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On morphologically similar species in the genus *Sicista* (Rodentia, Dipodoidea)

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Abstract. Morphologically similar species of the genus *Sicista* occurring within the boundaries of the former Soviet Union are reviewed. A narrow species concept is applied, principally based on the results of extensive chromosomal studies. Three species complexes and eight species are recognized. Some new diagnostic characters in the localization of the NOR and heterochromatin as well as in the size and shape of the sperm head are described.

Key words. Karyotypes, NOR, heterochromatin localization, sperm morphology, systematics, sibling species, *Sicista*, Palaearctica, FSU.

Introduction

Advances in karyology during the last three decades, including the analysis of chromosomal complements, have been instrumental in demonstrating that taxa regarded as “broad polytypic species” are in fact composed of several more narrowly defined species. As a result, the number of recognized species in taxonomically rather well-studied groups such as mammals is increasing, and we appear to return to the narrow species concept (Vorontsov 1980).

The current view of the systematics of the Palaearctic genus *Sicista*, whose range stretches from the Scandinavian Peninsula to Sakhalin and from Lower Pechora to China and Kashmir, also shows this tendency.

For a long time the taxonomy of this genus was based on the comparative analysis of body dimensions, colour patterns, and the morphology of the external reproductive organs. At this stage the taxonomy of *Sicista* was contradictory and disagreement existed as to the number of species in this genus (Vinogradov 1925; Ognev 1948; Ellerman & Morrison-Scott 1951; Gromov et al. 1963; Kuzjakin 1963; Bobrinski et al. 1965).

More recently the application of cytogenetical techniques has significantly increased the number of recognized taxa. 12 species of birch mice are now distinguished on the territory of the Former Soviet Union only (Sokolov et al. 1981, 1982, 1986a, b, 1989; Sokolov & Baskevich 1988, 1992), and have provisionally been listed in the world checklist of mammals (Holden 1993). Most of the species are morphologically very similar, although their morphology has not yet been documented in detail. The aim of this paper is to review these morphologically similar species of *Sicista*, to evaluate their similarities and differences, and to introduce some new diagnostic characters.

Material and methods

The material studied includes the specimens of birch mice mentioned in our previous articles (Sokolov et al. 1981, 1986a, b, 1989; Sokolov & Baskevich 1988, 1992). Additional material

includes specimens of *S. strandi* from Cis-Caucasus, Stavropol district, Sergievka area (2 ♂, 1 ♀), from North Ossetia, Mountain Zeka area (2 ♂, 1 ♀), specimens of *S. kluchorica* from Azau station in Kabarda-Balkaria (2 ♂), and of *S. caucasica* (4 ♂) from the village Archyz in the Stavropol district.

Specimens used for chromosomal banding were collected at the following localities: *S. betulina* (2 ♂) from the mountain Goverla area in the Carpathians; *S. strandi* (2 ♂, ♀) from the Stavropol district, Sergievka area; *S. severtzovi* (♀) from the Kursk region, Central Chernozem Reserve; *S. subtilis nordmanni* (2 ♂) from the Donets region.

Preparations of mitotic chromosomes were obtained by means of the general air-drying technique. The C-banding staining procedure was carried out according to Sumner (1972) and NOR-banding according to the method of Howell & Black (1980).

Sperm measurements were taken with the aid of an ocular micrometer at a magnification of x1500 from air-dried and Giemsa stained smears of epididymal sperm. Maximum length and width were measured. 20 cells of 1 to 2 animals of each species were measured.

Sperm measurements were taken from specimens of birch mice collected at following localities: *S. betulina* — Noginsk area, Moscow region and mountain Goverla area in the Carpathians; *S. strandi* — Kursk region and Kabarda-Balkaria, Haimashi; *S. severtzovi* — Kursk area; *S. subtilis nordmanni* — Donets and Cherson regions; *S. caucasica* — village Archyz area in the Stavropol district; *S. kluchorica* — upper reaches of the Kluchor; *S. kazbegica* — Northern Georgia, Kazbeg district, Suatisi gap and Northern Ossetia, North Ossetian Reserve; *S. armenica* — Minor Caucasus, North-Eastern Armenia.

