A C T A   T H E R I O L O G I C A

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Chromosomes of Siberian Shrews

[With 5 Tables & 16 Figs.]

A description is given of the karyotypes of *Sorex araneus, S. arcticus, S. daphaenodon, S. caecutiens, S. centralis* and *S. minutus* from Central Siberia (basin of the River Ob). It was found that in the Altay Autonomous District a form of *S. araneus* occurs which is cytologically different from the race *B*. Polymorphism of pairs of 4, 7 and 8 chromosomes is present in different Central Siberian populations of this species. The diploid number of chromosomes in *S. daphaenodon* $2N = 27$ (♂) and in *S. articus* $2N = 33$ (♂). There is an identical set of sex chromosomes *XX/XYY* in all these species. *Sorex caecutiens, S. centralis* and *S. minutus* have 42 chromosomes and sex chromosomes *XX/XY*. The autosomes of these species are, however, morphologically differentiated. Γhe classification of Holarctic shrews is discussed, taking into consideration cytogenetic data.

1. INTRODUCTION

Insectivora, one of the oldest groups of *Eutheria*, form the subject of many cytogenetic studies. Among *Soricidae* the species which has proved the most interesting, and simultaneously the best known from the cytogenetic aspect, is the common shrew *(Sorex araneus)*, in which multiple sex chromosomes — *XYY* were found to exist (Bovey, 1949; Sharman, 1956), and Robertsonian polymorphism of autosomes. It has so far been ascertained that polymorphic populations occur over the whole range of the species in Europe (Ford *et al.*, 1957; Ford & Hamerton, 1958, 1970; Meylan, 1964, 1965; Ford & Graham, 1964). Certain data suggest that there are also polymorphic populations on the eastern extreme of the range of *S. araneus* (Kozlovsky, 1970).

In addition to polymorphic shrews (race *B*) among which all populations are characterized by an identical number of chromosome arms ($NF=40$), it was found West European race *A* possessing $NF = 42$ (Meylan, 1964, 1965). It is likely that these two races are reproductively isolated, and in this connection Ott (1968) proposes a separate species name for cytological race *A*.

Among other Palaearctic species of the genus *Sorex* the following have been examined up to the present: *Sorex caecutiens*, *S. unguiculatus*, *S. shinto*, *S. centralis*, *S. minutus* and *S. minutissimus*. Monomorphic karyotypes were found in all these species (Halkka & Skarén, 1964; Meylan, 1965a; Takagi & Fujimaki, 1966, Skarén & Halkka, 1966, Fredga, 1968; Shimba & Itoh, 1969; Halkka *et al.*, 1970; Borgaonkar, 1969). In two Neoarctic species (*S. cinereus* and *S. fumeus*) an identical number of chromosomes — $2N=66$ were found (Meylan, 1968), whereas in *Sorex arcticus* it has been suggested that there are different karyotypes in individuals from the Old and New World (Meylan, 1968; Kozlovsky, 1971).

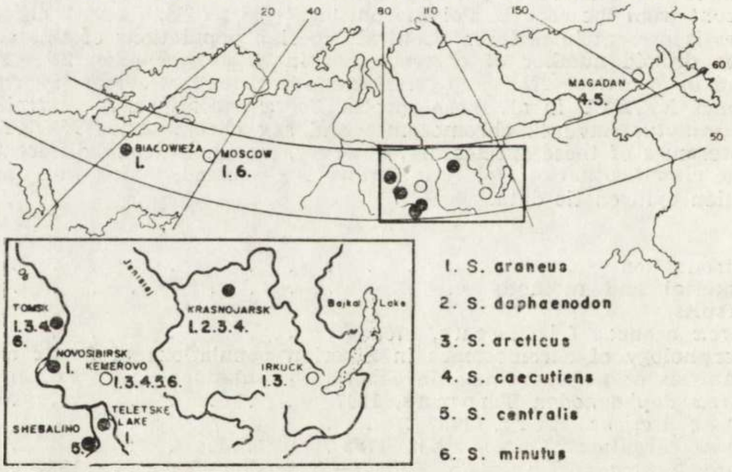

Fig. 1. Map showing distribution of shrews examined. Dark points indicate the places from which material used in the present study originated, lights spots — data from various studies by Orlov and Kozlovsky.

In these circumstances it would appear useful once again to undertake studies on the chromosomes of shrews originating from other localities. Karyotypes of species of the genus *Sorex* already described have therefore been presented in the present paper: *S. araneus*, *S. arcticus*, *S. caecutiens*, *S. centralis* (=*S. isodon*) and *S. minutus* and in addition the karyotype of *Sorex daphaenodon* has been described for the first time.

2. MATERIAL AND METHODS

The material used in the present study was collected during the course of the expedition made by the Laboratory of Population Genetics of the Institute of Cytology and Genetics SB AS USSR (Novosibirsk) from 1968—1971, and consisted of a total of 49 individuals of six species belonging to the genus *Sorex* (*S. araneus*, *S. arcticus*, *S. daphaenodon*, *S. caecutiens*, *S. centralis* and *S. minutus*) obtained from Central Siberia: Krasnojarsk region, Tomsk region, Altay Autonomous District (vicinity Shebalino and Teletske Lake) and from the Novosibirsk district. The number of animals used for the study, their sex and place in which they were caught are given in Table 1, and the capture site indicated on a map (Fig. 1).

Individuals caught in the Białowieża National Park (Poland), also during the period from 1968—1971, were used for comparisons of karyotype morphology of *Sorex araneus* from Europe and Asia.

Table 1

Specimens examined.

Species	No. of shrews ♂♂	♀♀	Locality
Sorex araneus	1	—	Boguchan, Right river of Chuna (Krasnojarsk region).
	11	4	Bakchar (Tomsk region).
	1	1	Teletske Lake (Altay Autonomous District).
	10	4	Academgorodok (Novosibirsk region).
Sorex articus	1	—	Boguchan
	1	—	Bakchar
Sorex daphaenodon	1	—	Boguchan
Sorex caecutiens	1	1	Boguchan
	6	2	Bakchar
Sorex centralis	2	1	Shebalino region (Altay Autonomus Distr.).
Sorex minutus	1	—	Bakchar

Chromosome preparations were made from bone marrow, using colchicine injections (1 ml of 0.5% water solution) and hypotonic shock (0.9% solution of sodium citrate for 45 min at a temperature of 37°). The preparations were stained with Giemza stain (Azur-Eosin). The skins and skulls of the Siberian individuals used for the chromosome studies are kept in the collection of the Laboratory of Population Genetics at Novosibirsk. Measurements of the area of chromosomes were made using a planameter (Pl) 1 — PZO — Warszawa).

3. RESULTS

3.1. *Sorex araneus* Linnaeus, 1758

Linear measurements of chromosome length commonly used in cytogenetic studies are burdened with considerable error, due chiefly to the different degree of contraction of chromosomes of different metaphasal plates. On this account we used measurements of the area of chromosomes, results (Table 2 and 3) being given as relative values, in percentages of the female's haploidal set. Calculation of arm ratio of biarmed chromosomes (Table 2) was also based on measurements of the area of arms.

