

Reconstruction of the postglacial colonization of *Sorex araneus* into northern Scandinavia based on karyotype studies, and the subdivision of the Abisko race into three

Karl Fredga

ABSTRACT. To clarify the number, distribution and origin of chromosome races of common shrews in northern Scandinavia, 117 specimens were karyotyped from 12 new localities, six in Sweden and six in Norway. Including previous investigations, altogether 257 specimens from 26 localities in northern Fennoscandia have been analysed. Inspection of this complete dataset shows that the Abisko chromosome race, which occupies a wide range in northern Scandinavia, should be subdivided into three races: Abisko (Ai) in the north, Ammarnäs (Am) in the centre, and Hattsjö (Ha) in the south. The characteristics of these races and their distributions are described. The colonization of small mammals into northern Scandinavia is closely associated with the history of deglaciation. Most likely, common shrews of the Abisko race were the first to spread westwards along the northern coast of Norway. Later, when the ice and water had disappeared from northern Sweden, a new and wider immigration route from the east was opened for shrews of the Ammarnäs race. Another possibility is that northern Sweden and Norway were colonized from the west by shrews which had survived the last glaciation on the isle of Andöya in northwest Norway. The Hattsjö race, located between the Ammarnäs and Sidensjö races, may be regarded as a hybrid race.

KEY WORDS: *Sorex araneus*, chromosome races, colonization history, Scandinavia.

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Реконструкция постледниковой колонизации северной Скандинавии на основе анализа кариотипов *Sorex araneus* и разделение расы Абиско на три расы

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РЕЗЮМЕ. Для выяснения характера распределения хромосомных рас обыкновенной бурозубки в северной Скандинавии был проведен кариотипический анализ 117 животных из 12 новых локалитетов, шести шведских и шести норвежских. Включая предыдущие исследования, всего было проанализировано 257 экземпляров из 26 точек северной Фенноскандии. Было показано, что хромосомная раса Абиско, широко расселенная в северной Скандинавии, должна быть разделена на три расы: Абиско (Ai) на севере, Аммарнас (Am) в центре и Хаттсьё (Ha) на юге. В статье представлено географическое распределение этих рас и их характеристики. Колонизация северной Скандинавии мелкими млекопитающими тесно связана с историей дегляциации. Наиболее вероятным представляется следующий сценарий. Бурозубки расы Абиско первыми расселялись на запад вдоль северного берега Норвегии. Позднее, когда льды и воды исчезли в северной Швеции, открылся новый и более широкий путь иммиграции, которым воспользовались бурозубки расы Аммарнас. Возможен и иной сценарий, по которому северная Швеция и Норвегия были заселены с запада бурозубками, пережившими оледенение на острове Андоя в северо-западной Норвегии. Расу Хаттсьё, занимающую территорию между ареалами рас Аммарнас и Сиденсьё, можно рассматривать как гибридную расу.

КЛЮЧЕВЫЕ СЛОВА: *Sorex araneus*, хромосомные расы, история колонизации, Скандинавия.

Introduction

During the height of the last glacial period, about 20 000 calendar years ago, most parts of Northern Europe were covered with ice. When the ice retreated virgin land appeared which was re-colonized by land mammals. In Scandinavia two major colonization routes were used, from the south via land bridges between

Denmark and southern Sweden or from the northeast through Finland. Some species, like the common shrew, *Sorex araneus*, used both routes and the two contingents meet in the northern part of central Sweden. They not only belong to different chromosome races but also to different karyotypic groups, the West European karyotypic group (WEKG) and the North European karyotypic group (NEKG) (Fredga, 1996). The contact zone

between the two groups has been studied in detail in an area NW of the town of Örnsköldsvik (Fredga & Narain, 2000).

By definition, a chromosome race of *S. araneus* is a group of geographically contiguous or recently separated populations that share the same set of metacentrics and acrocentrics by descent (Hausser *et al.*, 1994). Thus the karyotypes of (adjacent) populations in an area may mirror their origin and colonization history of that area.

Up to now common shrews in northern Sweden have been regarded to belong to the same race, the Abisko race, covering an area from 63°30' N at the Gulf of Bothnia to 68°30' N at Abisko in the far northwest (Fredga, 1996). However, published data include few specimens from the central part of this vast area, and as pointed out by Fredga (1996), it is impossible to decide whether these shrews belong to the Abisko or Savukoski races, because the arms *g*, *m*, *o* and *r* are unfused.

In the year 2000 the karyotypes of common shrews were studied at six localities in Norway and one in northern Sweden (Fredga, 2003). The race identification of the population on Andöya, a large island in northwest Norway, was unclear, and the same applied to the population at Överkalix in Sweden. Still a large area in northern Sweden remained uninvestigated, and

the race inhabiting this area was designated Ai? (Fredga, 2003). To solve the problem I organized an expedition to the uninvestigated area and to the northernmost parts of Norway in 2003. The results of the trip are presented here. The Abisko chromosome race is divided into three races and their characteristics are described. Possible late glacial and postglacial colonization routes of shrews into northern Scandinavia are discussed.

Material and methods

The expedition took part in 15 August – 1 September, 2003. We collected 303 small mammals of ten species, including 146 common shrews, from 12 localities, six in Sweden and six in Norway. The animals were caught with Swedish live traps, “Ugglan Special”, after 8–72 trap nights at each site.

Chromosome preparations were made from 117 common shrews, 4–16 specimens from each site. Mitotic chromosome preparations were made “in the field” from bone marrow cells after colchicine treatment *in vitro* (Fredga, 1987). All individuals were karyotyped in the microscope and every chromosome arm was identified by G-banding. The trypsin-Giemsa technique of Wang & Fedoroff (1972) was applied.

Table 1. Locality, polymorphism of chromosomes *gm*, *jl*, *hn*, *ip*, *kq* and *or*, number of autosomes (2NA) and sample size of common shrews analysed from northern Scandinavia in the present investigation.

No. in Fig. 1	Locality	Chromosome arms						2NA	Number of specimens	Sample size
		<i>gm</i>	<i>jl</i>	<i>hn</i>	<i>ip</i>	<i>kq</i>	<i>or</i>			
6	Hällnäs	H	M	M	M	M	T	21	3	13
		T	M	M	M	M	T	22	2	
		H	M	M	H	M	T	22	2	
		H	H	M	M	M	T	22	1	
		T	M	M	H	M	T	23	2	
		H	M	M	H	H	T	23	1	
		T	M	M	T	M	T	24	1	
		T	H	H	H	M	T	25	1	
7	Storuman	H	M	M	M	M	T	21	2	16
		T	M	M	M	M	T	22	1	
		H	H	M	M	M	T	22	1	
		H	M	M	M	H	T	22	1	
		T	M	M	H	M	T	23	1	
		T	M	M	M	H	T	23	1	
		H	H	M	M	H	T	23	1	
		H	M	M	H	H	T	23	1	
		H	M	M	M	T	T	23	1	
		T	M	M	M	T	T	24	2	
		T	H	M	H	H	T	25	1	
		T	M	M	T	H	T	25	2	
T	M	M	H	T	T	25	1			
8	Tärnaby	T	M	M	M	H	T	23	1	5
		H	H	M	M	H	T	23	1	
		T	M	M	M	T	T	24	3	
9	Burträsk	T	M	M	M	M	T	22	6	12
		T	M	M	M	H	T	23	6	

Table 1 (continued).

