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# Population genetics of north temperate shrews (Soricidae). A review

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The published data on the electrophoretically detectable variation in and the genetic differentiation of north temperate shrews are reviewed with a database of 54 loci from nine studies (39 enzymes of which 27 are variable). This paper summarizes the mean heterozygosity ($H$) and the average number of polymorphic loci ($P$) for 17 species belonging to three genera. Genetic variation within and between shrew species is substantial but not uniform. More research should be conducted on small-scale variation especially in *Sorex araneus* but also in the other species. Intriguing observations for subdivision of populations, temporal changes in genetic variability and differencies between the sexes are discussed.

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## 1. Introduction

Most electrophoretic studies on genetic variation in and differentiation of small mammals have been conducted on rodents, while studies on insectivorous mammals are rare. Only a few papers dealing with shrews, and mostly with the species belonging to *Sorex*, have been published during recent years, although one of the earliest papers in mammalian biochemical taxonomy included shrew material (*Sorex vagrans* and *S. obscurus*; Johnson & Wicks' (1959) work on serum proteins).

Mammals have generally been regarded as the least variable taxonomic group (Nevo 1978), but among mammals interspecific and intraspecific variation may be considerable. Mean heterozygosity ($H$) and the number of polymorphic loci ($P$) range widely: in interspecific comparisons $H$=0.000–0.106, $P$=0.00–0.73 and in intraspecific comparisons $H$=0.008–0.085, $P$=0.13–0.32 (Nevo 1978).

Genetic heterogeneity over very short geographic distances has been observed for many species of small mammals (e.g. Chesser 1983, Folz & Hoogland 1983 for *Cynomys ludovicianus*, Patton & Feder 1981 for *Thomomys bottae*, Selander et al. 1969, Defries & McClearn 1972, Bonhomme et al. 1984 for *Mus musculus*). For prairie dogs, pocket gophers and mice, the social structure of populations is generally considered as a major reason for small-scale variability (though see Baker 1981 for the house mouse). In other cases, random events such as drift, founder effect and bottle necks are assumed to be the major processes affecting the genetical structure of populations (e.g. Kilpatrick 1981).

The purpose of this paper is to review the published data on variation in and genetic differentiation of north temperate shrews.

## 2. Species studied

The common shrew *Sorex araneus* is a widely distributed and abundant species ranging from West Europe to Central Siberia. It has for a long time been the most intensively studied shrew in cytology, because of its extensive chromosomal polymorphism (see e.g. Halkka et al. 1986, 1987). More recently, Frykman et al. (1983) in Sweden and Searle (1985) in England have examined the enzyme gene variation in and between the different chromosomal races of the common shrew (see also Catzeflis 1984). Frykman & Simonsen (1984) have also studied *Sorex minutus*, *S. caecutiens* and *Neomys fodiens*.

Catzeflis et al. (1982) and Catzeflis (1984) have compared eight species of *Sorex* (*S. araneus*, *S. coronatus*, *S. granarius*, *S. samniticus*, *S. minutus*, *S. alpinus*, *S. isodon* and *S. caecutiens*), in addition to two *Neomys*, three *Crocidura* and two *Suncus* (*N. anomalus* and *N. fodiens*, *C. suaveolens*, *C. leucodon* and *C. russula*, *S. etruscus* and *S. murinus*). Catzeflis (1984) summarizes the taxonomy and phylogeny of the European *Sorex*.

Gebczynski (1985) has studied temporal genetic variation in *Sorex minutus*, and Gebczynski & Jacek (1980) have examined the overall biochemical variation in two *Sorex* and *Neomys* species (*S. araneus*, *S. minutus*, *N. fodiens* and *N. anomalus*) in the Bialowieza National Park in Poland. Data on enzyme gene variation in several populations of *S. araneus*, *S. caecutiens* and *S. minutus* in Finland are included in this paper (Heikkilä, unpubl.).