These results were compared with data for Białowieża (Table 2 and 3). As stated by Ford & Hamerton (1970) the morphology of all nine pairs of autosomes in *S. araneus* from the Białowieża population is identical with other West European populations (England and Switzerland) of the chromosome race *B* of *Sorex araneus* (Fig. 3, Plate III).

3.1.1. Morphology of chromosomes in Siberian populations of *Sorex araneus*

Differences in the average areas of different pairs of chromosomes between the study populations are fairly large, being greater in the group of large than small chromosomes. For instance the extreme values

Table 2

Average area and arm ratio of biarmed chromosomes of *Sorex araneus*.

No.	Biało-wieża	Novosi-birsk	Tomsk	Krasno-jarsk	Teletske Lake	Biało-wieża	Novosi-birsk	Tomsk	Krasno-jarsk	Teletske Lake
	Relative area of chromosomes					Arm ratio				
1	21.5	25.9	23.2	22.9	22.5	1.2	1.1	1.1	1.2	1.2
2	16.8	19.5	17.2	18.7	19.8	1.8	1.7	1.7	1.7	1.6
3	12.3	10.9	10.3	11.5	11.8	1.1	1.2	1.2	1.1	1.2
4	11.0	11.2	11.1	11.0	10.9	1.1	1.2	1.2	1.2	1.3
5	*9.4*	*8.7*	*9.3*	*9.2*	*12.3*	*2.5*	*2.1*	*2.0*	*2.2*	*1.2*
6	9.1	8.9	8.2	8.6	—	2.0	1.8	1.8	1.9	—
7	8.3	7.5	6.8	—	7.1	1.2	1.0	1.2	—	1.1
8	7.8	5.0	5.7	—	—	1.0	1.4	1.2	—	—
9	3.6	2.2	3.0	2.9	3.0	1.2	1.2	1.4	1.3	1.4
X	18.4	20.8	19.9	19.6	21.1	1.1	1.3	1.2	1.2	1.3
Y_1	1.6	2.2	2.9	2.0	2.5	—	—	—	—	—
Y_2	9.9	10.9	11.8	11.4	11.7	33.5	29.7	22.2	27.4	30.4

of average areas of the two largest pairs of chromosomes (No. 1 and 2) between different populations are greater than 3 units, the lowest values occurring in the Białowieża population. On the other hand the average area of chromosomes No 3 in the Białowieża population is approximately 2 units greater than the area of chromosomes of the pair in the Novosibirsk and Tomsk populations, and about 1 unit greater than in the populations from Krasnojarsk and the Teletske Lake district. The chromosomes of pairs No. 4 and 6 are only slightly differentiated. Also the extreme values for average areas of chromosomes 5 in the Białowieża, Novosibirsk, Tomsk and Krasnojarsk populations differ by only 0.7 of a unit, whereas in the population from the Teletske Lake district the average area of chromosomes of this pair is greater by over 3 units. The extreme values of average areas of chromosomes in pairs 7 and 9 differ by over 1 unit, and in pair 8 by over 2. In these last three pairs the maximum values are represented in the Białowieża population (Table 2).

The positions of centromeres on biarmed chromosomes were defined by calculating the arm ratio. As can be seen from Table 2, the centromeres of chromosomes No. 1, 3 and 4 are located in the median region position (m). The ratio of the arms of these three metacentric pairs varies within limits of 1.1 — 1.2 (except for pair 4 in shrews from the Teletske Lake district, in which the ratio is 1.3). Chromosomes 4 in the Novosibirsk population are represented by two metacentric or three heteromorphic elements. In the second case one of two acrocentrics, differing only slightly in dimensions (Table 3), has a distinctly shorter arm

Table 3
Average area of uniarmed chromosomes of *Sorex araneus* expressed as parts per cent of the total chromosome area of the female haploid set.

No.	Białowieża		Novosibirsk		Tomsk		Teletske Lake		Krasnojarsk	
4	—	—	3.5	A 3.7	—	—	—	—	3.1	A 3.3
6	—	—	—	—	—	—	2.7	C 3.5	A 3.3	3.1
7	3.3	A 3.3	3.2	A 3.4	3.2	A 3.5	—	—	3.3	B 3.4
8	2.8	A 3.1	2.9	A 3.0	—	—	2.6	B 3.0	2.7	B 3.1

A — Heterozygote (1 m+2 a). B — Twin-acrocentric morph. (4 a). C — Twin-acrocentric morph homologous to short arms of 5th and 6th pairs.

(cf. Fig. 4, Plate III). Position of the centromere in chromosomes of pair No. 5 which is the most differentiated. The arm ratio of the chromosomes of this pair in the Białowieża population is 2.5, the Krasnojarsk population 2.2, Novosibirsk 2.1 and Tomsk 2.0, whereas in the population from the Teletske Lake district it differs completely from the foregoing, being 1.2. Thus element 5 in the population from the latter district is metacentric (*m*), and in the others submetacentric (*sm*).

Four acrocentrics are homologous to pair 6 in the Teletske Lake district population (Fig. 7 and 8, Plate IV), the average areas of these four twin elements being 2.7 and 3.5 (Table 3). In the other populations, however, chromosomes No. 6 are submetacentric (*sm*) with an arm ratio of 1.8 — 2.0 (Table 2) (in Krasnojarsk population this pair forms trivalent).

It is clear from these comparisons that chromosomes of pairs 5 and 6 in the Teletske Lake district population are not homological with chromosomes 5 and 6 in the other populations. The slight differences in the areas of acrocentrics No. 6 in the population from Teletske Lake district cannot, as the result of centric fusion, form a submetacentric element similar to chromosomes 6 in the other populations. It may therefore be assumed that metacentrics 5 in the population from the Teletske Lake district is formed of homologues of the longer arms of elements 5 and 6 and the acrocentrics No. 6 in this population are homologues of the short arms of elements 5 and 6 in the other populations (Fig. 2).

Metacentric chromosomes with an arm ratio of 1.0 — 1.2, or heteromorphic trivalents form pair No. 7, and it is only in the Krasnojarsk population that this pair is represented by 4 uniarmed elements of similar dimensions (Table 3).

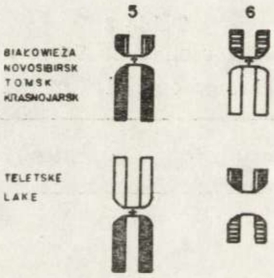

Fig. 2. Diagram representing homology of arms of chromosomes — pairs No 5 and 6 in the study populations of *Sorex araneus*.

Metacentrics 8 have an arm ratio of 1.0 — 1.4. In the Novosibirsk and Białowieża populations this pair may be represented by three heteromorphic elements, and in individuals from the populations of Krasnojarsk and Teletske Lake district twin-acrocentric homologues with very similar areas occur (Table 3). In all populations elements 9 are formed by metacentric chromosomes with an arm ratio from 1.2 to 1.4 (Table 2). The *X* chromosome is metacentric in all populations, with an arm ratio 1.1 — 1.3, but the arm ratio for subtelocentric Y_2 chromosome is from 22.2 (Tomsk) to 33.5 (Białowieża) (Table 2). These differences are due to the different degree of contraction of arms, since as shown by Sasaki's studies (1960), short arms undergo only a minimum degree of shortening.