No. in Fig. 1	Locality	Chromosome arms						2NA	Number of specimens	Sample size
		<i>gm</i>	<i>jl</i>	<i>hn</i>	<i>ip</i>	<i>kq</i>	<i>or</i>			
10	Älvsbyn	T	M	M	M	H	T	23	2	9
		T	M	M	M	T	T	24	7	
12	Överkalix	T	M	M	M	M	T	22	6	12
		T	M	M	M	H	T	23	3	
		T	M	M	M	T	T	24	3	
14	Lönsdal	T	M	M	M	H	T	23	1	12
		T	M	M	M	T	T	24	9	
		T	H	M	M	T	T	25	2	
15	Muonio	T	M	M	M	M	H	21	4	13
		T	M	M	M	M	T	22	5	
		T	H	M	M	M	T	23	2	
		T	H	M	M	H	T	24	1	
		T	M	M	M	T	T	24	1	
17	Ballangen	H	M	M	M	M	M	19	1	9
		M	M	M	M	M	H	19	1	
		T	M	M	M	H	M	21	1	
		T	M	M	M	M	H	21	4	
		H	M	M	M	H	H	21	1	
		T	M	M	M	M	T	22	1	
20	Straumfjordnes	M	M	M	M	M	M	18	1	8
		H	M	M	M	M	M	19	4	
		T	M	M	M	M	M	20	2	
		H	H	M	M	M	M	20	1	
21	Alta	T	M	M	M	M	M	20	3	6
		H	M	M	M	M	H	20	2	
		T	M	M	M	M	H	21	1	
22	Russenes	H	M	M	M	M	M	19	2	10
		T	M	M	M	M	M	20	2	
		H	M	M	M	M	H	20	1	
		H	H	M	M	M	M	20	1	
		T	M	M	M	M	H	21	4	
23	Karasjok	H	M	M	M	M	H	20	1	4
		T	M	M	M	M	H	21	1	
		H	M	M	M	M	T	21	1	
		T	M	M	M	M	T	22	1	

No. — locality number, M — homozygous metacentric, H — heterozygous, T — homozygous telocentric.

To cover the area of interest, the localities given below were chosen (names used are in bold face). The locality numbers refer to Tab. 1 and Fig. 1. In Fig. 1 other samples from previous studies are included, which are used in the final analysis of the whole region.

6. Kronlunds kursgård, 9 km NW **Hällnäs**, Sweden, N 64°19', E 19°33'.

7. Avasund fiscecamp, 4 km E **Storuman**, Sweden, N 65°04', E 17°09'.

8. Västansjö, 8 km NW **Tärnaby**, Sweden, N 65°45', E 15°05'.

14. Polarsirkelens höyffjellshotell, **Lönsdal**, Norway, N 66°48', E 15°24'.

17. **Ballangens** camping, 24 km SW Narvik, Norway, N 68°20', E 16°53'.

20. **Straumfjordnes**, 14 km NNE Nordreisa, Norway, N 69°53', E 21°12'.

21. Elvebacken, 5 km E **Alta**, Norway, N 69°58', E 23°24'.

22. **Russenes**, 50 km N Lakselv, Norway, N 70°29', E 25°04'.

23. **Karasjok**, 70 km S Lakselv, Norway, N 69°27', E 25°26'.

15. Rajamaa camping, 7 km SW **Muonio**, Sweden, N 67°54', E 23°33'.

10. Nyfors, 2 km W **Älvsbyn**, Sweden, N 65°40', E 20°58'.

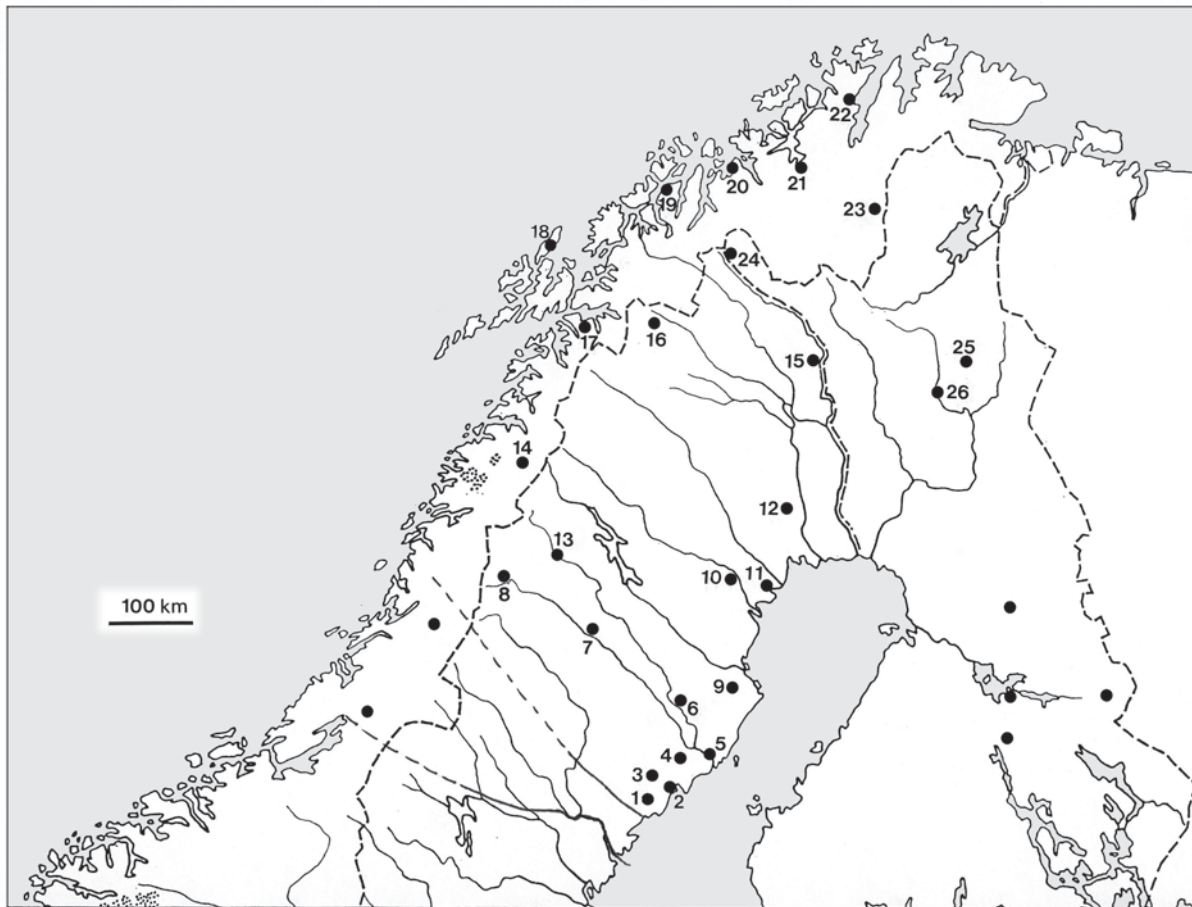


Figure 1. Map of northern Fennoscandia showing the sampling localities of the common shrews included in the paper. The numbers refer to Tabs 1 and 2. Localities without numbers show the relatively wide distribution of the Sidensjö race in Norway (Fredga, 2003), and sites of the Kuhmo race in Finland (Halkka *et al.*, 1987).

