St. Michaels, Alaska; it inhabits the boreal taiga and tundra of northwestern Yukon, extreme northwestern British Columbia, and most of Alaska (Junge & Hoffmann, 1981).

All of these shrews are superficially similar, and are usually among the larger species of *Sorex* in a given fauna. They all belong to the

Fig. 1. Distribution of *Sorex arcticus* and *Sorex tundrensis* in North America. Circles indicate collection localities of specimens used in this study; triangles, localities of fossils identified as *S. arcticus.*

subgenus *Sorex,* and posses a well- developed post-mandibular foramen but lack the pigmented ridge on the lingual face of the unicuspids (Junge & Hoffmann, 1981). The third unicuspid is larger than the fourth and there is no accessory tine on the medial face of the first upper incisor. The glans penis of each is long and cylindrical, tapering to a point, with no elaboration of the tip. Cytologically, *Sorex araneus* and *Sorex arcticus* are characterized by the presence of trivalent sex chromosomes (X, Y1, Y2) in the male (Meylan & Hausser, 1973). Since the most obvious differences between these species is size, the systematic relationships between the common shrew of Eurasia and the Palearctic "*S. arcticus*", on the one hand, and between the Nearctic arctic and tundra shrews, on the other, have been in some dispute.

Jackson, in his 1928 revision of the North American long-tailed shrews, considered the arctic and tundra shrews to be separate species, and listed several characters in which they differed. Rausch (1953) disagreed, considering the differences between the two taxa insufficient to warrent full specific status, although he did not formally place them in synonomy. He also pointed out that *arcticus* and *tundrensis* were closely related to *araneus*. Bee & Hall (1956) studied Alaskan populations and formally referred *tundrensis* to *arcticus*. The shrews included in *araneus* in the U.S.S.R. were studied by Stroganov (1957), who separated several taxa and referred them to *arcticus*. As a result of these revisions, four subspecies of *arcticus* (*arcticus, laricorum, maritimensis, tundrensis*) were recognised in North America, and seven in the U.S.S.R. (*baikalensis, borealis, buxtoni, petschorae, schnitnikovi, sibiriensis, transrypheus*). A eighth Palearctic subspecies, *parvicaudatus*, was described subsequently (Okhotina, 1976).

Fig. 2. Distribution of *Sorex tundrensis* subspecies in Eurasia. Circles indicate collection localities of specimens measured for this study: triangles indicate collection localities of Stroganov (1957), Dolgov (1967), Fedyk & Ivanitskaya (1972), Yudin *et al.* (1976), and Sokolov & Orlov (1980).

Youngman (1975) again reviewed the systematics of the North American subspecies. Six cranial measurements and four body measurements were made of populations of *S. a. arcticus* and *S. a. tundrensis* from Alaska and the Northwest Territory, Yukon, and Alberta, Canada.

Youngman found 92—100% joint non-overlap in all characters measured except length of hind foot, least interorbital breadth, and maxillary breadth in specimens of arctic shrews from Canada and tundra shrews from Tuktoyaktuk, N. W. T., the area where, if intergradation did occur, they would be expected to be the most alike. In addition, Youngman found that the unicuspids of the arctic shrew occupied a greater percentage of the maxillary toothrow than did those of the tundra shrew (38% vs. 35%, significant at the .01 level), and that certain features of the auditory ossicles also differed. On the basis of this study, Youngman re-elevated *tundrensis* to full specific status.

If *Sorex tundrensis* is afforded specific status, then *Sorex arcticus* still has Holarctic distribution, but the North American and Eurasian populations are separated from each other by the closely related tundra shrew. The purpose of this study was to re-examine Youngman's systematic separation of the arctic and tundra shrews, and to clarify the relationships between the Eurasian and North American populations in this group.

2. MATERIALS AND METHODS

Twelve skull and toothrow measurements were made of 147 skulls from museum collections. Skull measurements were made with dial calipers; toothrow measurements were made on a dissecting scope equited with a gradicle which was calibrated to the same dial calipers. Measurements included: 1) condylobasal length (Fig. 3, A-H), 2) cranial breadth (G-G'), 3) cranial depth (N-P), 4) mid-cranial depth (Q-R), 5) least interorbital width (L-L'), 6) glenoid width (U-V), 7) palatal length (A-F), 8) length of maxillary toothrow (B-D), 9) length of maxillary unicuspid toothrow (B-C), 10) length of maxillary molariform (P4/-M3/) toothrow (E-D'), 11) width across M2/-M2/ (J-J'), and 12) width of palate at U1/-U1/ (S-T).