3.1.2. Analysis of polymorphism in Siberian populations of *Sorex araneus*

With the exception of 2 shrews from the Teletske Lake district, in which we found incomplete homology of pairs, it was established that in the other Siberian populations polymorphism applies to pairs 4, 6, 7 and 8. It was only possible to analyse elements 3 and 4 on the basis of karyotypes, on account of the difficulty in distinguishing between them, but the heterozygotes 7 and 8, can be comparatively easily differentiated by comparison in good quality preparations (Ford & Hamerton, 1970). In this case also analysis was based only on microscopic observations. When the quality of the preparations was poorer and/or one of the pairs was a twin-acrocentric homozygote, analysis was made on the basis of karyotypes drawn up from photographs.

Table 4

Analysis of chromosome polymorphis in four Siberian population of *Sorex araneus*.

Locality	$2Na$	Pair 4	6	7	8	No. of shrews ♂♂	♀♀	Total
Tomsk	18	+	+	+	+	10	4	
	19	+	+	H	+	1	—	15
Novosibirsk	18	+	+	+	+	5	2	
	19	H	+	+	+	1	2	
	19	+	+	H	+	1	—	
	19	+	+	+	H	2	—	
	20	+	+	+	A	1	—	14
Krasnojarsk	23	+	H	A	A	1	—	1
Teletske Lake	22	+	A*	+	A	1	1	2

+=homozygous metacentric, H= heterozygous, A=homozygous acrocentric.
A* = 4 acrocentrics homologous to short arms of 5th and 6th pairs.

Collection of single karyotypes from Krasnojarsk and the Teletske Lake district did not permit of analysing the polymorphism of these populations. It was only possible to record that the single male from Krasnojarsk had $2N=26$, with ten acrocentric chromosomes forming twin acrocentric morphs of pairs 7 and 8, and trivalent of pair 6. Two individuals from the Teletske Lake district had 8 acrocentric autosomes $2N=24/25$. These autosomes are homologous to pair No. 8 and the short arms of pairs 5 and 6 (Figs 7 and 8, Plate IV).

In the Tomsk population we found a very high percentage of matecentric morphs. Out of the 15 animals examined in 14 all the autosomes were biarmed ($2Na=18$ — Fig. 6, Plate IV), and only one male was a heterozygote 7 ($2Na=19$ — Fig. 5, Plate III).

The Novosibirsk population, where the variations in number of autosomes comes within limits of 18 — 20, is far more differentiated. Five cytologically different morphs were found. Polymorphism applies to one only of three pairs of autosomes (Table 4).

3.2. *Sorex daphaenodon* Thomas, 1907

In the present study a description is given of the chromosomes of one male *S. daphaenodon* from the Krasnojarsk region. On the basis of the 78 metaphase plates examined the modal number of chromosomes was established as $2N=27$ (Fig. 9, Plate V), and this number was found in 58 plates (Table 5). The number of arms of chromosomes $NF=46$.

Sex chromosomes of males, as in case of *Sorex araneus*, form a trivalent XY_1Y_2. The X chromosome is a metacentric element similar in size to the three largest pairs of autosomes. The Y_1 chromosome is a small acrocentric, similar in length to that of the last pair of acrocentric autosomes. The Y_2 is a subtelocentric homologous to the longer arm of X chromosome.

Table 5

Chromosome counts in four species examined.

Species	n	⩽25	26	27	28	29	30	31	32	33	34	⩽39	40	41	42	43	Σ
S. daphaenodon	1	15	5	58													78
S. arcticus	2	3	1	1	6	3	7	5	33	8	1						68
S. caecutiens	10											15	5	17	57	2	96
S. centralis	3											6	5	7	40	—	58

The autosomes of *S. daphaenodon* were divided into three groups. The first group contains 5 pairs of large biarmed chromosomes, among which three pairs (1 — 3) are distinctly larger. The centromeres of these chromosomes lie at a distance of about $^1/_3$ of the length of the chromosomes. Pair 4 is submetacentric, pair. No. 5 consists of chromosomes with median centromeres. The second group is formed by four pair (No. 6—9) of small biarmed chromosomes not differing in length. The third group consists of three pairs of telocentric chromosomes of gradually decreasing dimensions. Satellites occur on the chromosomes of pair 10. On some of the plates they can be observed in both chromosomes (Fig. 10, Plate V), on other plates satellites are visible in one chromosome only (Figs. 9 and 11, Plate V).

3.3. *Sorex arcticus* Kerr, 1792

Studies ware made of the chromosomes of two males of *S. arcticus* from Tomsk and Krasnojarsk (Fig. 1). Microscopic analysis revealed a modal number of chromosomes equal to 32 in both individuals (Table 5). Analysis of karyotypes showed that the metaphase plates with 32 chromosomes are monosomic. In the series of large subtelocentrics there is one odd chromosome (No. 6), this being found in six karyotypes (Fig. 12, Plate VI). Only 8 plates were found possessing 33 chromosomes, among which there were six large pairs of submetacentrics (Fig. 13, Plate VI). $NF=56$.

In males the sex chromosomes form a trivalent (XY_1Y_2) in exactly the same way as in *Sorex araneus* and *S. daphaenodon*. The X chromosome is distinctly longer than the first pair of autosomes and has a median centromere. The Y_1 is an acrocentric similar in dimensions to the penultimate pair of acrocentric autosomes. The Y_2 chromosome is a subtelocentric with a distinctly marked short arm. In respect of length this chromosome corresponds to the longer arm of X chromosome.

The autosomes of *Sorex arcticus* consist of 11 pairs of biarmed and four pairs of uniarmed chromosomes of gradually decreasing dimensions. Among the biarmed chromosomes pairs No. 1, 2, 4, 5, 6, 7 and 8 are submetacentric (*sm*), the centromeres in chromosomes of pair No. 3 are located subtelocentrically (*st*), but medially (*m*) in chromosomes 9, 10 and 11. Pairs 12 — 15 are telocentric, and satellites were not found to be present in any of these pairs.

3.4. *Sorex caecutiens* Laxmann, 1788

The chromosomes of 10 individuals of *S. caecutiens* were examined. Analysis of 96 metaphase plates showed that the modal number of chromosomes $2N$ in this species was 42, this being found in 57 plates (Table 5), and sex chromosomes were of the XX/XY type. NF was 68.

Chromosomes 1, 2, 4, 5, 9 and 16 are metacentric (*m*), and of these pair 16 is far smaller in dimensions than the others. There are submetacentric chromosomes 3, 6, 7, 8 of large, and in pairs 14, 15, 18 and 20 of small elements. Chromosomes 20 have satellites (short arms). The remaining pairs (10, 11, 12, 13, 17 and 19) are telo- or subtelocentric. There are also satellites on the short arms of the chromosomes 19. The X chromosome is a telocentric far larger than the longest pair of telocentric autosomes, Y chromosome is subtelocentric, similar in dimensions to the 17th pair of autosomes (Fig. 14, Plate VII).

3.5. *Sorex centralis* Thomas, 1911 (=*S. isodon* Turov, 1924)

Examination was made of 58 metaphase plates obtained from three individuals of *S. centralis*, determining the diploid number of chromosomes $2N=42$ (Table 5). The set of sex chromosomes is the same as in *S. caecutiens;* X — a large telocentric, Y — small subtelocentric. $NF=$ $=68$.