9. **Burträsk**, 29 km SSW Skellefteå, Sweden, N 64°31', E 20°39'.

In August 2000 12 common shrews were collected at Överkalix. The analysis of this sample is also included in the present report:

12. Lillavan, Vännäsberget, 8 km NW Överkalix, Sweden, N 66°23', E 22°44'.

Results

As expected, all specimens belonged to the traditional Abisko race. Chromosome polymorphism was present at all 13 localities, but the degree of polymorphism and the chromosome arms involved varied. This is evident from Tab. 1. For example, at Storuman 13 different karyotypes were present among 16 specimens, $2NA=21-25$, whereas at Burträsk only two karyotypes were identified among 12 specimens, $2NA=22-23$. At five localities in the centre of the region the chromosome arms *g*, *m*, *o* and *r* were unfused in all 58 specimens studied. In the eight samples south and north of this area the frequency of unfused arms *g* and *m* varied from 56 to 90 per cent. A striking difference between these two areas was that the arms *o* and *r* were essential-

ly always unfused in the south and that *i* and *p* were always fused in the north. The chromosome *jl* occasionally occurs as one atelocentric (*j*) and one telocentric (*l*) chromosome. This rare type of variation was found in 7 of the 13 localities, always in the heterozygous state.

The results of the present study are summarized in Tab. 1. These data are combined with previous investigations from northern Fennoscandia (Halkka *et al.*, 1987, 1994; Fredga, 1996, 2003), and all data are presented in Tab. 2, which includes 257 specimens from 26 localities, 15 in Sweden, 8 in Norway and 3 in Finland. Tab. 2 gives the frequencies of metacentrics for the variable chromosomes and number of autosomes. In order to visualize the quite complicated situation, pie charts showing the frequencies of unfused (black) and fused (white) states of the individual chromosome arms were constructed (Figs 2A-F). In these figures the localities 1 and 2, 4 and 5, 10 and 11, and 25 and 26 were combined because they are located close to each other and the sample size in one of the localities is small.

The available data suggest that the Abisko race should be subdivided into three races: Hattsjö (3), Am-

Table 2. Summary of chromosome data of common shrews studied in northern Fennoscandia.

No. in Fig. 1	Locality	Sample size	Chromosome arms						2NA		Ref.
			<i>gm</i>	<i>jl</i>	<i>hn</i>	<i>ip</i>	<i>kq</i>	<i>or</i>	mean	range	
1	Gideå S	1	50.0	100	100	0	100	0	23.0	(23)	1
2	Lögdeå S	17	70.6	85.3	88.2	52.9	94.1	0	22.2	21–24	1
3	Hattsjö S	24	70.8	93.8	84.5	52.1	93.8	0	22.1	20–24	1
4	Bjurholm S	2	75.0	75.0	75.0	50.0	100	0	22.5	22–23	2
5	Umeå S	9	11.1	100	94.4	66.7	100	5.6	22.4	21–24	1
6	Hällnäs S	13	26.9	92.3	96.2	69.2	96.2	0	22.4	21–25	3
7	Storuman S	16	21.9	90.6	100	75.0	53.1	0	23.2	21–25	3
8	Tämaby S	5	10.0	90.0	100	100	20.0	0	23.6	23–24	3
9	Burträsk S	12	0	100	100	100	75.0	0	22.5	22–23	3
10	Älvsbyn S	9	0	100	100	100	11.1	0	23.8	23–24	3
11	Antnäs S	1	0	100	100	100	0	0	24.0	(24)	1
12	Överkalix S	12	0	100	100	100	62.5	0	22.8	22–24	3
13	Ammarnäs S	7	0	92.9	100	100	7.1	0	24.0	23–25	1
14	Lönsdal N	12	0	91.7	100	100	4.2	0	24.1	23–25	3
15	Muonio S	13	0	88.5	100	100	88.5	15.4	22.2	21–24	3
16	Abisko area S	17	14.7	88.2	97.1	100	88.2	79.4	20.6	20–22	1
17	Ballangen N	9	22.2	100	100	100	88.9	55.6	20.7	19–22	3
18	Andøya N	18	0	100	100	100	0	0	24.0	24	4
19	Tromsø N	12	100	100	100	100	100	100	18.0	18	4
20	Straumfjordnes N	8	43.8	93.8	100	100	100	100	19.25	18–20	3
21	Alta N	6	16.7	100	100	100	100	75.0	20.2	20–21	3
22	Russenes N	10	20.0	95.0	100	100	100	75.0	20.2	19–21	3
23	Karasjok N	4	25.0	100	100	100	100	25.0	21.0	20–22	3
24	Kilpisjärvi F	11	27.3	86.4	100	100	95.5	77.3	?	?	5
			<i>go</i>					<i>mr</i>			
25	Savukoski F	6	5.6	100	100	100	83.3	0	22.2	21–24	5, 6
26	Sodankylä F	3									

Frequencies (%) of metacentrics are given for the various arm combinations, 2NA — number of autosomes. Samples 1–8 belong to the Hattsjö race, 9–15 and 18 to the Ammarnäs race, 16–17 and 19–24 to the Abisko race. Samples 25 and 26 are pooled. They represent the Savukoski race. S — Sweden, N — Norway, F — Finland.

References: 1 — Fredga, 1996; 2 — Fredga, 1998, unpubl. data; 3 — present study; 4 — Fredga, 2003; 5 — Halkka *et al.*, 1994; 6 — Halkka *et al.*, 1987.

marnäs (13) and Abisko (16). The figures in brackets refer to the location of the type localities in Fig. 1. The names are chosen in accordance with the nomenclature rules (Hausser *et al.*, 1994). These races may be defined as follows:

Hattsjö race (Ha). XX/XY₁Y₂, *af, bc, g/m, h/n, i/p, j/l, k/q, o, r, tu.*

Description: Fredga (this paper).

Type locality: Hattsjö, Sweden, N 63°36', E 18°58'.

Distribution: N Sweden, bordering on the Sidensjö race in the south and to the Ammarnäs race in the north.