Results and discussion

Based on detailed taxonomical analyses of birch mice from the territory of the Former Soviet Union (Sokolov et al. 1981, 1982, 1986a, b, 1987, 1989; Baskevich 1988; Sokolov & Baskevich 1988, 1992), we conclude that morphologically similar birch mice previously recognized as polytypic species (*S. betulina*, *S. subtilis*) or regarded as taxonomically complicated unit (*S. caucasica*) form three species complexes containing two to four species each:

- 1) *S. betulina* (Pallas, 1778), *S. strandi* (Formozov, 1931);
- 2) *S. subtilis* (Pallas, 1773), *S. severtzovi* (Ognev, 1935);
- 3) *S. caucasica* Vinogradov, 1925, *S. kluchorica* Sokolov, Baskevich & Kovalskaja, 1981, *S. kazbegica* Sokolov, Baskevich & Kovalskaja, 1986, *S. armenica* Sokolov & Baskevich, 1988.

It has been shown by Sokolov et al. (1981, 1982, 1986a, b, 1987, 1989), Baskevich (1988), and Sokolov & Baskevich (1988, 1992) that the forms of each complex are very similar in their external characters such as pelage colour pattern or male reproductive tract morphology. For example, all specimens of the first species group have been considered earlier as part of the polytypic species *S. betulina* (Vinogradov 1937; Ognev 1948, and others). (The form "*pseudonapaea*", whose species rank has been suggested earlier, was excluded from consideration due to the presence of reliable morphological peculiarities; see Strautman 1949, and Sokolov et al. 1982).

S. betulina and *S. strandi* are characterized by the presence of a longitudinal black stripe along the back from the head to the base of the tail and features of the glans penis; the main diagnostic characters are two great horn thorns jutting out of the glottis and a special type of comb formed of small horn thorns covering the terminal part of the glans penis ventrally (Vinogradov 1925, 1937; Ognev 1948; Sokolov et al. 1989).

The species of the morphologically similar complex *S. subtilis* and *S. severtzovi* are also characterized by a common colouration (presence of an intensive central black band along the back from the head to the base of the tail and two lateral, less conspicuous dark bands) and by a similar structure of the outer genitals (glans penis with a large number of small horn thorns covering the surface of the organ and one great horn thorn jutting out of the glottis; see Vinogradov 1925, 1937; Ognev 1948; Sokolov et al. 1986a). Moreover, the bacula and sperm heads of *S. subtilis* and *S. severtzovi* are similar in shape and size (Sokolov et al. 1986a; see also table 2).

The monochromatic birch mice of the Caucasus, *S. caucasica*, *S. kluchorica*, *S. kazbegica* and *S. armenica* also share colouration (no longitudinal black stripe) and the similar structure of the external genitalia (glans penis without great horn thorns jutting out of the glottis, small horn thorns covering the surface of the glans penis only: Vinogradov 1925; Sokolov et al. 1981, 1986b; Sokolov & Baskevich 1988).

Within the groups mentioned, chromosomes are the main characters by which the species can be diagnosed, but other character sets (such as craniodental and molecular data) have not been carefully studied. However, in a few instances details of the fur colouration may allow to distinguish between representatives of *S. severtzovi* and *S. subtilis* (Sokolov et al. 1986a), and between *S. caucasica* and *S. kluchorica* (Sokolov et al. 1981).

Karyotype studies may often furnish an answer to the question whether a reproductive isolation between the taxa under study may exist or not, which is particularly important when comparing allopatric populations or forms for which hybridization experiments are impossible (Orlov 1974). In this respect the comparative cytogenetics of birch mice has greatly contributed to the systematics of the genus (Sokolov et al. 1981, 1982, 1986a, b, 1987, 1989; Baskevich 1988; Sokolov & Baskevich 1988, 1992).

The chromosomal data from morphologically similar species of birch mice are summarized in table 1.

Specimens of northern birch mice belonging to the 32 chromosome form have been recorded from 17 localities covering a wide range from dense forests of eastern Poland and the Carpathians to western Transbaikalia (Walknowska 1969; Vorontsov & Malygina 1973; Sokolov et al. 1989). Birch mice with 44 chromosomes are known from the Central Chernozem Reserve (Kursk district) (Sokolov et al. 1989), the Cis-Caucasus (Stavropol region) (own data) and from four localities of the northern slopes of the Great Caucasus (Sokolov et al. 1989 and own data). According to chromosome studies the taxa *betulina*, *taigica* and *montana* belong to the 32 chromosome form and *strandii* to the 44 chromosome form (Sokolov et al. 1989).