In the karyotype of *S. centralis,* as in the case of *S. caecutiens,* there are 9 pairs of biarmed chromosomes, among which pairs 1, 2, 4 and 9 are metacentric. Of the remaining chromosomes those of pair 16 may be considered metacentric, although in some plates the chromosomes of this pair can be classified as submetacentric. Submetacentric chromosomes are represented by pairs 3, 6, 7, 14, 15, 18 and 19. There are satellites in the chromosomes 18. The chromosomes 10, 11, 12, 13, 17 and 20 are telo- and subtelocentric. (Fig. 15, Plate VII).

There are thus morphological differences between the karyotypes of *Sorex centralis* and *S. caecutiens.* In this last species pair 18 is submetacentric, in *S. centralis* metacentric, and in addition pair 20 in *S. caecutiens* is submetacentric and has a satellite, while in *S. centralis* it is distinctly telocentric, without a satellite, and is of far smaller dimensions than in the preceding species.

3.6. *Sorex minutus* Linnaeus, 1766

In addition examination was made of three metaphase plates of a male of *Sorex minutus* from the Tomsk region. In all three plates the diploid number was found to be 42, as was earlier found for this species (Meylan, 1965 a; Orlov & Alenin, 1968).

The karyotype of *S. minutus* consists of 5 large and one small pair (No. 16) of biarmed chromosomes and of 14 pairs of uniarmed chromosomes. The *X* chromosome is a large telocentric, *Y* chromosome a small telocentric (Fig. 16, Plate VIII).

4. DISCUSSION

The geographical range of *S. araneus* covers the whole of Europe except for Ireland, the Iberian Peninsula and islands in the Mediterranean. From the east a boundary is formed by the River Yenisei and Baikal Lake (Dolgov, 1967). Meylan (1964) found two cytological races on the western extreme of these animals' range; race *A* has $NF=$ $=42$, race $B — NF=40$. These races differ in respect of one tandem fusion and three pericentric inversions (Ford & Hamerton, 1970). Recently shrews were found in Sweden with karyotypes different from the above two races (Fredga, cit. after Ford & Hamerton, 1970). Also Orlov & Kozlovsky (1969) discovered in *Sorex araneus* from Kemerovo (Fig. 1) a karyotype differing from the karyotype of race *B* in respect of the pericentric inversion of pair 4. These authors also suggest that the short arms of pairs 4 and 7 are homologous to the four acrocentrics 7 in the Kemerovo population. It would seem that this is the same morph as that described in the present study from the Teletske Lake district. Orlov & Kozlovsky (1969) changed the numeration of pairs 4 and 5, 6 and 7, and consequently they do not coincide with our numeration, accepted after Ford & Hamerton (1970).

The areas of different chromosomes in *S. araneus* from the Siberian population studied differ both from each other and from the Białowieża population, but the arm ratio (except for pair 5 from Teletske Lake) differs very little. Thus differences in average areas of chromosomes are more due to differences in contraction than to aberration, and consequently it can be assumed that the karyotypes of *S. araneus* from the Novosibirsk, Tomsk and Krasnojarsk populations do not in principle differ from the karyotypes of European populations of *Sorex araneus* — race *B*.

Orlov & Kozlovsky (1969) found that the diploid number of chromosomes was invariably 24/25 in 22 of the individuals of *S. araneus* from Kemerovo which they examined. This same number was found in 2 individuals of *S. araneus* from the Teletske Lake district. It may be assumed that there is a persistent morph 24/25, differing from race *B*, in Siberia. Persistent morphs with different numbers of chromosomes, most often 20/21, also occur in different European shrew populations of race *B* (Meylan, 1964, 1965). A monomorphic population 20/21 was discovered in the Moscow area (Orlov & Kozlovsky, 1969), but this forms the only data available on the chromosomes of *S. araneus* from the centre of this species' range. In Siberian populations of *S. araneus* of race *B* polymorphism applies to pairs 4, 6, 7 and 8. There was a slightly larger amount of material available from two populations only (Novosibirsk and Tomsk), and in both of them we found a considerable predominance of metacentric homozygotes ($2Na=18$, $2N=20/21$). The range of $2N$ variation in these Siberian populations comes within limits of 20 — 23. Far higher numbers of chromosomes were found: 25 (♂), 27 (♀), 27 (♂) (Kozlovsky, 1970) in the eastern extreme of the range of *S. araneus* (Irkuck — Fig. 1). There was also one male from the Krasnojarsk area which had $2N=26$. It must be remembered that in the western extreme of the range of *S. araneus* — race *B* there are also large numbers of chromosomes — $2N$ up to 31 (Meylan, 1964).

The multiple sex chromosomes (type *XX/XYY*) form a separate problem. It has been suggested that this type of sex chromosomes in *Sorex araneus* was formed as the result of translocation between the original telocentric *X* chromosome and the telocentric autosome, homologue of Y_2. Autoradiographic studies have confirmed this (Fredga, 1970).

The presence in males of a set of XY_1Y_2 chromosomes was discovered in both chromosome races of *S. araneus* (Sharman, 1956; Meylan, 1964; *et al.*). Meylan (1968) suggested the presence of the trivalent of sex chromosomes and $2N=28/29$, with $NF=38$ in *Sorex arcticus* from Canada. Kozlovsky (1971) confirmed in Siberian material of *S. arcticus* that there is a trivalent of sex chromosomes in males (XYY) with different numbers of chromosomes: $2N=33$ (Kemerovo) and $2N=37$ (Irkuck) (Fig. 1), with $NF=52$ common to both populations. The trivalent of sex chromosomes described by Kozlovsky (1971) differs from the trivalent of *Sorex araneus;* biarmed Y_2 chromosome is also slightly different morphologically in the two populations. In the present study we have not confirmed these differences — trivalent XYY in *S. arcticus* in the Tomsk and Krasnojarsk populations is identical to that in *S. araneus*, and in addition $2N=33$ (in males) and $NF=56$ was found in both populations.

The considerable preponderance of monosomic metaphase plates in *Sorex arcticus* (cf. Table 5) is astonishing and difficult to explain.

The differing quality of the preparations makes it impossible to compare the karyotypes of this species from the Tomsk and Krasnojarsk populations with the karyotypes from the Kemerovo and Irkuck populations described by Kozlovsky (1971). Differences in $2N$ and NF suggest that there are structural differences between the karyotypes of *S. arcticus* from different Siberian populations. It may be possible to resolve this question on the basis of repeated studies of the chromosomes of *S. arcticus* from various other populations. On the other hand *Sorex arcticus* from Canada ($2N=28/29$ and $NF=38$, Melyan, 1968), differs considerably from the Siberian representatives of this species.

This same trivalent of sex chromosomes occurs in males of *Sorex daphaenodon*. The number of chromosomes $2N=27$ is relatively small and comes within the range of variation of $2N$ in *S. araneus*, but NF in *S. daphaenodon* is greater by 6 units than NF in *Sorex araneus* race B, being 46. A karyotype very similar to *S. daphaenodon* has been described by Kozlovsky (1971a) in *Sorex caucasicus:* $2N=25$ (♂), $NF=46$. A trivalent of sex chromosomes XY_1Y_2 also occurs in this species.