Additional information: This race has previously been included in the Abisko race (Fredga, 1996; Zima *et al.*, 1996).

Ammarnäs race (Am). XX/XY₁Y₂, *af, bc, g, m, hn, ip, j/l, k/q, o, r, tu.*

Description: Fredga (this paper).

Type locality: Ammarnäs, Sweden, N 65°58', E 16°13'.

Distribution: N Sweden and N Norway bordering on the Hattsjö race in the south and the Abisko race in the north. Present on Andøya (Norway).

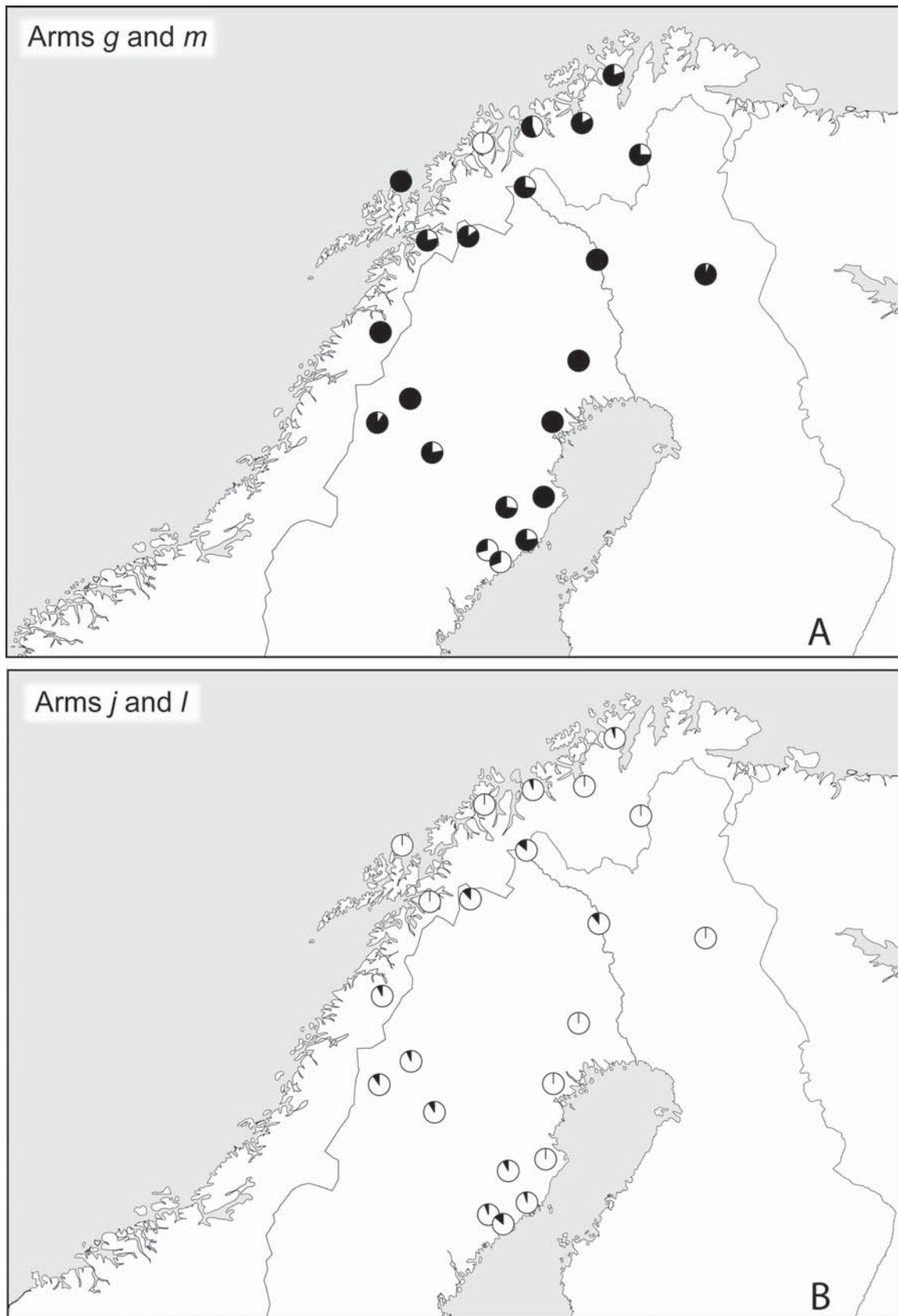


Figure 2. Frequency of unfused (black) and fused (white) states of the individual chromosome arms. When fused the arms are combined into metacentrics in the same way in the Abisko, Ammarnäs and Hattsjö races.