George (1984, 1988) has studied the systematics and evolution of the New World *Sorex*, but she has also published the mean heterozygosity and percentage polymorphism values for 26 *Sorex* species (*S. araneus*, *S. arcticus*, *S. arizonae*, *S. bendrii*, *S. caecutiens*, *S. cinereus*, *S. dispar*, *S. fontinalis*, *S. fumeus*, *S. gracillimus*, *S. haydeni*, *S. hoyi*, *S. longirostris*, *S. merriami*, *S. minutus*, *S. monticolus*, *S. nanus*, *S. ornatus*, *S. pacificus*, *S. palustris*, *S. preblei*, *S. tenellus*, *S. trowbridgii*, *S. tundrensis*, *S. unguiculatus*, *S. vagrans*), with *Notiosorex crawfordii* and *Cryptotis parva* as outgroups.

The species included in the present study, the sample sizes, the number of loci scored, mean heterozygosities and the percentage of polymorphic loci are listed in Table 1.

## 3. Results and discussion

### 3.1. Number of alleles in polymorphic loci

It is difficult to compare the allele frequencies in different data sets because of the uncertainty in cross-identifying alleles from different papers. The number of alleles in polymorphic loci can however be used as a measure of genetic variation within and between species. A total of 54 loci (39 enzymes) has been scored for shrews by eight authors during the last ten years. Of the 54 loci, 27 have been found to be variable (Table 2). It is clear that certain loci have been studied more intensively and frequently than others, and provide therefore more comparable data. *Ak* (two loci), *esterases* (at least four loci), *G-6-pdh*, *Got* (two loci), *Gdp* (two loci), *Hb*, *Idh* (two loci), *Ldh* (two loci), *Lap* (two loci), *Mdh* (two loci), *Pgm* (three loci) and *6-Pgd* have been the most popular and also the most variable loci used in these studies.

Considering the commonest polymorphic loci in *S. araneus*, *Ak* seems to express two alleles in Switzerland (Catzeflis et al. 1982) and Finland (George 1988, though the Finnish sample is very small, only five individuals). Variation in *esterase* loci ranges from one to four alleles per population, depending on the locus stained. In Finland, the 4-methyl umbelliferylacetate-stained esterase seems to have its own electromorph in south-eastern Finland (frequency 0.04), where it is restricted to the chromosomal race III (Heikkilä unpubl.; for the chromosomal races of *S. araneus* in Finland see Halkka et al. 1986, 1987).

Two *esterase* loci exhibit two or three alleles in Swiss, Hungarian and Austrian (*Est-1*) populations, but are monomorphic in Italian populations (Catzeflis et al. 1982). Different alleles are present in different European populations, and the total number of alleles is five (*Est-1*) and four (*Est-2*) (Catzeflis 1984).

The *Pgm* loci in England (Searle 1985) exhibit great variation in the number of alleles. Four, three and five alleles have been scored in *Pgm-1*, *Pgm-2* and *Pgm-3*, respectively. *Pgm-3* seems to have one rare allele only in the Oxford race of *S. araneus*. In other parts of Europe, *Pgm* comprises five alleles altogether (Catzeflis et al. 1982). According to Frykman et al. (1983), possibly two different alleles can be found in Swedish populations, but in Finland *Pgm* seems to be monomorphic (Catzeflis et al. 1982, Heikkilä unpubl.).

*6-Pgd* had three alleles in a sample collected from England (George 1988), while in Switzerland, Finland (Catzeflis et al. 1982) and Sweden (Frykman et al. 1983) *6-Pgd* has two alleles. Heikkilä (unpubl.) found *6-Pgd* to be monomorphic in Finland (246 specimens).

The number of alleles in the *Mpi* locus in *S. araneus* varies from six in England (Searle 1985) to four in Sweden (Frykman et al. 1983) and Finland (Heikkilä unpubl.). *Mpi* appears to be very informative in *S. araneus*, but unfortunately it has been studied only in English, Swedish and Finnish populations. *Mpi* seems to have unique alleles in Finland and Sweden restricted to particular chromosomal races (for Finland see Halkka et al. 1987, for England Searle 1985 and for Sweden Frykman et al. 1983), suggesting that there may be barriers to gene flow between the different races. Only a few karyotypic hybrids have been found in Sweden (Frykman & Bengtson 1984), while in England hybrid zone samples included "some" individuals with a hybrid karyotype (Searle 1985).

