The Number of Karyotypic Variants in the Common Shrew (Sorex araneus)

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Owing to intensive research carried out in different countries, a very complicated variation of common shrew karyotype was revealed, including polymorphism and polytypy. Thirtyseven different Robertsonian metacentrics, 13 different homozygous karyotypes containing only metacentric autosomes, and about 30 different homozygous karyotypes containing metacentric and acrocentric autosomes have actually been found in natural populations. We have calculated the number of theoretically possible karyotypic variants in the common shrew. There may occur 66 Robertsonian metacentrics, 10 395 different homozygous karyotypes containing only metacentric autosomes, and 129 757 different homozygous karyotypes containing at least two acrocentric pairs. There are probably certain factors in nature limiting free combinations of chromosome arms in fusions. Nevertheless, it is probable that some new combinations will be described during further research, especially in hybrid zones and near edges of the present-day distribution of the common shrew.

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1. INTRODUCTION

The chromosome research in the common shrew (*Sorex araneus* Linnaeus, 1758), began in the fifties, and has been evolving very rapidly, particularly in recent years (*e.g.*, Belcheva & Kolevska, 1986; Fedyk, 1986; Hausser *et al.*, 1986; Reumer & Meylan, 1986; Searle, 1986a, b, 1987, 1988; Wójcik, 1986; Fedyk, 1987; Fedyk & Leniec, 1987; Fredga, 1987; Halkka & Söderlund, 1987; Halkka *et al.*, 1987; Searle & Wilkinson, 1987; Wójcik & Zima, 1987; Wójcik & Searle, 1988). According to available data actually published, the number of karyologically examined specimens of the common shrew can be estimated at about 4000, and populations from approximately 350 localities have been studied. The nomenclature proposed by Halkka *et al.* (1974) is used for chromosome arms (G-band) identification in common shrew karyotype. Each substantial chromosome arm is designated by a letter $a — u$, and a is the largest arm (Fig. 1). The karyotype of this species is characterized by

variations caused by Robertsonian rearrangements. Karyotypic differences between specimens or populations can inhere in different number of autosomes $2n_a$, and/or in different sets of metacentrics composed of some or all of the chromosome arms *g* through *r*. The metacentrics *af, bc, tu* and the sex chromosomes appear to be invariant. Owing to intensive research carried out by many workers in different countries, a very complicated pattern of variation was revealed, including polymorphism (*i.e.* variability inside individual populations) and polytypy (*i.e.* variability between geographical populations).
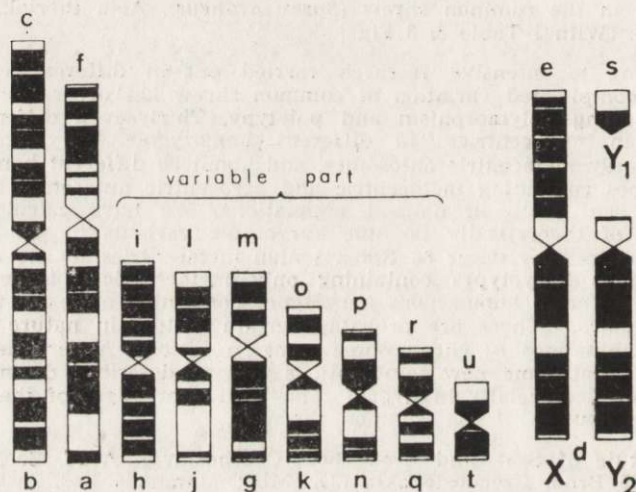

Fig. 1. A schematic drawing of the G-banded karyotype of the common shrew with the designation of the individual chromosome arms.

2. ACTUALLY FOUND VARIANTS OF KARYOTYPE

Over 30 variants of common shrew karyotypes have actually been found in natural shrew populations in the extensive Paleartic range of this species (Table 1). The most of them have been described in the European part of the area of distribution, and only three variants have been ascertained in western Siberia, *i.e.* in the eastern edge of the species range (Král *et al.*, 1981). It is supposed that ancestral karyotype of common shrew was acrocentric and that all metacentrics were formed by Robertsonian fusions (Meylan & Hausser, 1973; Searle, 1984). This assumption is supported by the results of the examinations made in the regions situated near the extreme southwestern edge of the present-day distribution of the common shrew where the most acrocentric karyotypes were found (Ford Hamerton, 1970; Hausser, 1978; Hausser & Bos-

Table 1

Actually known chromosome races and forms of *Sorex araneus*, variable part of the karyotype (arms *g—r*). Chromosomes not necessarily listed in order of size, and the maximum number of metacentrics is shown. Metacentrics are indicated in format *xry*, and acrocentrics in format *x, y*. Asterisks indicate the hybrids.