Stepwise discriminant function analysis was performed on the University of Kansas Academic Computer Center Honeywell 66/60, using the program BMDP/7M79. Three groups were employed for the analysis; "arcticus" included shrews identified as *S. a. arcticus* and *S. a. laricorum*; "tundrensis" included Alaskan *S. tundrensis;* and "Siberian" included several subspecies identified as *S. arcticus* from the U.S.S.R.

3. RESULTS

Five variables entered into the best discriminant model (in order of decreasing contribution); cranial depth, palatal length, glenoid width, condylobasal length and least interorbital width. The plot for cannonical axes 1 and 2 is shown in Fig. 4. There is no overlap between the prediction intervals for the "arcticus" group and the combined "tundrensis" and "Siberian" groups, but some overlap between the "tundrensis" and "Siberian" groups (Fig. 4, Table 1). The "arcticus" group had longer and

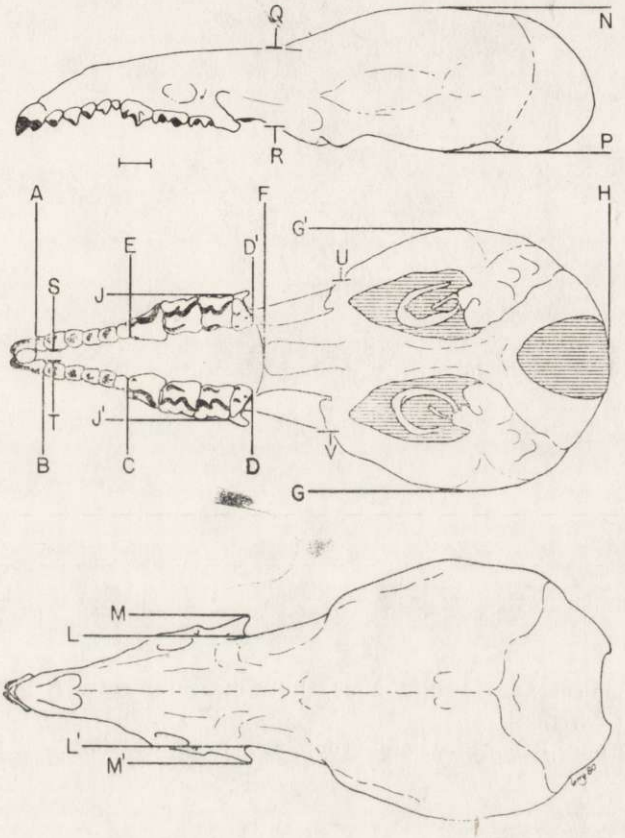

Fig. 3. Lateral and ventral views of skull of *Sorex dispar*, showing measurements referred to in text. A—H, condylobasal length; G—G′ cranial width; N—P, cranial depth; Q—R, mid-cranial depth; L—L′, least interorbital width; U—V, glenoid width; A—F, palatal length; B—D, length of maxillary toothrow; B—C, length of maxillary unicuspid toothrow; E—D′, length of maxillary molariform (P4/—M3/) toothrow; J—J′, width across M2/—M2/; anda S—T, width of palate at U1/—U1/.

higher skulls which were relatively narrower than those of the other groups, and had longer, narrower palates. The "tundrensis" group had longer, lower skulls than the "Siberian" group, and the palate was relatively longer.