Several authors (Stangl 1986, Sulivan et al. 1986, Cothran & Zimmerman 1985, Robbins et al. 1985, Tucker & Schmidly 1981) have demonstrated contact zones with variable rates of hybridization and gene flow in species and chromosomal forms of *Peromyscus*, *Onychomys* and *Geomys*. For instance in *Onychomys*, several unique alleles have been found in the different chromosomal forms *O. arenicola*, *O. torridus* and *O. leucocaster* (Sulivan et al. 1986). For the formation and maintenance of hybrid zones see the rewiew by Barton & Hewitt (1989).

To summarize the allelic variation observed in *S. araneus*, the number of alleles in particular loci ap-

Table 1. Sample size ($N$), number of loci ($N_L$), mean heterozygosity ($H$) (0.01 level) and the number of polymorphic loci ($P$) in shrews.

| Species | $N$ | $N_L$ | $H$ | $P$ | Source of data |
|---|---|---|---|---|---|
| *Sorex araneus* | 23 | 11 | 0.057 | 72.72 | Gebczynski & Jacek 1980 |
| | 31 | 22 | 0.022 | 40.90 | Catzeflis et al. 1982 |
| | 113 | 27 | 0.041 | 62.96 | Catzeflis 1984 |
| | 100 | 35 | 0.028 | 31.43 | Frykman & Simonsen 1984 |
| | 10 | 26 | 0.023 | 11.5 | George 1984 |
| | 286 | 6 | *** | *** | Searle 1985 |
| | 8 | 26 | 0.02 | 11.54 | George 1988 |
| | 246 | 23 | 0.04 | 30.43 | Heikkilä (unpubl.) |
| *Sorex alpinus* | 11 | 22 | 0.011 | 27.27 | Catzeflis et al. 1982 |
| | 14 | 26 | 0.026 | 23.08 | Catzeflis 1984 |
| *Sorex arcticus* | 2 | 26 | 0.019 | 7.7 | George 1984 |
| | 2 | 26 | 0.02 | 7.69 | George 1988 |
| *Sorex caecutiens* | 10 | 26 | 0.054 | 15.38 | Catzeflis 1984 |
| | 7 | 35 | 0.024 | 8.57 | Frykman & Simonsen 1984 |
| | 10 | 26 | 0.050 | 34.6 | George 1984 |
| | 5 | 26 | 0.02 | 3.85 | George 1988 |
| | 37 | 23 | 0.02 | 17.39 | Heikkilä (unpubl.) |
| *Sorex cinereus* | 19 | 26 | 0.039 | 26.9 | George 1984 |
| | 19 | 26 | 0.04 | 23.08 | George 1988 |
| *Sorex coronatus* | 14 | 22 | 0.026 | 13.64 | Catzeflis et al. 1982 |
| | 32 | 27 | 0.031 | 18.52 | Catzeflis 1984 |
| *Sorex hoyi* | 4 | 26 | 0.010 | 3.8 | George 1984 |
| | 4 | 26 | 0.01 | 3.85 | George 1988 |
| *Sorex isodon* | 12 | 26 | 0.045 | 19.23 | Catzeflis 1984 |
| *Sorex minutus* | 36 | 11 | 0.047 | 63.64 | Gebczynski & Jacek 1980 |
| | 4 | 22 | 0.019 | 4.55 | Catzeflis et al. 1982 |
| | 21 | 26 | 0.039 | 23.08 | Catzeflis 1984 |
| | 15 | 35 | 0.036 | 25.71 | Frykman & Simonsen 1984 |
| | 92 | 22 | 0.025 | 45.45 | Gebczynski 1985 |
| | 5 | 26 | 0.023 | 11.5 | George 1984 |
| | 5 | 26 | 0.02 | 11.54 | George 1988 |
| | 25 | 23 | 0.02 | 17.39 | Heikkilä (unpubl.) |
| *Sorex monticolus* | 13 | 26 | 0.03 | 19.23 | George 1988 |
| *Sorex palustris* | 12 | 26 | 0.016 | 23.1 | George 1984 |
| | 12 | 26 | 0.02 | 19.23 | George 1988 |
| *Sorex trowbridgii* | 10 | 26 | 0.015 | 11.5 | George 1984 |
| | 10 | 26 | 0.02 | 11.54 | George 1988 |
| *Sorex tundraensis* | 4 | 26 | 0.019 | 7.7 | George 1984 |
| | 4 | 26 | 0.02 | 7.69 | George 1988 |
| *Sorex vargans* | 19 | 26 | 0.038 | 42.3 | George 1984 |
| | 4 | 26 | 0.04 | 15.38 | George 1988 |
| *Neomys anomalus* | 8 | 11 | 0.044 | 63.64 | Gebzynski & Jacek 1980 |
| | 22 | 32 | 0.015 | 34.37 | Catzeflis 1984 |
| *Neomys fodiens* | 10 | 11 | 0.046 | 72.72 | Gebzynski & Jacek 1980 |
| | 41 | 32 | 0.029 | 40.62 | Catzeflis 1984 |
| | 9 | 35 | 0.030 | 5.71 | Frykman & Simonsen 1984 |
| *Crocidura suaveolens* | 50 | 28 | 0.015 | 67.85 | Catzeflis 1984 |