Known range	Karyotype	Reference
Scotland, Wales	*jl, hi, gm, ko, np, qr*	Searle (1984)
England, Denmark	*jl, hi, gm, kq, no, pr*	Searle (1984), Fredga (1987)
SW England, Wales	*jl, hi, gm, ko, n, p, q, r*	Searle (1987)
C Sweden	*jl, hi, gm, kp, nr, oq*	Fredga & Nawrin (1977)
C Sweden	*jl, hi, gm, ko, nr, pq*	Fredga (1987)
C Sweden*	*jl, hi, gm, kq, n, r, o, p*	Fredga (1987)
S Sweden	*jl, hi, gm, ko, nq, pr*	Fredga & Nawrin (1977)
W Germany, Hungary, Czechoslovakia, Yugoslavia	*jl, hi, gm, k, n, o, p, q, r,*	Dulić (1978), Olert & Schmid (1978), Zima & Král (1985)
N Switzerland	*jl, hi, gm, kr, no, p, q*	Hausser et al. (1986)
Moscow region USSR	*jl, hi, gm, kp, no, qr*	Ivanitskaya (1985)
NW Czechoslovakia, SW Poland	*jl, hi, gm, ko nr, p, q*	Zima &Král (1985), Wójcik unpubl.
N Poland	*jl, hi, gm, ko, n, p, q, r*	Wójcik & Fedyk (1985)
W & C Poland	*jl, hi, gm, ko, np, q, r*	Wójcik (1986), Fedyk & Leniec (1987)
NE Poland*	*jl, hi, gr, ko, mn, p, q*	Fedyk & Leniec (1987)
NE Poland*	*jl ,hi, gr, ko, np, m, q*	Fedyk (1987)
E Poland	*jl, ik, gr, hn, mp, o, q*	Fredga & Nawrin (1977), Fedyk (1980)
NE Poland	*jl, ik, gr, hq, mn, o, p*	Wójcik (1986), Fedyk & Leniec (1987)
NE Poland	*jl, hk, gr, io, mn, p, q*	Wójcik (1986), Fedyk & Leniec (1987)
NE Poland*	*jl, hk, gr, io, np, m, q*	Fedyk (1987)
N Sweden, Finland	*jl, ip, hn, gm, kq, or*	Halkka et al. (1974, 1978), Fredyga & Nawrin (1977)
SE Finland	*jl, ip, hn, gm, kr, oq*	Halkka et al. (1987)
S Finland	*jl, ip, hn, gq, ko, mr*	Halkka et al. (1987)
SW Finland	*jl, ip, hn, mr, oq, g, k*	Halkka et al. (1987)
SE Finland	*jl, ip, hk, gq, mo, nr*	Halkka et al. (1987)
SW Finland (Aland)	*jl, ip, g, h, k, m, n, o, q, r*	Halkka et al. (1987)
W Siberia USSR	*jl, ik, hn, go, mp, qr*	Aniskin & Volobujev (1981), Král et al. (1981)
W Siberia USSR	*jl, gk, hi, mn, op, qr*	Aniskin & Volobujev (1981), Král et al. (1981)
W Siberia USSR	*jl, gk, ho, iq, mn, pr*	Aniskin & Volobujev (1981)
S Switzerland	*hj, gi, lo, kn, m, p, q, r*	Hausser et al. (1986)
France (near Chamonix)	*g, h, i, j, k, l, m, n, o, p, q, r*	Hausser & Bosshard (pers. comm.)