Multiple sex chromosomes among mammals are rare (cf. Fredga, 1970). Within *Insectivora* they occur only in the above-mentioned species of the genus *Sorex*, and in *Echinops telfairi* (Borgaonkar, 1967). There is therefore no doubt that the complex of multiple sex chromosomes in species of the genus *Sorex* has a common origin. They are characterized by the smallest number of chromosomes (20 — 37) among all the species of the genus *Sorex* examined up to the present. This is additional evidence of the close relationship between *Sorex araneus, S. daphaenodon,* *S. arcticus* and *S. caucasicus*, to which Kozlovsky (1971a) earlier drew attention.

The remaining species have sex chromosomes of the *XX/XY* type, and they are also characterized by higher $2N$ values. Two Neoarctic species, *Sorex fumeus* and *S. cinereus*, have $2N=66$, with $NF=98$ and 70 (Meylan, 1968). *Sorex cinereus* also occurs in Asia (Chukotka) (Hoffmann & Peterson, 1967; Yudin, 1969), but the chromosomes of this Asiatic form are not known. Among Eurasian species that possessing the greatest number of chromosomes is *Sorex alpinus* — $2N=58$ (Meylan, 1964). The diploid number 42 occurs in *S. caecutiens*, (Skarén & Halkka, 1966; Fredga 1968), *S. centralis* (=*S. isodon)* (Halkka & Skarén, 1964; Halkka *et al.* 1970), *S. unguiculatus* and *S. shinto* (Takagi & Fujimaki, 1966; Shimba & Itoh, 1969). The *NF* in these species is 68.

Very similar karyotypes were found in *Sorex vir* ($2N=42$, $NF=70$, Orlov & Kozlovsky, 1971) and in *S. minutus* ($2N=42$, $NF=56$, Meylan, 1965 a; Orlov & Alenin, 1968), whereas it was different in *Sorex minutus volnuchini* ($2N=40$, $NF=60$, Kozlovsky, 1971a). It is very likely that in *S. minutissimus* there are differentiated karyotypes $2N=38$ and 42, with *NF* about 70 (Halkka *et al.*, 1970; Orlov & Kozlovsky, 1971). *Sorex raddei* possesses a karyotype intermediate between these two groups — ($2N=36$, $NF=68$; Kozlovsky, 1971a).

Hoffmann (1971) suggests dividing Holarctic shrews into six groups. A common group would consist of all species possessing multiple sex chromosomes: *S. araneus, S. daphaenodon, S. arcticus* and *S. caucasicus*. This fact confirms the correctness of Hoffmann's classification (1971). In addition to these species, closely related from the cytological point of view, this group also included *S. centralis, S. unguiculatus* and *S. vir* with 42 chromosomes, *S.raddei* with $2N=36$ and *S. asper* and *S. roboratus* with unknown karyotypes. Karyological data suggest that this group should be divided into three subgroups:

1. *Sorex araneus* (both cytological races), *S. arcticus, S. daphaenodon* and *S. caucasicus* — shrews with sex chromosomes *XX/XYY*.
2. *S. centralis, S. unguiculatus* and *S. vir* — with 42 chromosomes.
3. *S. raddei* — with an intermediate karyotype $2N=36$.

Among the other shrews the chromosomes of *S. caecutiens* (group 2 — in Hoffmann's classification) are known — $2N=42$.

The karyotype of *S. caecutiens* is identical with the karyotype of *S. unguiculatus* (Fredga, 1968; Takagi & Fujimaki, 1966), but it is impossible to postulate the inclusion of this species with the 42-chromosome shrews of the preceding group on the basis of karyological comparisons only. Group 6 in Hoffmann's (1971) classification is formed from species belonging to the subgenus *Otiosorex* (Hoffmann & Peterson, 1967). Among these *S. cinereus* from North America has 66 chromosomes and $NF=70$ (Meylan, 1968), and thus only two pairs of biarmed chromosomes. As it is known that centric fusions played an important role in the evolution of the karyotypes of different species of the genus *Sorex* [1], it must be assumed that *Sorex cinereus* has the most primitive karyotype of all the shrew karyotype examined up to the present.

The review of fossil forms (Rapenning, 1967) permits of establishing that the strain from which contemporary *Soricidae* evolved appeared before the Oligocene, *Soricidae* were introduced from Eurasia to North America in the early Miocene, while the genus *Sorex* appeared in the late Pliocene. It may therefore be assumed that the karyotype of *S. cinereus* is similar to the karyotype of ancestral shrews from the end of the Pliocene and beginning of the Miocene, which occupied areas in the basin of the North Pacific. It will be interesting in the future examine the karyotypes of relict species from islands in the Bering Sea area (*Sorex jacksoni, S. pribilofensis* and *S. hydrodromus*).

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[1] This both applies to the polymorphism of *S. araneus* race *B* and explains the evolution of the karyotype of *S. raddei*.

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CHROMOSOMY SYBERYJSKICH RYJÓWEK

Streszczenie

W pracy opisano chromosomy sześciu gatunków ryjówek: *Sorex araneus, S. daphaenodon, S. arcticus, S. caecutiens, S. centralis, S. minutus* z pięciu miejscowości środkowej Syberii (Fig. 1: Tabela 1). Ryjówki aksamitne (*S. araneus*) z okolic Jeziora Teletskiego posiadają kariotypy różniące się morfologią chromosomów par No 5 i 6 od kariotypów *S. araneus* chromosomowej rasy *B.* Pary te są homologiczne dłuższym ramionom (para No 5) i krótszym ramionom (para No 6) tych dwu par w pozostałych populacjach (Fig. 2). W pozostałych populacjach zidentyfikowano kariotypy typowe dla *S. araneus* cytologicznej rasy *B,* identyczne z kariotypami tego gatunku z populacji białowieskiej (Fig. 3—8: Tablice III—IV). Populacje te są polimorficzne pod względem par No 4, 6, 7 i 8, z dużą przewagą metacentrycznych homozygot $2Na$=18 (Tabela 4).

U *Sorex daphaenodon* ustalono modalną liczbę chromosomów $2N$=27 (♂) (Fig. 9—11: Tablica V), natomiast u 2 samców *S. arcticus* modalna liczba $2N$=32 (monosomiczny kariotyp — Fig. 12; Tablica VI) a tylko w 8 przypadkach na 68 badanych płytek stwierdzono prawidłowy kariotyp — $2N$=33 (Fig. 13, Tablica VI: Tabela 5). Wszystkie te trzy gatunki posiadają morfologicznie identyczne chromosomy płci typu XX/XY_1Y_2.

U *Sorex caecutiens, S. centralis* i *S. minutus* potwierdzono diploidalną liczbę chromosomów $2N$=42 (Tabela 5), chromosomy płci typu *XX/XY*, autosomy tych gatunków są morfologicznie zróżnicowane (Fig. 14—16, Tablica VII—VIII). Prze-

dyskutowano klasyfikację holarktycznych ryjówek wprowadzoną przez Hoffmanna (1971). Biorąc pod uwagę dane kariologiczne zaproponowano podział 1-szej grupy w systemie Hoffmanna na trzy podgrupy:

1. Ryjówki z wielokrotnymi chromosomami płci i 2*N* 20—37 (*Sorex araneus, S. daphaenodon, S. arcticus* i *S. caucasicus*).
2. Ryjówki posiadające 42 chromosomy i chromosomy płci *XX*/*XY* (*S. unguiculatus, S. centralis i S. vir*).
3. *Sorex raddei* — z kariotypem pośrednim: 2*N*=36, *XX*/*XY*.