Where the boundary between the two chromosomal forms runs needs further study. We suggest that a contact zone or area of limited sympatry exists in the region of the right bank of the river Dnepr (Sokolov et al. 1989).

The degree of chromosomal difference between the 32 and 44 chromosome forms (almost all chromosomes of the 32 chromosome form are biarmed, those of the 44 chromosome form mostly acrocentric) allows us to consider them as independent species: *S. betulina* (Pallas, 1778) ($2n = 32$) and *S. strandii* (Formozov, 1931 ($2n = 44$)) (Sokolov et al. 1989). They differ from each other also by the patterns of heterochromatin localization (fig. 1 a, b) and by the sperm head measurements (table

Table 1: Karyotypes of morphologically similar species of birch mice. 2n = diploid number of chromosomes; NF = fundamental number; M = meta-, SM = submeteta-, ST = subtelo-, A = acrocentrics.

Species complexes	Species	2n	NF	Autosomal set (pairs of autosomes)	Heterochromosomes	
					X	Y
I	<i>S. betulina</i>	32	64, 63	11 (M+SM)+4 ST	SM	A
	<i>S. strandi</i>	44	52	1 M+3 SM+17 A	A	A
II	<i>S. severtzovi</i>	18	28	4 (M+SM)+large SM+4 A	A	A
		19	29			
		20	30	4 (M+SM)+middle SM+4 A	A	A
	<i>S. subtilis nordmanni</i>	26	48	11 (M+SM)+1 A	A	A
	<i>S. s. subtilis</i>	24	41—44		A	A
	<i>S. s. vaga</i>	24	41—42	8 (M+SM)+3 pairs of autosomes with variable morphology	A	A
III	<i>S. s. sibirica</i>	24	44—45		A	A
	<i>S. caucasica</i>	32	48	4 M+4 SM+7 A	A	A
	<i>S. kluchorica</i>	24	44	8 M+2 SM+1 A	A	A
	<i>S. kazbegica</i>	42	52	3 SM+1 ST+1 SM+15 A	A	A
		40	50	3 SM+1 ST+1 M+14 A	A	A
	<i>S. armenica</i>	36	52	4 M+2 SM+2 ST+9 A	A	SM

Table 2: Sperm head measurements (in μm) in morphologically similar species of birch mice.

Species complex	Species	Length (L)		Width (D)		L/D
		$x \pm s$	var.	$x \pm s$	var.	
I	<i>S. betulina</i>	4.1 ± 0.03	3.8—4.3	2.6 ± 0.03	2.4—2.9	1.6
	<i>S. strandi</i>	6.2 ± 0.07	5.0—7.1	4.0 ± 0.10	3.2—4.8	1.5
II	<i>S. severtzovi</i>	5.8 ± 0.09	5.0—6.5	3.1 ± 0.06	2.8—3.8	1.9
	<i>S. subtilis nordmanni</i>	5.5 ± 0.08	4.8—6.1	3.1 ± 0.05	2.8—3.6	1.8
III	<i>S. caucasica</i>	4.9 ± 0.05	4.4—5.3	3.7 ± 0.04	3.4—4.0	1.3
	<i>S. kluchorica</i>	4.5 ± 0.04	4.5—5.0	3.7 ± 0.05	3.3—4.2	1.2
	<i>S. kazbegica</i> (2n = 42)	6.5 ± 0.09	5.8—7.3	4.0 ± 0.06	3.5—4.4	1.6
	(2n = 40)	6.4 ± 0.08	5.7—7.0	4.0 ± 0.06	3.6—4.6	1.6
	<i>S. armenica</i>	5.4 ± 0.05	5.1—5.7	3.9 ± 0.06	3.5—4.5	1.4

2). The latter two characters are proposed as additional diagnostic criteria for the identification of the two species.