In a jackknifed classification, the posterior probability of correctly identifying a member of the "arcticus" group is 100%. There is a 93% posterior probability of correctly identifying a "Siberian" specimen and an 89% probability of correctly identifying "tundrensis". If a tundra shrew is incorrectly idendified, however, it will seem to belong to the "Siberian" group; conversely, the "Siberian" shrews are incorrectly

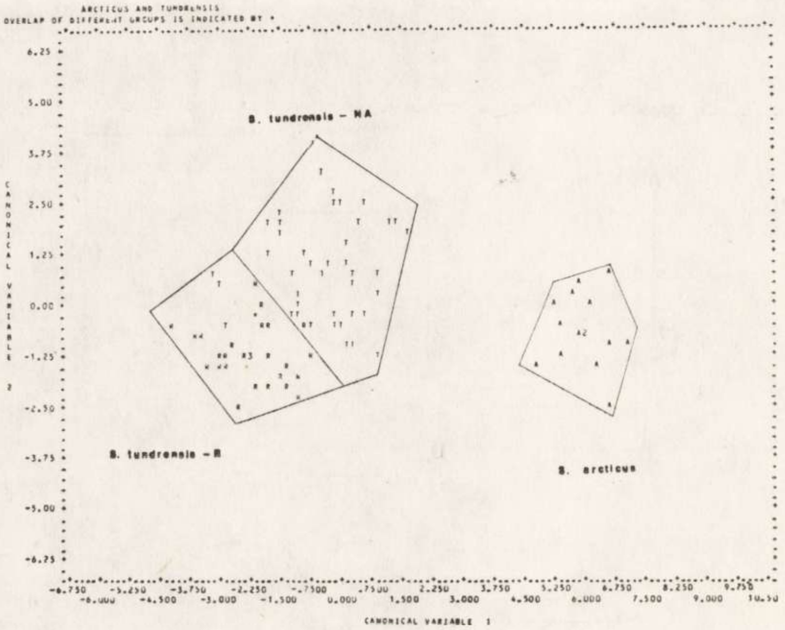

Fig. 4. Cannonical axes 1 and 2 of skull measurements. A= "arcticus" group, 2 = mean of "arcticus" group; T = "tundrensis" group, 1 = mean of "tundrensis" group; R = "Siberian" group, 3 = mean of "Siberian" group.

Table 1

Means (M), coefficient of variation (CV) and standard deviation (SD) of skull measurements used in discriminant function analysis, n=number in each group.

	"arcticus" n=13			"tundrensis" n=45			"Siberian" n=26		
Variable	M	SD	CV	M	SD	CV	M	SD	CV
Condylobasal length (A—H)	19.08	.22	.01	17.81	.30	.02	17.36	.25	.01
Cranial depth (N—P)	6.10	.24	.04	5.58	.25	.04	5.78	.17	.03
Cranial width (G—G′)	9.35	.15	.02	8.92	.18	.02	8.77	.14	.02
Least interorbital width (L—L′)	3.42	.12	.04	5.09	.12	.04	3.40	.11	.03
Midskull depth (Q—R)	3.47	.14	.04	3.23	.07	.02	3.28	.40	.12
Palatal length (A—F)	7.51	.13	.02	6.90	.22	.03	6.41	.18	.03
Length of maxillary toothrow (B—D)	6.94	.11	.02	6.42	.17	.03	6.13	.15	.03
Length of maxillary unicuspid toothrow (B—C)	2.98	.10	.03	2.54	.24	.09	2.39	.19	.08
Length of maxillary molariform tooth (E—D′)	4.25	.09	.02	4.05	.17	.04	3.83	.14	.04
Width of palate at U1—U1 (S—T)	.36	.05	.12	.39	.05	.12	.36	.03	.10
Width across M2/—M2/ (J—J′)	4.46	.09	.02	4.35	.13	.03	4.23	.14	.03
Glenoid width (U—V)	5.50	.09	.02	5.10	.19	.04	4.86	.10	.02

identified as "tundrensis". Neither of them will be misidentified as "arcticus", nor will "arcticus" be mistaken for either "tundrensis" or "Siberian". This analysis of morphometric data confirms Youngman's separation of *S. tundrensis* from *S. arcticus*. The Eurasian specimens are much closer morphologically to *S. tundrensis* than to *S. arcticus*, and are hereafter referred to that taxon.

4. DISCUSSION

Upon examination of a series of skulls from arctic and tundra shrews, certain differences become apparent (Junge & Hoffmann, 1981). Skulls of the arctic shrew are larger and more robust than those of the tundra shrew. In palatal view, the unicuspids of *S. arcticus* appear squared off and bulbous; although the posterior teeth are smaller than the anterior, the difference appears small. In *S. tundrensis*, the unicuspids are not as robust, not bulbous, and appear as a more steeply graded series, decreasing in size from front to back (Junge & Hoffmann, 1981). The unicuspids occupy a larger proportion of the total maxillary toothrow in *arcticus* than in *tundrensis*, averaging in this study 43% versus 39.8%.