EXPLANATION OF PLATES III—VIII

Plate III

Fig. 3. Karyotype of male *Sorex araneus* in the Białowieża population 2*N* = 23, double heterozygote of pairs No 7 and 8.

Fig. 4. Karyotype of female *Sorex araneus* in the Novosibirsk population 2*N* = 21, heterozygote No 4.

Fig. 5. Karyotype of male *Sorex araneus* in the Tomsk population: heterozygote No 7.

Plate IV

Fig. 6. Karyotype of male *Sorex araneus* in the Tomsk population: metacentric homozygote — 2*N*=21.

Figs. 7 & 8. Karyotypes of male and female *Sorex araneus* from the Teletske Lake area, 2*N*=24/25. Pair No 5 is formed by two metacentric chromosomes (*m*), eight acrocentric autosomes arranged in pairs No 6 and 8.

Plate V

Fig. 9. Karyotype of male *Sorex daphaenodon*, 2*N*=27.

Figs. 10 & 11. Metaphase plates of *Sorex daphaenodon*, pair No 10 indicated by arrows.

Plate VI

Fig. 12. Karyotype of male *Sorex arcticus*, 2*N*=32, monosomy of pair 6.

Fig. 13. Karyotype of male *Sorex arcticus*, 2*N*=33.

Plate VII

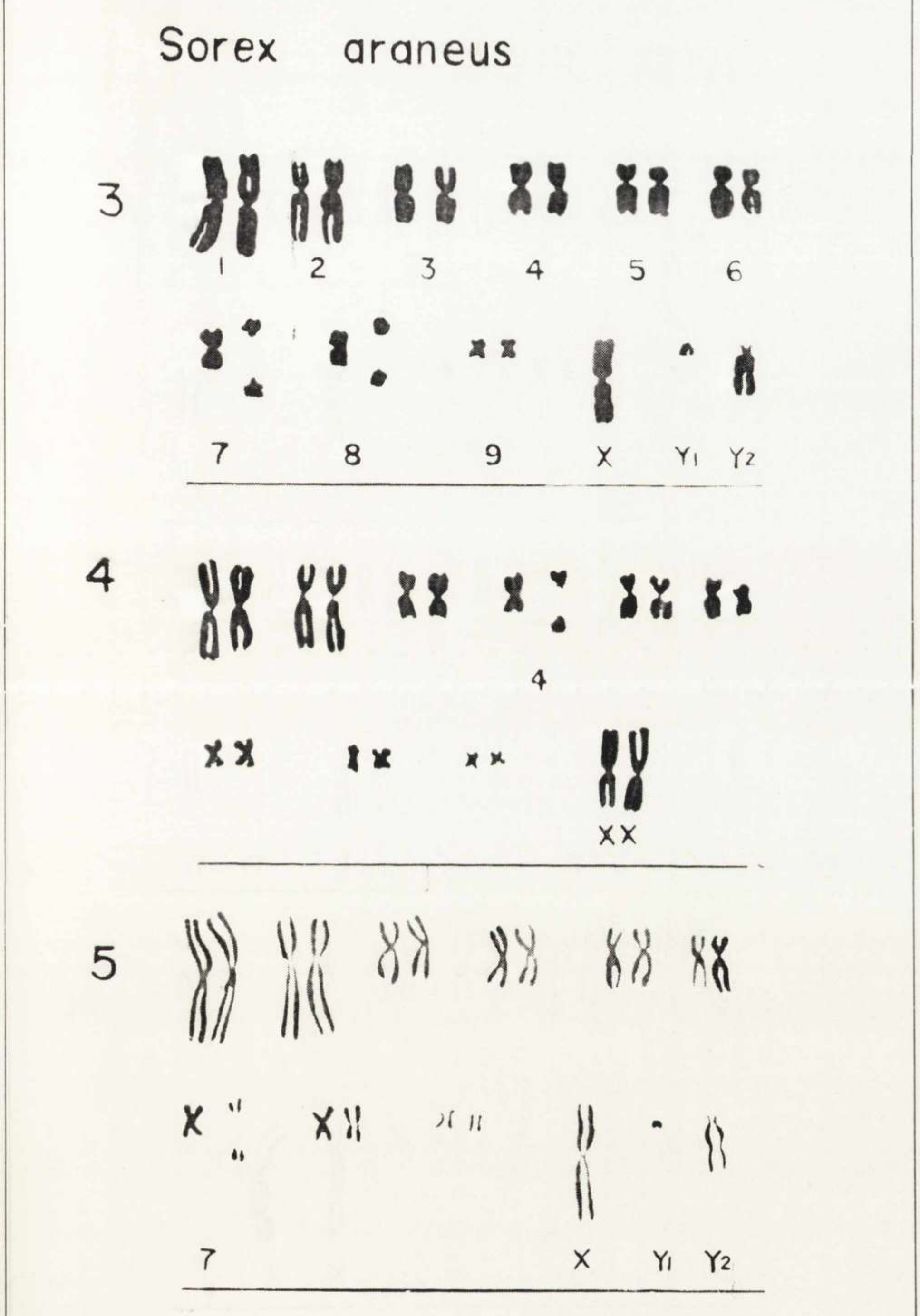
Fig. 14. Karyotype of male *Sorex caecutiens*, 2*N*=42.

Fig. 15. Karyotype of female *Sorex centralis*, 2*N*=42.