A comparison of the karyotypes of different subspecies of southern birch mice has revealed strong chromosomal differences between the form “*severtzovi*” and other subspecies (Sokolov et al. 1986a, table 1). These differences include a different chromosome number and also a different morphology of the chromosomes. On this basis it was suggested that southern birch mice from the Kursk district represent a separate species, *S. severtzovi* (Ognev, 1935) (Sokolov et al. 1986a). Its distributional range was described by Ognev (1948). The species occurs from the Central Chernozem region to the north up to approximately 53—54 degrees north. The southern boundary where *S. severtzovi* comes into contact with *S. subtilis nordmanni* needs further study.

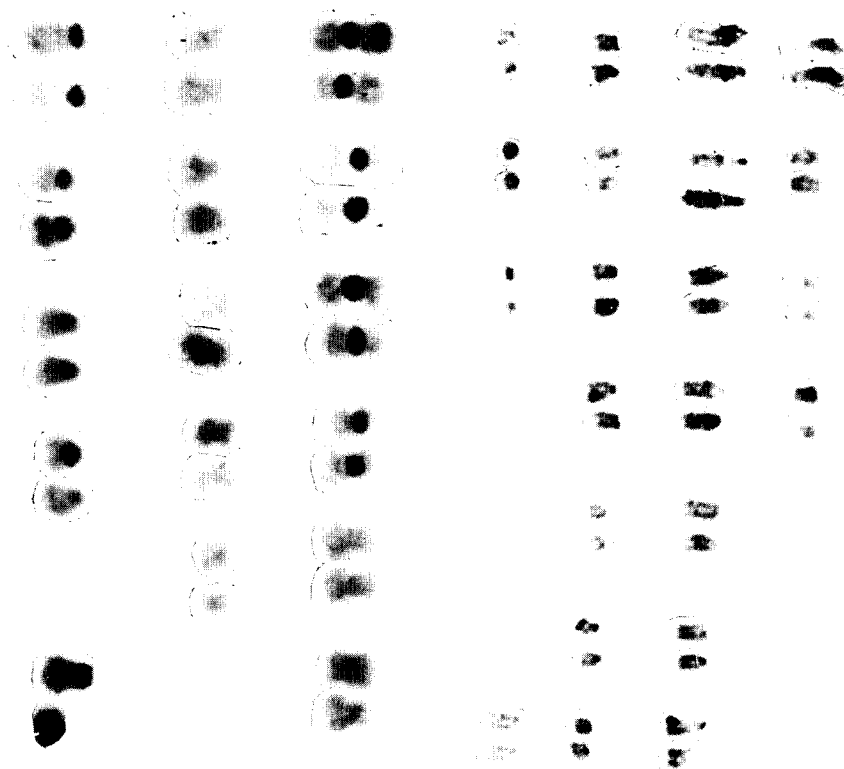


Fig. 1: C-banding. Karyotypes of a) *S. strandi*, female from Stavropol region, Sergievka area ($2n = 44$, $NF = 52$); b) *S. betulina*, male from Eastern Carpathians, Goverla mountain area ($2n = 32$, $NF = 64$).

At present, karyotype morphology is one of the main diagnostic characters for *S. severtzovi* and its similar congener *S. subtilis*. The karyotypes of both species also differ by the NOR localization (fig. 2a, b). In the chromosome set of *S. s. nordmanni* the NOR is located at the terminal parts of the short arms of the ninth (submetacentric) pair of autosomes, while in *S. severtzovi* these structures are in the secondary constrictions of the largest pair of acrocentrics.

Another complex of morphologically similar species of birch mice is represented by monochromatic (unstriped) mice of the Caucasus. They also differ from each other in chromosomal morphology. Five chromosome forms (table 1) are assigned to four species: 32 chromosomes (*S. caucasica*), 24 chromosomes (*S. khuchorica*), 42 or 40 chromosomes (*S. kazbegica*) and 36 chromosomes (*S. armenica*) (Sokolov et al. 1981, 1986b, Sokolov & Baskevich 1988, 1992).