shard, pers. comm.), as well as by the comparison of karyotypes of different related species of *Sorex* (Meylan & Hausser, 1973; Wójcik & Searle, 1988). On the basis of this assumption, several phylogenetic groups of common shrew can be recognized (Searle, 1984). The races (with metacentrics *hi* and *gm*) of West European phylogenetic group occur in central, northwestern, south and southeastern Europe, and near Moscow (Fig. 2). The races (with metacentrics *ik* and *gr*) of the East European
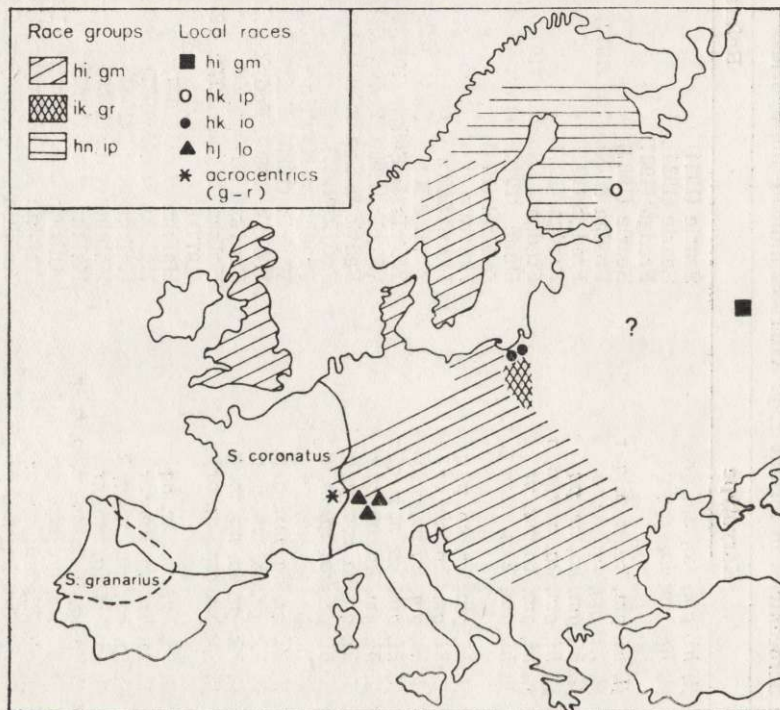

Fig. 2. Distribution of different race groups and local races of *Sorex araneus* in Europe. Continuous line — range of *S. coronatus*, and dotted line range of *S. granarius*.

phylogenetic group were found in eastern Poland. We suppose that the local races (with metacentrics *hn* and *ip*) which were described in Finland and north Sweden belong to another phylogenetic group. The local race "Valais" (with metacentrics *gi*, *hj*, *kn*, *lo*) in the Alps (Switzerland) is probably of Italian origine (Hausser *et al.*, 1986). Populations with a primitive karyotype with all chromosome arms from *g* to *r* in acrocentric form (12 acrocentric pairs) have been observed near Chamonix in the Western Alps (Hausser & Bosshard, pers. comm.). The Siberian races represent probably separate phylogenetic group.

The contact zones between different races and/or different phylogenetic groups have been described in England, in Poland, in Sweden, and in Switzerland (Frykman & Bengtsson, 1984; Fedyk, 1986; Hausser *et al.*, 1986; Searle, 1986b; Fredga, 1987). The hybrid karyotypes and the local hybrid races have been described in those contact zones.

We can conclude that in the natural populations examined up to now, 37 different Robertsonian metacentrics, 13 different homozygous karyotypes containing only metacentric autosome, and about 30 different homozygous karyotypes containing metacentric and acrocentric autosomes have been found (in this respect, the occurrence of fusion in a heterozygous states was supposed to evidence real possibility of finding it in a homozygous state as well).

3. THEORETICAL NUMBER OF VARIANTS

We have calculated the number of theoretically possible karyotypic variants in the common shrew. We had to assume, that all chromosome arms from g to r have a free and equal possibility and capacity to form new arm combinations. The number of possible variants is very high. Supposing that observed karyotypic variability is determined by the Robertsonian system involving 12 acrocentric autosomal pairs (A) which can be freely combined by fusions to form different metacentrics, theoretically there may occur:

$$\binom{A}{2} = \binom{12}{2} = 66$$

metacentric morphs with a specific arm combination (Fig. 3);

$$\frac{A!}{2^{A/2} \times (A/2)!} = \frac{12!}{2^6 \times 6!} = 10\ 395$$

different homozygous karyotypes containing only Robertsonian metacentrics ($2n_a = 18$); and

$$\sum_{m=0}^{A/2-1} \frac{A!}{(A-2m)!\ 2^m \times m!} = \sum_{m=0}^{5} \frac{12!}{(12-2m)!\ 2^m \times m!} = 129\ 757$$

different homozygous karyotypes containing at least two acrocentric pairs ($2n_a = 20 - 30$).