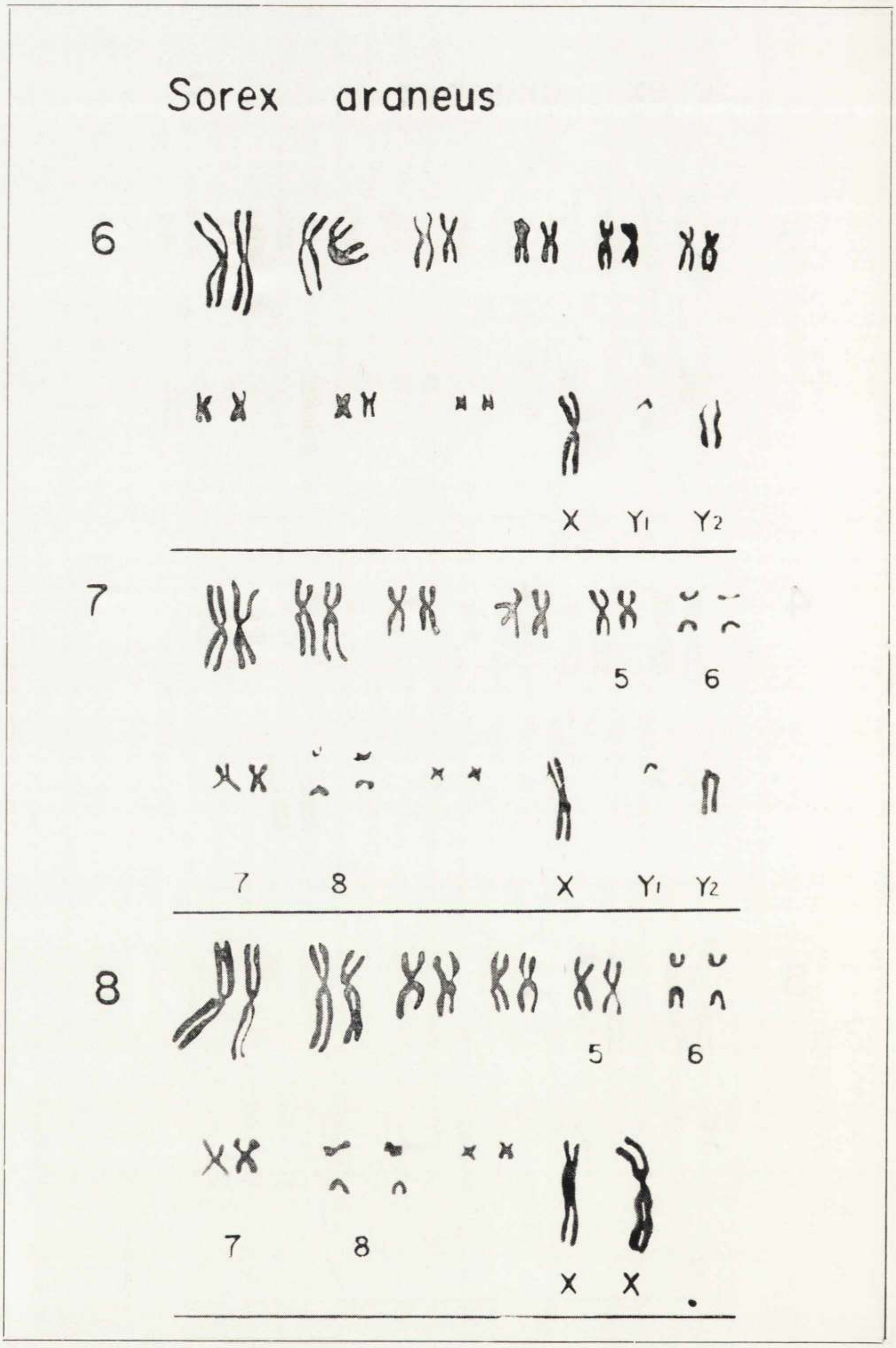
Plate VIII

Fig. 16. Karyotype of male *Sorex minutus*, 2*N*=42.

PLATES III—VIII



S. Fedyk & E. Yu. Ivanitskaya auctores phot.



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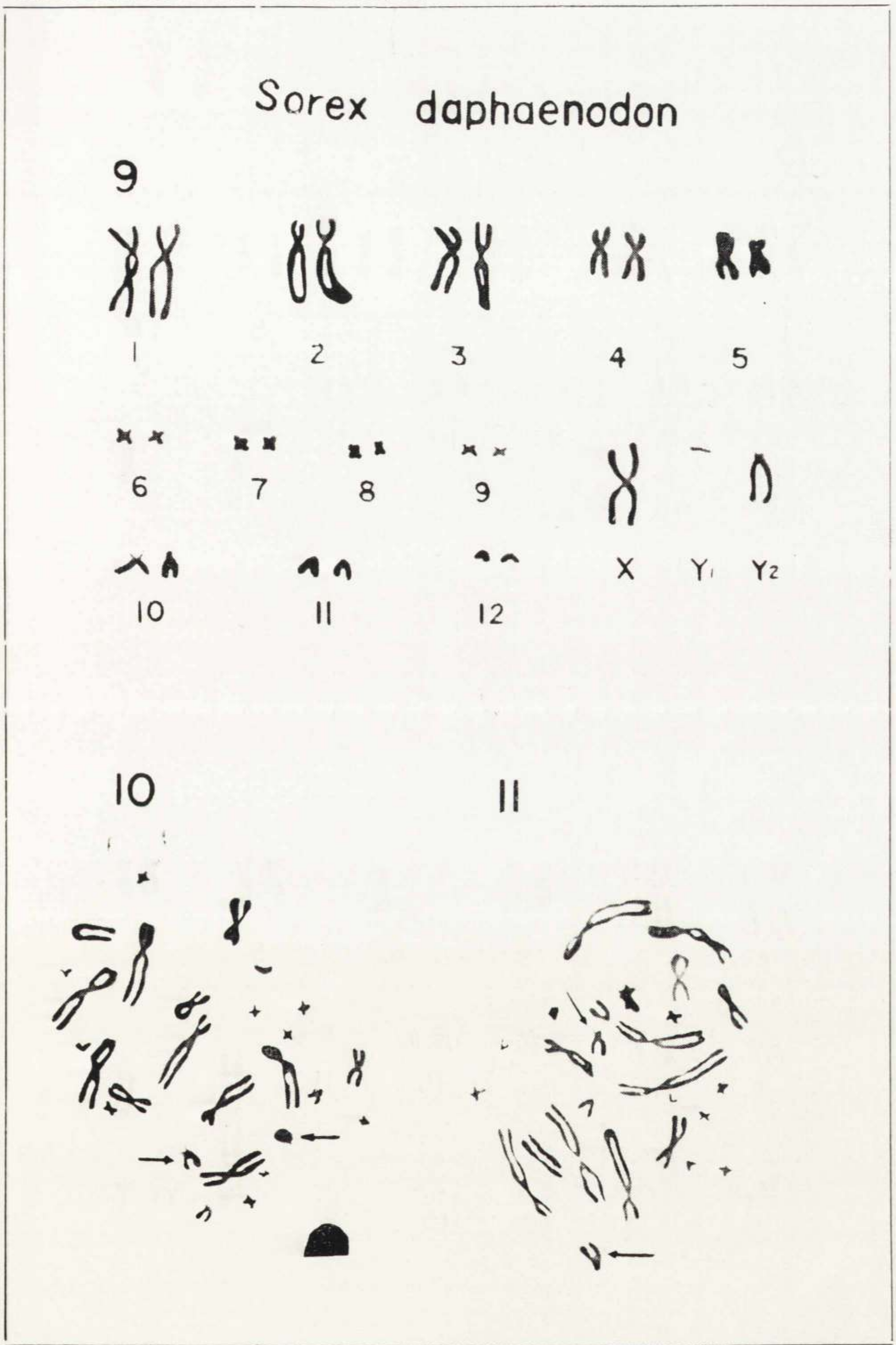