The ranges of the arctic and tundra shrews are separated by an area approximately 75 kilometers wide in the central Yukon, in which neither has been found, although there are records of other shrews captured there (Youngman, 1975). If intergradation between the two species was taking place in this area, but had not been sampled, one would expect that the size differences between the two species would be minimized in areas immediately adjacent to the gap. This is not the case; specimens collected from oppocite sides of the gap do not have similar body size (Youngman, *op. cit.*), or cranial dimensions (this study).

Chromosome analysis has been important in differentiation of species in the *araneus* — *arcticus* species complex (Fedyk & Ivanitskaya, 1972; Meylan & Hausser, 1973; and references cited therein). The group is characterized by trivalent sex chromosomes; there are two Y chromosome in the male. European *Sorex araneus* (chromosome type B) (Meylan, 1964, 1965) have diploid autosome numbers (2Na) ranging from 18 to 32; the autosomal fundamental number (NFa) is 36 (Meylan & Hausser, *op. cit.*) Siberian populations of *araneus* exhibit 2N of 18—23; Fedyk & Ivanitskaya (1972) do not consider them significantly different from the karyotypes of European type B *araneus*. Siberian *Sorex tundrensis* exhibit fundamental numbers (NF) of 52 (NFa=48) (Kemerov and Irkutsk districts) (Kozlovsky, 1971), and 56 (NFa=52) Tomsk and Krasnoyarsk); Fedyk & Ivanitksaya (*op. cit.*) suggest that there may be structural differences in karyotypes between Siberian populations. *S. a. arcticus* in Canada has NFa=34 (Meylan & Hausser, 1973); both it and Siberian *tundrensis* differ karyotypically from *araneus*, as well as from each other. *S. t. tundrensis* from Alaska has yet to be karyotyped.

The subspecies limits and designations of *tundrensis* in Eurasia are somewhat confused. Stroganov (1957) recognised *S. t. buxtoni* J. Allen, 1903; *S. t. borealis* Kastschenko, 1905; *S. t. baikalensis* Ognev, 1913; *S. t. petschorae* Ognev, 1921; *S. t. schnitnikovi* Ognev, 1921; *S. t. sibiriensis* Ognev, 1921; and *S. t. transrypheus* Stroganov, 1956. Corbet (1978) recognized only two Palearctic subspecies, *borealis* and *transrypheus*, as well as a questionable third, *S. jenissejensis margarita* Fetisov, 1950, which was listed by Stroganov as a synonym of *sibiriensis*. Corbet's *borealis* included *baikalensis, petschorae*, and *sibiriensis* (referred to *S. daphaenodon* by Ellermann and Morrison-Scott, 1951), as well as *amasari* Ognev, 1921; *ultimus* Ognev, 1926; *jenissejensis* Dukelsky, 1930; *middendorfi* Ognev, 1933; and *irkutensis* Ognev, 1935 (except as noted, referred to *S. caecutiens* by Ellerman and Morrison-Scott, *op. cit.*) The latter three taxa were included in *sibiriensis* by Stroganov, who referred *amasari* to *baikalensis* and *ultimus* to *borealis*. Stroganov placed the type locality of *borealis* as Bogdanidy River, Taimyr Peninsula, below 71 degrees N latitude, whereas both Corbet and Ellerman and Morrison-Scott list it as Tomsk.

Corbet considered the holotype of *buxtoni* referable to *Sorex caecutiens* Laxmann, 1788. One of us (RSH) has examined the holotype, and concurs with Corbet; however, Corbet also commented that "one of the two paratypes in the BM(NH) is *S. daphaenodon* and the other *S. caecutiens*." We consider both of these specimens to be *S. caecutiens* but the type series, most of which is in the American Museum of Natural History (New York) includes both *caecutiens* and *tundrensis*. Gromov & Baranova (1981) listed without comment the subspecies *borealis, buxtoni, schnitnikovi*, and *transrypheus*. They also assigned *sanguinidens* G. Allen 1914, to *tundrensis*, although it is considered a subspecies of *Sorex daphaenodon* by both Corbet and Stroganov. An insular subspecies, *parvicaudatus*, has been described from Moneron Island, off the southwest end of Sakhalin Island (Okhotina, 1976).