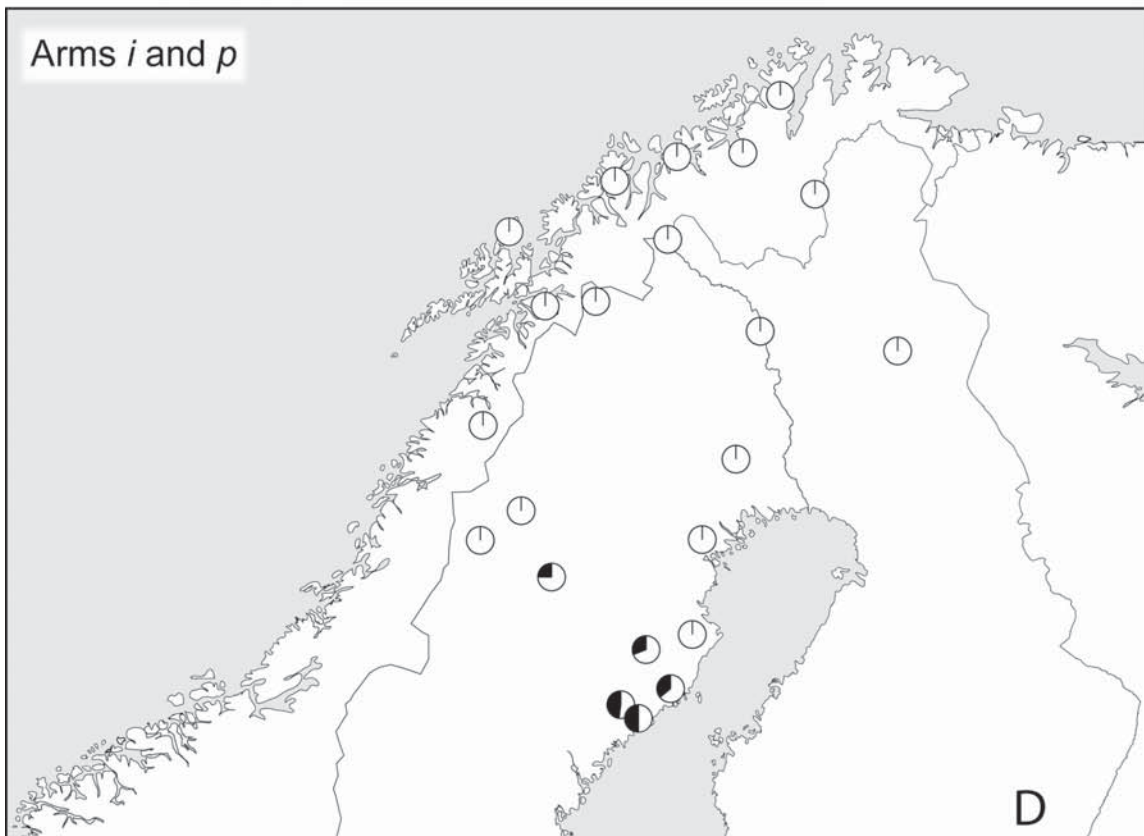
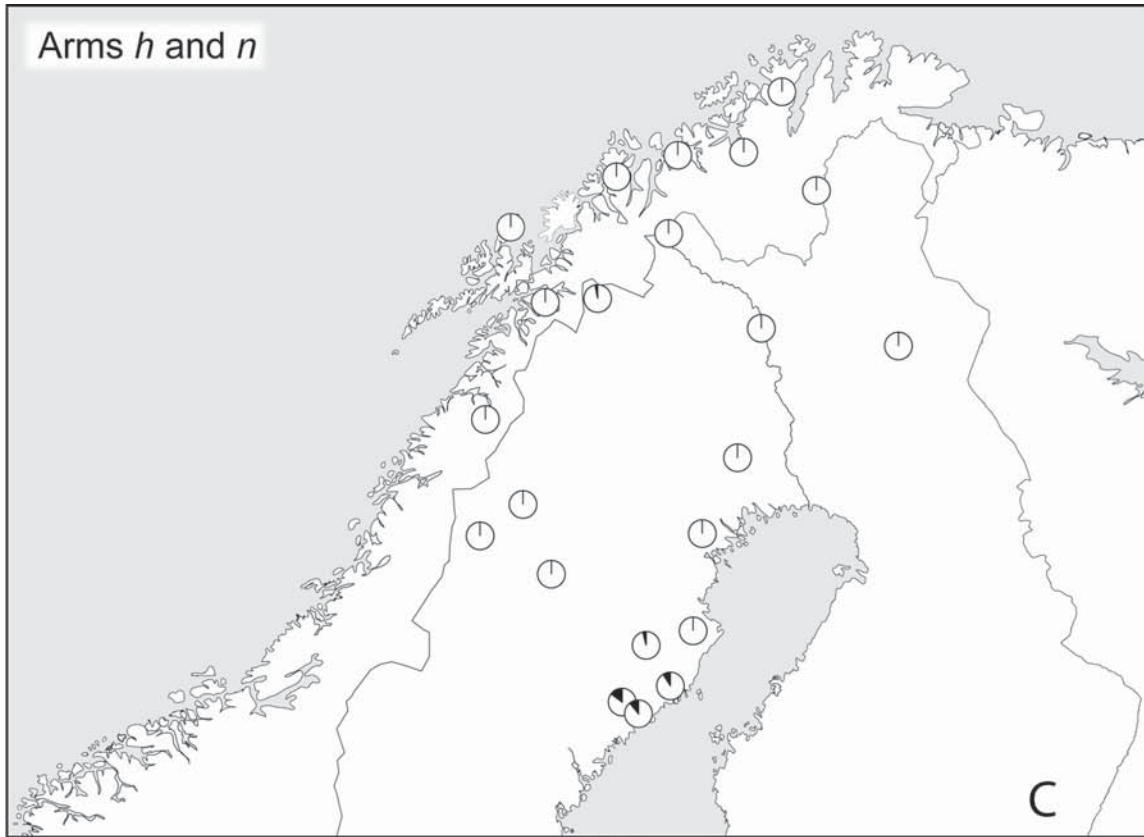


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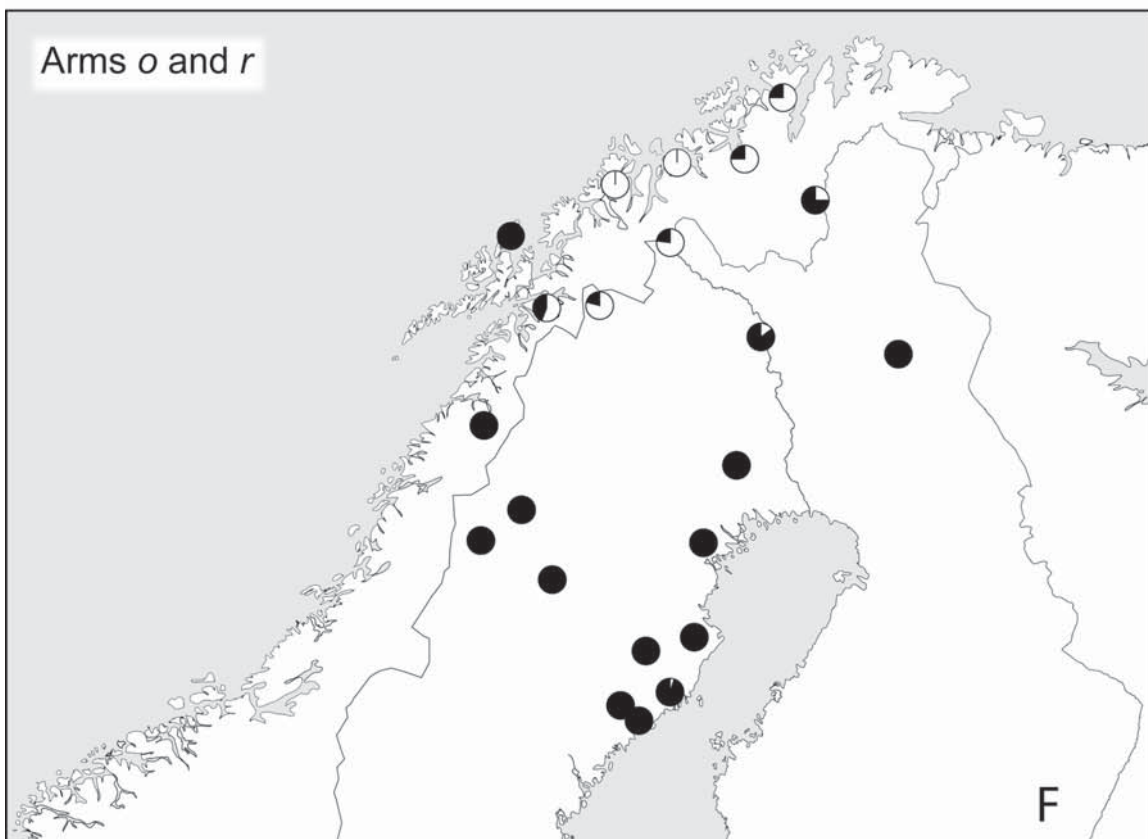
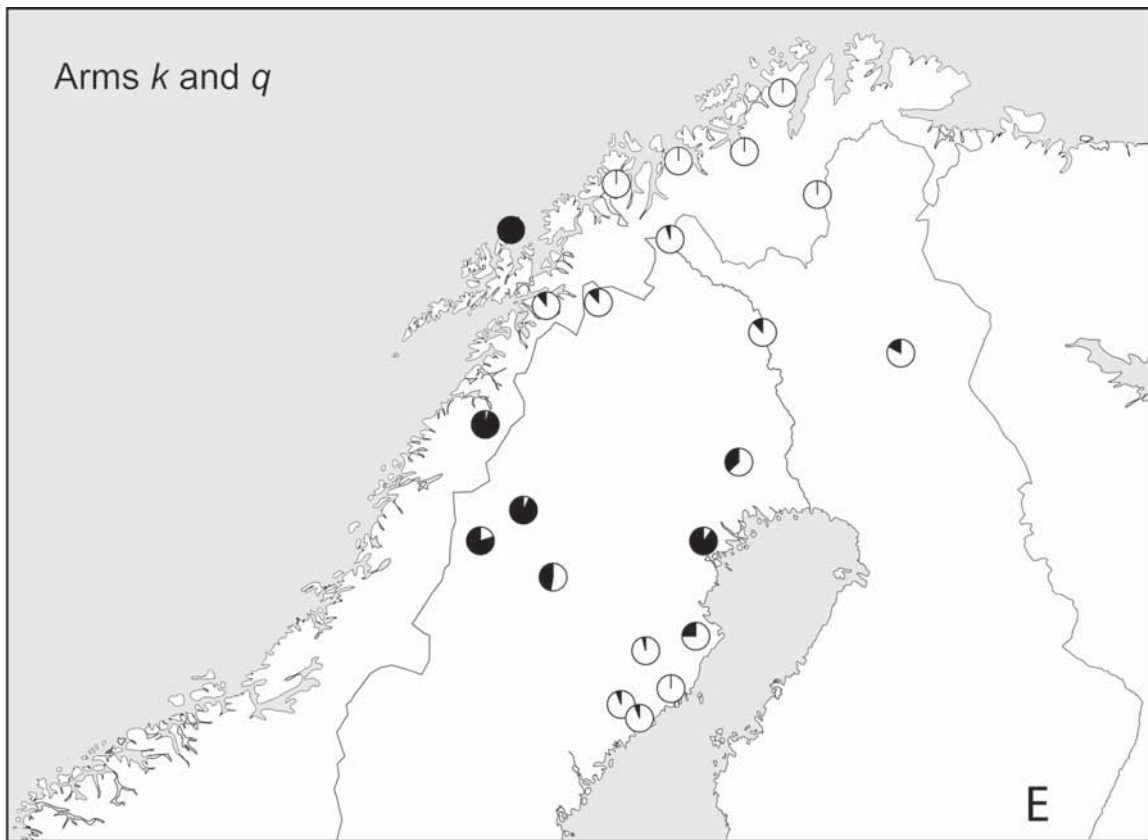