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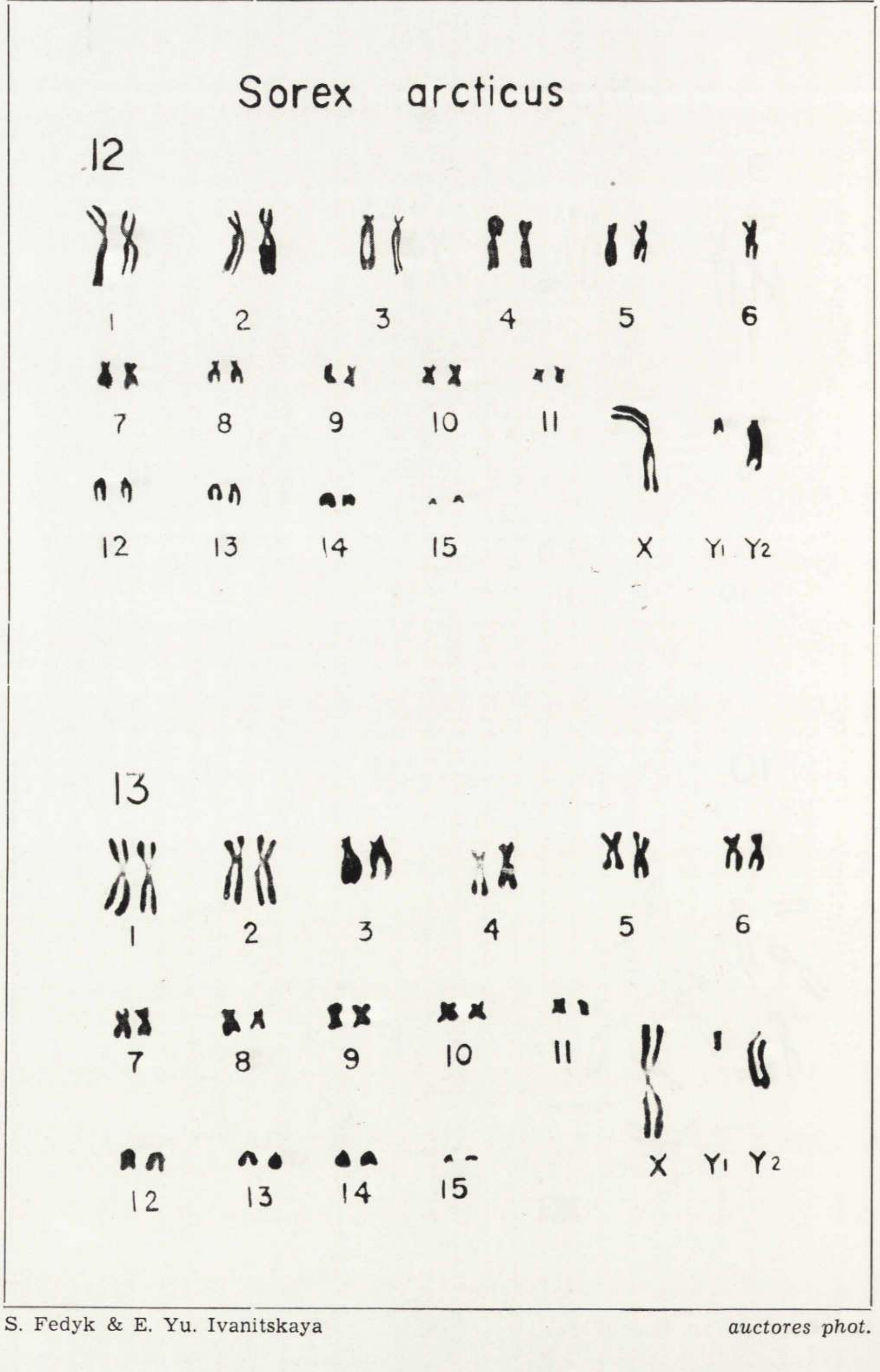

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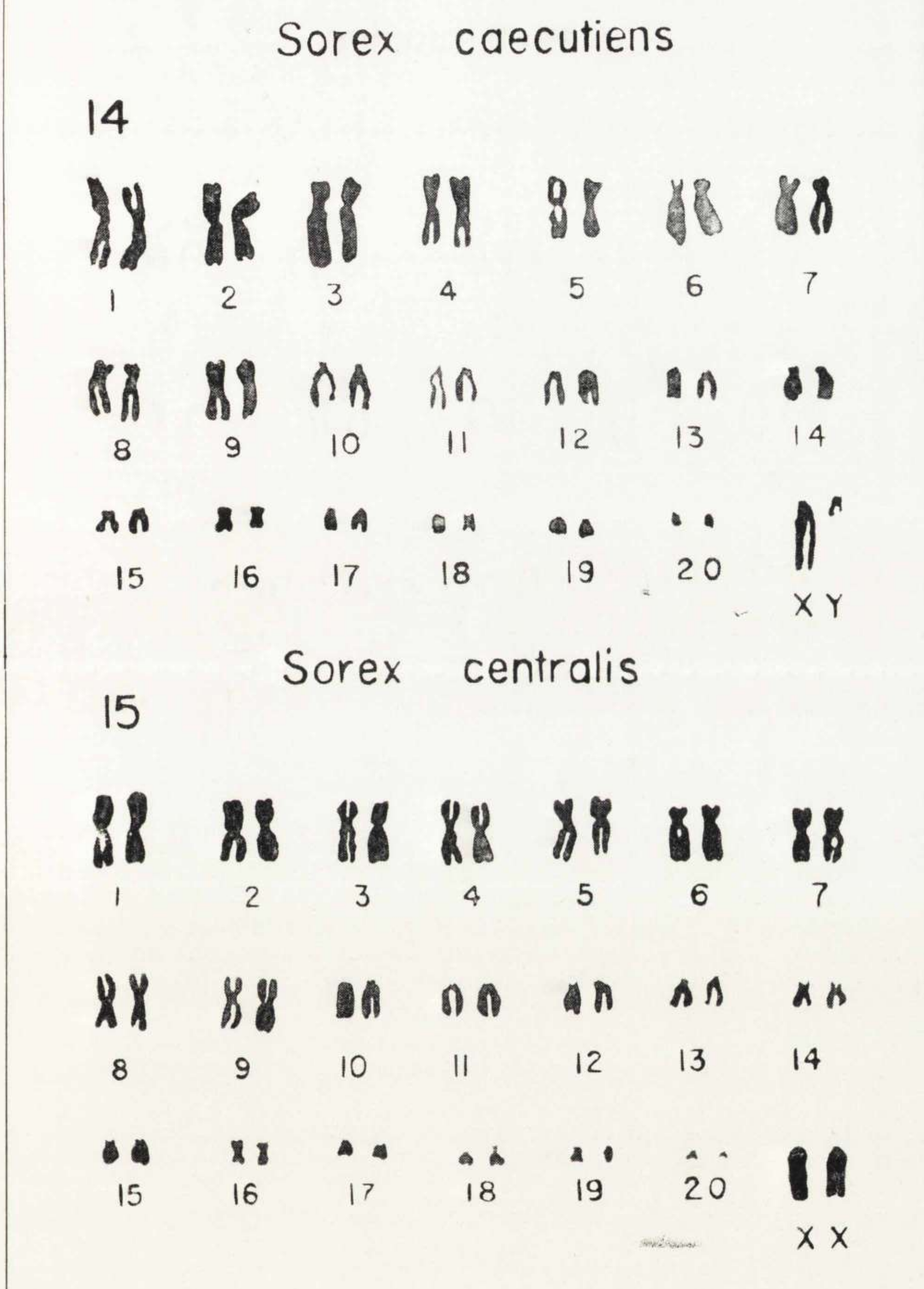
Sorex caecutiens
14
1 2 3 4 5 6 7
8 9 10 11 12 13 14
15 16 17 18 19 20 XY
Sorex centralis
15
1 2 3 4 5 6 7
8 9 10 11 12 13 14
15 16 17 18 19 20 XX

Sorex minutus