The forms of *S. kazbegica* with 40 and 42 chromosomes are most closely related: the chromosome sets differ only by a single rearrangement, a tandem translocation. The two forms are also close in their distribution and faunal history (Sokolov & Baskevich 1992) and are therefore considered as populations of *S. kazbegica*. The remaining forms are characterized by a large number of chromosome rearrangements and are therefore regarded as separate species, because fertile crosses among forms with such significant chromosome discrepancies are not possible. There are also dif-

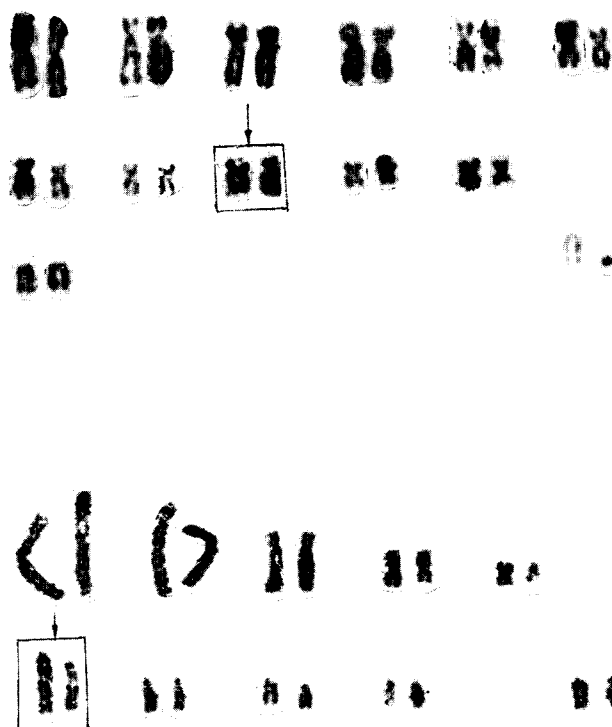


Fig. 2: NOR-banding. Karyotypes of a) *S. subtilis nordmanni*, male from Donetsk district, Chotutovski steppe ($2n = 26$, $NF = 48$); b) *S. severtzovi*, female from Kursk region, Central Chernozem Reserve ($2n = 20$, $NF = 30$).

ferences in the size of the sperm heads between most species of unstriped birch mice (table 2), in addition to differences in the shape of the baculum of *S. caucasica* and *S. kluchorica*, and some other morphological features (Sokolov et al. 1981, 1986b; Sokolov & Baskevich 1988, 1992). However, it should be stressed that the main diagnostic characters in this complex of morphologically similar species are chromosomal number and morphology.

On the basis of the above mentioned diagnostic characters the distribution of birch mice species of the Caucasus is as follows (Sokolov et al. 1987b, Sokolov & Baskevich 1992, and recent data). *S. caucasica* occurs in the west, *S. kluchorica* in the west to the western central part, *S. kazbegica* in the central Great Caucasus, and *S. armenica* in the Minor Caucasus. In general, the unstriped birch mice of the Caucasus are allopatric.

In our earlier publications we called morphologically similar species of birch mice sibling species (Sokolov et al. 1981, 1986a, b, 1989; Sokolov & Baskevich 1988). Sibling species are morphologically similar or identical species which separate as a result of isolating mechanisms of evolution (Mayr 1963). And it is correct in our case. Mayr (1963) postulated sympatry of sibling species. Only two species pairs in the group under study probably have overlapping ranges and thus can be classified as sibling species in the strict sense. The unstriped birch mice of the Caucasus, therefore, are considered as sibling species in a wider sense of this concept.

Based on present knowledge, the morphologically similar species of birch mice represent about 66 % of all *Sicista* species occurring within the territory of the Former Soviet Union. At present their main diagnostic characters are clear chromosomal differences. However, future studies of the morphology of birch mice based on multivariate studies of craniodental morphology, and multivariate analyses of the external genital morphology discussed above may provide a better view of both chromosomal and morphological evolution in this genus.

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Zusammenfassung

Es wird eine Übersicht der morphologisch ähnlichen Birkenmausarten (Gattung *Sicista*) gegeben, die im Gebiet der früheren Sowjetunion vorkommen. Dabei wird ein enges Artkonzept zugrundegelegt, welches vor allem auf den Ergebnissen intensiver Chromosomenstudien fußt. Drei Artengruppen mit insgesamt acht Arten werden behandelt. Einige neue diagnostische Merkmale werden vorgestellt; diese betreffen die Lage der NOR-Regionen auf den Chromosomen sowie die Verteilung von Heterochromatin und die Größe und Form der Spermienköpfchen.

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