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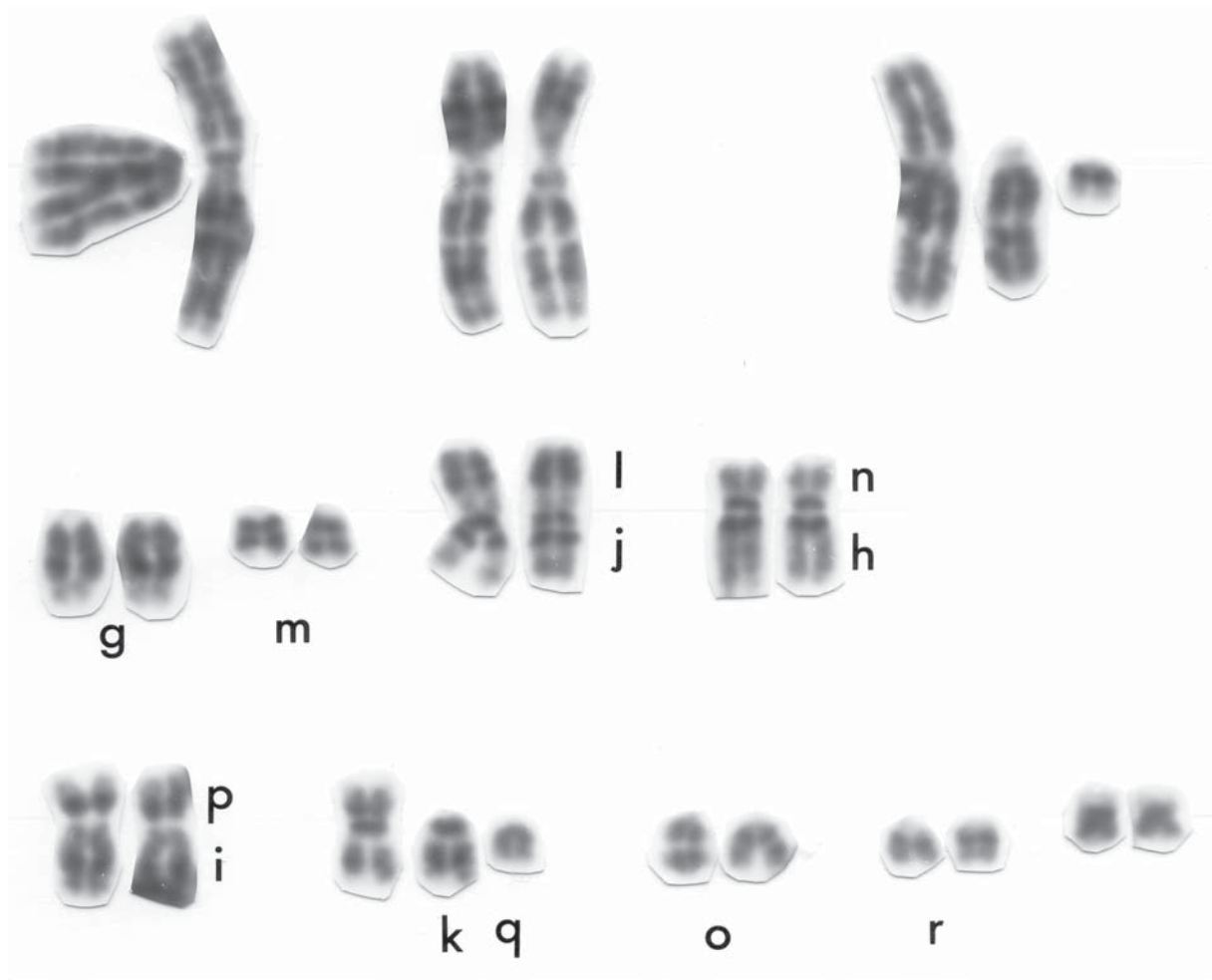


Figure 3. G-banded karyotype of a male *Sorex araneus* of the Ammarnäs race from Överkalix (2NA=23). The arms involved in Robertsonian polymorphism are indicated according to the standard nomenclature (Searle *et al.*, 1991). Characteristic for the Ammarnäs race is that arms *g*, *m*, *o* and *r* are always unfused, arms *hn* and *ip* are always fused, and arms *k* and *q* may be both unfused and fused.