The subspecies map presented here (Fig. 2) is based on our review of the literature. Collection sites shown by triangles are from Stroganov (1957), Dolgov (1967), Fedyk & Ivanitskaya (1972), Yudin, *et al.* (1976), and Sokolov & Orlov (1980) and subspecies boundaries are modified from the same sources. Localities from which specimens measured in this study were collected are indicated by circles. To which subspecies the specimens of *S. tundrensis* formerly given the name *buxtoni* should be assigned is uncertain, pending further study. We therefore designate them as "buxtoni" in Fig. 2, until their taxonomic status is resolved. The boundary between *baikalensis* and *sibiriensis* west of the tip of Lake Baikal is so placed as to include Kozlovsky's (1971) and Fedyk & Ivanitskaya's (1972) specimens in *sibiriensis*, even though two distinct karyotypes (NFa=48, 52) are included. On the basis of autosomal fundamental number differences, it appears that there may be at least two species of tundra shrews in Eurasia (see also Kral & Ivanitskaya, 1973); however assignment to separate species is premature at this time, pending a thorough review of all Eurasian populations.

There are Pleistocene fossil remains identified as those of the arctic shrew from Irvingtonian and Rancholabrean sites in North America (Kurten & Anderson, 1980, and references cited therein); there are, however, no records of fossil shrews identified as *S. tundrensis*. The Pleistocene range of *S. arcticus* lies entirely south of its present range (Fig. 1); the occurrences are associated with taiga, and are within the *Symbos-Cervalces* faunal complex of Martin & Neuner (1978). At the end of the Pleistocene, the arctic shrew invaded newly ice-free areas to the north and west of its Pleistocene range.

The tundra shrew probably had an East Asian/Beringian distribution during the Pleistocene (Hoffmann, 1981), advancing south and east as the ice retreated in North America (Youngman, 1975). Although Eurasian and North American populations of the tundra shrew have been separated at least since the flooding of the Bering Land Bridge, they do not appear to have diverged much morphologically. Therefore we conclude that both populations are conspecific, pending additional chromosome studies and acquisition of a larger sample of Eurasian specimens for further analysis.

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Specimens Examined

Abbreviations:

NMC — National Museum of Canada, Ottawa, Canada

USNM — National Museum of Natural History (Smithsonian), Washington, D.C

KU — University of Kansas, Museum of Natural History, Lawrence, Kansas

MGU — Moscow State University, Zoological Museum, Moscow, U.S.S.R.

Sorex arcticus arcticus

CANADA: Alberta: South Edmonton, USNM 69149, 69159, 69147, 69153, 69156, 69160, 69162, 69164, 69168, 69151.

Northwest Territory: Mackenzie District: Fort Rae, 40 mi S. Trout Rock, USNM 110049; Fort Rae, USNM 110062; Fort Norman, UNSM 134097; Fort Simpson, Mackenzie River, USNM 38826; Fort Resolution, Great Slave Lake, USNM 59634, 59630. Yukon: vicinity of Yukon Crossing, NMC 33419.

Sorex arcticus laricorum

USA: Michigan: Schoolcraft Co, Seney National Wildlife Refuge, T44N, R13W, Sec. 5. USNM 514194—5, 514199—201, 514205—7, 524490—1.

Minnesota: Sherburne Co, Elk River, KU 45296—303.

North Dakota: Ward Co, Velva, 9 mi S. of, KU 115917.