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4. DISCUSSION

Only a small proportion of theoretically possible variants has actually been found in natural shrew populations. Possible and actually existing combinations of arms in biarmed autosomes are summarized in Fig. 3. Thirty-seven out of the 66 possible Robertsonian metacentrics have been ascertained in natural populations. It is interesting and important to note that among small arms (m—r) nearly all possible fusion combinations (except the mq one) have been found in nature. Among large arms (g—l) only 7 out of the 15 possible combinations are known. Of the 36 possible fusions between large and small arms 16 have been documented. Individual arms can be involved in 2 (j, l) to 10 (o) different metacentrics.

	h	i	j	k	l	m	n	o	p	q	r
g	gh	(gi)	gj	(gk)	gl	(gm)	gn	(go)	gp	(gq)	(gr)
h		(hi)	(hj)	(hk)	hl	hm	(hn)	(ho)	hp	(hq)	hr
i			ij	(ik)	il	im	in	(io)	(ip)	(iq)	ir
j				jk	(jl)	jm	jn	jo	jp	jq	jr
k					kl	km	(kn)	(ko)	(kp)	(kq)	(kr)
l						lm	ln	(lo)	lp	lq	lr
m							(mn)	(mo)	(mp)	mq	(mr)
n								(no)	(np)	(nq)	(nr)
o									(op)	(oq)	(or)
p										(pq)	(pr)
q											(qr)

Fig. 3. A synopsis of possible and documented combinations of arms in Robertsonian metacentrics. The documented combinations are circled. Based on data from Table 1.

The number of karyotype variants actually found in natural populations is rather low in comparison with that expected theoretically. When calculating the theoretical number of variants it was assumed that all chromosome arms (g—r) have a free and equal possibility and capacity to form new arm combinations (each to other). This seems not to be true in nature, and certain constrains limiting the extent of variation have to be considered. It is highly probable that all theoretically possible variants do not occur in nature. The process of chromosome fusions is self limiting, and the number of possible variants drops sharply as successive arm fusions become established in the populations. Differ-

ential fusion activity of individual arms is also expected to occur. For instance, the chromosome arms j and l, which occur as a metacentric nearly in whole range of this species apparently have a stronger fusion actvity that another arms. The same holds for the arm combinations hi and gm of the western race group, the ik and gr of the eastern race group, and the hn and ip of some Scandinavian races. These combinations seem to have different fusion activity than the other from respective areas. Nevertheless, it is probable that some new combinations will be described during further research, especially in hybrid zones and near edges of the present-day distribution of the common shrew. Actually we are not well informed about the cytogenetic status of populations in a number of large geographical areas.

The possibility of a mistaken identification of chromosome arms should be considered, especially in some small elements (*e.g.*, m, and o), and "there may be greater variability on paper than in nature" (Halkka *et al.*, 1987). From this point of view, an elaboration of the standards of the G-band patterns in different variants of common shrew karyotype would be highly desirable. This suggestion was also recommended in the conclusions of the "Meeting on Population and Evolutionary Cytogenetics of *Sorex araneus*" held in Oxford in 1987.

The karyotypic status of a population can be exactly described only by a commonly used system of alphabetic designation of individual arms and an indication of their status (acrocentric vs. fused). At present any simplification of this system would be undesirable.

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LICZBA WARIANTÓW KARIOTYPU U RYJÓWKI AKSAMITNEJ
(SOREX ARANEUS)

Streszczenie

Scharakteryzowano aktualnie znane rasy i formy chromosomowe ryjówki aksamitnej. W naturalnych populacjach stwierdzono dotychczas 37 różnych robertsonowskich metacentryków, opisano 13 różnych homozygotycznych kariotypów zawierających tylko metacentryczne autosomy i około 20 różnych homozygotycznych kariotypów zawierających metacentryczne i akrocentryczne autosomy (Tabela 1, Ryc. 2 i 3).

Wyliczono teoretycznie możliwą liczbę wariantów kariotypowych u ryjówki aksamitnej. Przy założeniu, że każde ramię od *g* do *r* miałoby taką samą możliwość formowania nowych kombinacji ramion, teoretycznie może występować 66 różnych robertsonowskich metacentryków, 10 395 różnych homozygotycznych kariotypów zawierających tylko metacentryczne autosomy, oraz 129 757 różnych homozygotycznych kariotypów zawierających najmniej dwie akrocentryczne pary autosomów. Mimo, że w naturze występuje wiele czynników ograniczających swobodne fuzje ramion chromosomowych, można przypuszczać, że w przyszłości będą stwierdzane nowe kombinacje ramion w kariotypach ryjówki aksamitnej, szczególnie na obszarach kontaktu różnych ras chromosomowych.