Additional information: This race has previously been included in the Abisko race (Fredga, 1996; Zima *et al.*, 1996). The karyotype of the Ammarnäs race was first demonstrated in Fig. 5 of Frykman *et al.* (1983).

Abisko race (Ai). XX/XY₁Y₂, *af*, *bc*, *g/m*, *hn*, *ip*, *j/l*, *k/q*, *o/r*, *tu*.

Description: Fredga (this paper).

Type locality: Abisko, Sweden, N 68°22', E 18°50'.

Distribution: Northernmost parts of Sweden, Norway and Finland.

Additional information: Shrews of the Hattsjö and Ammarnäs races were previously included in the Abisko race (Fredga, 1996; Zima *et al.*, 1996; Fredga & Narain, 2000; Andersson *et al.*, 2004, 2005).

The characteristics of the races are apparent by their chromosome formulae given above. The Hattsjö race may have the arms *h*, *n*, *i* and *p* unfused, in contrast to the other two races, which always have *hn* and *ip* fused.

The Ammarnäs race always has *g* and *m* unfused. The Abisko race often has *o* and *r* fused, in contrast to the other two races, which essentially always have *o* and *r* unfused. Examples of karyotypes of the newly defined Abisko and Hattsjö races are shown in Figs 3 and 4 in Fredga (1996), and of the Ammarnäs race in Fig. 5 of Frykman *et al.* (1983). A G-banded karyotype of the Ammarnäs race is shown in Fig. 3.

The approximate distributions of the chromosome races in northern Fennoscandia are shown in Fig. 4.

Among the samples included in Tab. 2, those from Andöya and Tromsö are exceptional. Both lack polymorphism and both have extreme karyotypes (Fredga, 2003).

The Andöya population belongs to the Ammarnäs race and the arms *g*, *m*, *k*, *q*, *o* and *r* appear as telocentrics and are never fused (2NA=24, N=18). Andöya is the northernmost of the Lofoten-Vesterålen islands in Northern Norway (locality 18 in Fig. 1). It is located outside the main distribution range of the Ammarnäs

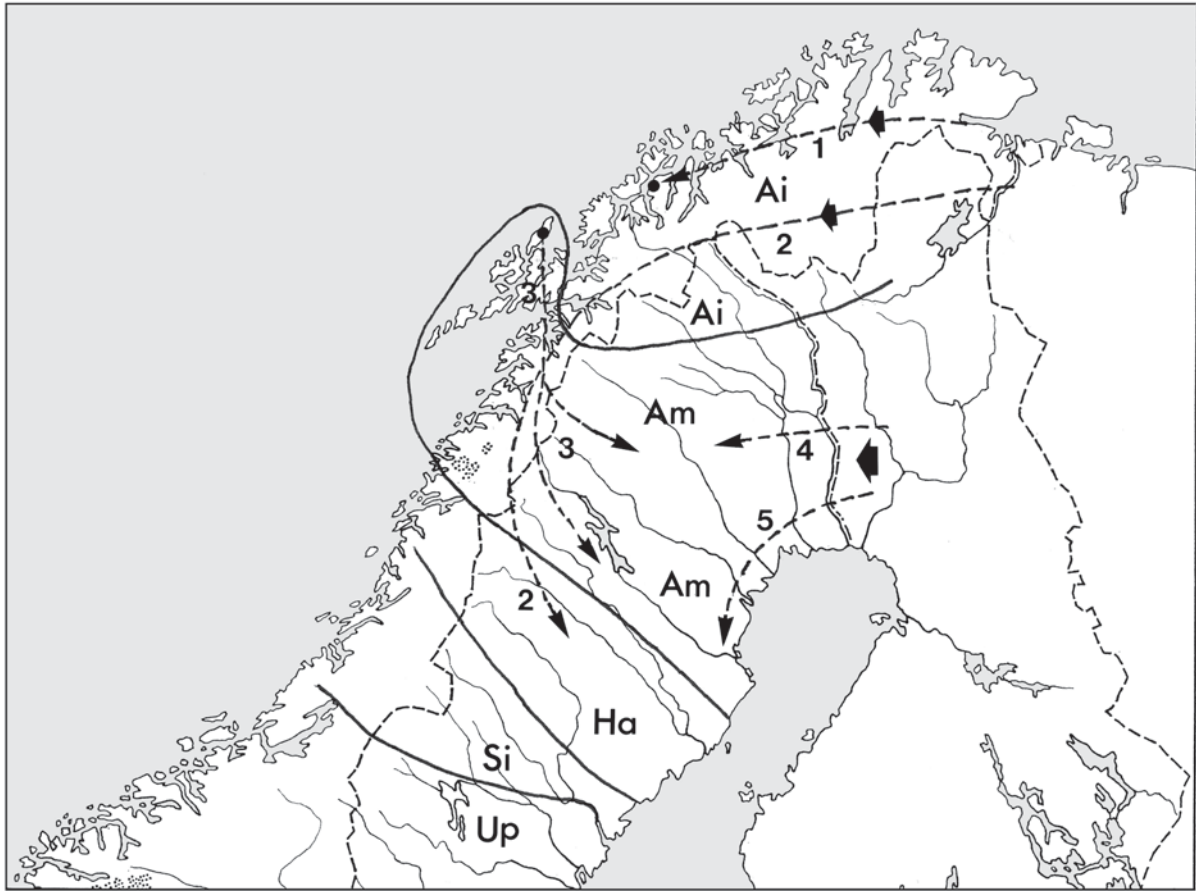


Figure 4. Map showing the approximate distribution of the chromosome races in northern Fennoscandia (solid lines). Up — Uppsala, Si — Sidensjö, Ha — Hattsjö, Am — Ammarnäs, and Ai — Abisko races. Possible colonization routes of common shrews into Scandinavia are indicated by dashed lines and arrows. Arrow 1 represents the Abisko race, arrow 2 a less likely route for the Hattsjö race, arrows 3 and 4–5 alternative routes for the Ammarnäs race (see text).

race. A large number of telocentrics is common for island populations, but may also represent a “primitive” karyotype. It is tempting to speculate that the shrews at Andöya are the descendants of shrews who survived the last glaciation on this island.

The Tromsö sample is from Tromsdalen on the mainland just east of the little Tromsö island (locality 19 in Fig. 1). The karyotype is characterized by having all chromosomes biarmed ($2NA=18$, $N=12$) and is the endpoint in chromosome fusions of the Abisko race.