Sorex t. tundrensis

USA: Alaska: Eagle, mountains near, USNM 131000—3, 131007, 131011, 131023, 131028, 131032, 131034, 131036; St. Michael, USNM 99281—5, 99287—91; Yukon River, USNM 38825/6395; Kokwok River, 80 mi upstream, USNM 180562, 180565, 180567; Doonnochchogaweet Mts., USNM 180578; Kanuluk, USNM 201849—50; near Bethel, USNM 201878, 201886; Kilikmak Valley, Kilikmak Creek, headwaters of, USNM 505006, 505008, 505011, 505013; Anderson River, Arctic Circle, USNM 38393; Anderson River, Eskimo, USNM 38397, 38399, 38401, 38403, 38405, 38407—8; Arctic America, Peels River, USNM 38414; Good News Bay, USNM 224900, 224924; Kuskokwin River, east fork, USNM 242753; Savage River, USNM 244050; Stuyahok Landing, USNM 244772; Hooper Bay, USNM 244775—6; Sawtooth Mountains, USNM 245474, 245476—7; Driftwood, 200 mi SW Pt. Barrow, USNM 292982, 292984; Umiat, 1.5 mi W 0.75 mi N of, lat. 69,22,18N long. 152,8,10W, 370 ft, KU 43199—207, 43209—43218; Umiat, 0.9 mi W and 0.9 mi N of, lat. 69,22,53N long. 152,10,58W, 380 ft, KU 50414—5; Bettles, lat. 66,54N long. 151,34W 671 ft, KU 43225—6; Brooks Range, Gavia Lake, N. White Hills, lat. 69,35N long. 150,0W 460 ft, KU 50411—12.

CANADA: Northwest Territory: Horn Lake, 37 mi NW Ft. McPherson, NMC 33419.

Northwest Territory: Reindeer Station, Caribou Hills, NMC 19079—80; Tuktuk, NMC 24368; Reindeer Depot, lat. 68,42N, long. 134,11W, NMC 37335, 37340—37345; Tuktoyaktuk, NMC 24376—24379, 24383—24384, 24369, 24371, 24373—5; Chick Lake, lat. 65,52N long. 128,03W, NMC 42840.

Yukon: Old Crow, NMC 33695; Summit Lake, lat. 67,43N long. 136,29W NMC 37064—66; Chapman Lake, 20 mi S of, lat. 64,35N long. 138,23W NMC 29389; Firth River, 15 mi S of mouth of Joe Creek, lat. 68,49N long. 140,33W NMC 30297.

Sorex tundrensis baikalensis

USSR: RSFSR: Primorsk Kr., Nagezhdinsk Distr., Razdol'noe, KU 121366.

Sorex tundrensis borealis

USSR: RSFSR: Verkne Kolymsk, USNM 200774; Lower Anui River, USNM 200773; Chukotka, Palyavan River, MGU 88237, 88244, 88248, 88250, 88253, 88258—9, 88264—5, 88268—9, 88271—3, 88277—8, 88282, 88285, 88288—9, 88292, 88296, 88300—1, 88300—1, 88304—5, 88311, 88313.

Sorex tundrensis petschorae

USSR: RSFSR: Tyumensk Obl., Purovsk Distr., Samburg, KU 121364—5.

Sorex tundrensis schnitnikovi

USSR: RSFSR: Gorno-Altaisk Kr., Chagan-Burgazi Pass USNM 175429, 175431.

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Note added in proof: Since this paper was submitted, (Okhotina, Zool. Ž., 62: 409—417. 1983) has independently reached similar conclusions.

Zpc

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POKREWIEŃSTWA W OBRĘBIE HOLARKTYCZNEGO ZESPOŁU GATUNKÓW *SOREX ARCTICUS — SOREX TUNDRENSIS*

Streszczenie

Powszechnie w literaturze zalicza się populacje ryjówek północno-amerykańskie i eurazjatyckie do *Sorex arcticus*, a z Yukonu i Alaski do *S. tundrensis*. Wyniki analizy morfometrycznej trzech populacji (Ryc. 1, 2, 3) wskazują, że eurazjatyckie rypówki są bardziej zbliżone do *tundrensis* niż do *arcticus* (Tabela 1) i są one zaliczane do tego taksonu. Podstawowa liczba autosomów (NFa=34) także różni się od liczby autosomów w eurazjatyckich populacjach *tundrensis* (NF=52, 56; NFa=48, 52); niestety północno-amerykańskie *tundrensis* nie mają określonego kariotypu. Autorzy przytaczają w pracy mapę rozmieszczenia eurazjatyckich podgatunków (Ryc. 2). Analiza chromosomów okazów odnoszonych do *S. t. sibirensis* wskazuje, że są w tym obszarze prawdopodobnie 2 odrębne gatunki ryjówek, lecz zmiany nazewnictwa byłyby jeszcze przedwczesne a sprawa wymaga dalszych badań.