Discussion

Chromosomes. The present study has shown that it is justified to divide the Abisko race of *Sorex araneus* into three, called Hattsjö (Ha), Ammarnäs (Am) and Abisko (Ai). The apparent similarity between the Hattsjö and Abisko races with respect to arms *g* and *m* is most likely not by descent, and therefore it is justified to separate these two races. The Hattsjö race may be a “hybrid race” which has originated in the hybrid zone between the Ammarnäs and Sidensjö (Si) races, or

originally between the Ammarnäs and Uppsala (Up) races. In the Ammarnäs race the arms *g* and *m* are never fused (*g, m*), in the Sidensjö and Uppsala races these arms are always fused (*gm*), and in the Hattsjö race these arms are both unfused and fused (*g/m*). Another support for the “hybrid hypothesis” is that both the Ha and Si races occupy relatively narrow zones compared to the Am and Up races.

Colonization history. Many terrestrial mammals have colonized Sweden and Norway from at least two directions after the latest glaciation (Jaarola *et al.*, 1999). Previous studies (Fredga & Nawrin, 1977; Fredga, 1996) have demonstrated that the common shrew colonized Sweden from two directions after the latest glaciation, from the southwest and northeast. The five southern races in Sweden (Åk, Hä, Öl, Up and Si) belong to the West European karyotypic group (WEKG), whereas the three northern races (Ha, Am and Ai) belong to the North European karyotypic group (NEKG). The zone of contact between populations of the two karyotypic groups has been studied in some detail (Fredga & Narain, 2000). The Sidensjö and Hattsjö races meet

and hybridize in a 16 km wide hybrid zone in northern Sweden (centre of zone: N 63°31', E 18°04'). The hybrids are fertile (Narain & Fredga, 1998) and gene flow across the hybrid zone seems not to be reduced (Andersson *et al.*, 2004) in spite of considerable chromosomal differences between the two races Si and Ha. I would like to stress that in all previous publications the Hattsjö race was included in the Abisko race.

The present study focuses on the re-colonization of shrews along the northern route. The last glaciation (Weichselian) started about 115 000 years ago. The maximum extent of the glacial ice sheet occurred about 20 000 years ago, when the ice covered most of northern Europe (Andersen & Borns, 1997; Lundqvist, 2002). The retreat of the ice sheet began soon after, opening up routes from the south and northeast for the re-colonization of Fennoscandia by terrestrial animals (Björck & Svensson, 2002). Ca 11 600 years ago a narrow strip along the north coast of Norway was free of ice, and ca 500 years later this strip was enlarged and connected with ice free areas on the west coast of Norway and eastwards with the ice free Kola peninsula and the area west of the White Sea. Ca 10 200 years ago large parts of northern Sweden were covered by ice, but the northernmost parts of Sweden and Finland were ice free. Considerable areas of today's eastern Sweden and western Finland were flooded by water, which made it impossible for shrews to spread southwards along the coast of the Gulf of Bothnia. This colonization route, east of the remains of the ice cover, was opened about 9 500 years ago.

My results indicate that shrews of the Abisko race were the first to colonize Sweden and Norway along the Norwegian coast ca 11 100 years ago (route 1 in Fig. 4). Tromsö may be the end point of this colonization event. Later on a second colonization wave may have continued southwards along the west coast of Norway (route 2 in Fig. 4) and given rise to the Hattsjö race (see below). The Abisko race may have originated somewhere west of the White Sea by fusions of arms *g* and *m*, and *o* and *r*, in shrews with the Ammarnäs karyotype.

Shrews of the Ammarnäs race may have colonized northern Scandinavia according to either of the following two hypotheses:

(i) From the east when this route was opened ca 10 200 years ago shrews spread westwards, and later on all the way to the west coast of Norway (site 14) (route 4 in Fig. 4), and ca 9 500 years ago southwards along the east coast of Sweden (site 9) (route 5 in Fig. 4). We do not know the origin of the Ammarnäs race. Is it on the eastern or western side of the Muonio and Torne rivers (which constitute the borderline between Sweden and Finland)? Today the shrews on the western side are of the Ammarnäs race, but on the eastern bank the chromosome constitution is unknown. However, it is likely that the ancestors of the Ammarnäs race are to be found in northern Finland, because in Laukkuvaara, Savukoski, and Luosto, Sodankylä, two Finnish localities about 150 km east of the rivers, 8 out of 9 specimens had the karyotype characteristic of the present Ammarnäs race

(Halkka *et al.*, 1987). Only one specimen was heterozygous for the arm combination *go*, which is characteristic for the Savukoski, Kuhmo and Ilomantsi races in northern, central and eastern Finland. This single shrew is the type specimen of the Savukoski race, which was separated from the Kuhmo race by the ISACC "because of isolated distribution and presence of arms *m* and *r* as acrocentrics" (Zima *et al.* 1996). Halkka *et al.* (1987) included the Savukoski race in the Kuhmo race.

(ii) From the Isle of Andöya (site 18) when the mainland became ice-free (route 3 in Fig. 4) shrews spread eastwards to the Torne river, and perhaps further eastwards, and southwards to the area of the present Hattsjö race. The shrew population on Andöya may have survived the last glacial maximum on the island. It is of the Ammarnäs race, monomorphic, and with the arms *g*, *m*, *k*, *q*, *o*, *r* unfused. This may be regarded as a "primitive" character, but is also characteristic of insular populations (e.g. the Öland race on the Isle of Öland and the Lemland race on the Åland Islands). At least parts of Andöya were ice-free during the last glacial maximum (Vorren *et al.*, 1988; Möller *et al.*, 1992), and it is possible that the environment fulfilled the basic habitat requirements of the common shrew, which is a surprisingly tough species. A detailed discussion on glacial survival of small mammals in northwest Norway is given by Brunhoff *et al.* (2006).

Shrews of the Hattsjö race have most likely originated by hybridization when shrews of the North and West European karyotypic groups met (see p.94). Another, less likely, scenario is that a second wave of representatives of the Abisko race continued southwards along the west coast of Norway and then followed the Ume river south-eastwards to the coast of the Baltic (route 2 in Fig. 4). These shrews should then be the ancestors of the Hattsjö race. The Abisko population along the Norwegian coast was later replaced by the Ammarnäs race (site 14).

The cytochrome *b* gene of the mitochondrial DNA has been sequenced in common shrews from northern Scandinavia and the frequencies of various haplotypes determined (Andersson, 2004). However, the mtDNA structure is discordant with the chromosomal groupings and does not help answer the question about the colonization history of *Sorex araneus* in northern Scandinavia.

Conclusions

Three chromosome races of the common shrew occur in northern Scandinavia: Abisko, Ammarnäs and Hattsjö. Shrews of the Abisko race were the first to colonize Norway and Sweden from the east along the Norwegian coast. Shrews of the Ammarnäs race later colonized northern Sweden from Finland, or from a population that had survived the last glaciation on the Isle of Andöya in northwest Norway. The Hattsjö race is regarded as a hybrid race that originated when populations of the Ammarnäs race met shrews that had colonized Sweden from the south.

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