*** Values not available.

Table 2. The loci scored in the different population genetic studies on shrews. The variable loci are marked with an asterisk (*).

| Locus | Abbreviation | Tissue[1] | Source of data[2] |
|---|---|---|---|
| Acid phosphatase | PA (ACP) | L,K | 2,3,9 |
| Aconitase | *ACO | L | 4 |
| Adenosine deaminase | *ADA | L,H | 4,9 |
| Adenylate kinase | *AK (ADK) | (2) L,H,K | 2,4,5,8,9 |
| Alcohol dehydrogenase | *ADH | L | 4 |
| Albumin | *AB (ALB) | H,K | 3,5,8 |
| Catalase | CAT | L | 4 |
| Creatine kinase | CK | H | 2,3 |
| Diaphorase | DIA | L | 4 |
| Esterase | *ES(EST,ESB) | (4) L,K,P | 1,2,3,4,5,6,7,8,9 |
| Fumarate hydrogenase | FH | L | 4 |
| Glucose dehydrogenase | GDH | H,K | 5 |
| Glucose-6-phosphate- dehydrogenase | *G-6-PD (G-6-PDH) | H,K | 2,3,4,5,8,9 |
| Glucosephosphate isomerase | *GPI | H,K | 4,8 |
| Glutamate oxaloacetate | *GOT (AAT) | (2) L,K | 2,3,4,5,8,9 |
| Glutamic-pyruvic transaminase | GPT | H | 4 |
| a-Glycerophosphate dehydrogenase | *a-GBD (-GBDH) (2) | L | 2,3,4,5,8,9 |
| Glyseraldehyde-3-phosphate dehydrogenase | GAPDH | L | 9 |
| Hemoglobine | *HB | H,K | 2,3,5,6,8 |
| Hexokinase | HK | L | 4 |
| Isocitrate dehydrogenase | *IDH | (2) H,K | 2,3,4,5,8,9 |
| Indophenol oxidace | *IPO | (3) K | 3 |
| Lactate dehydrogenase | *LDH | (2) H,K | 1,2,3,4,5,6,7,8,9 |
| Leucine-aminopeptidase | *LAP | (2) L,H,K | 1,2,3,6,9 |
| Malate dehydrogenase | *MDH | (2) L,H,K | 1,2,3,4,5,6,8,9 |
| Malic enzyme | *ME (MOD) | L,H,K | 3,4,5,8 |
| Mannose phosphate isomerase | *MPI | H,K | 4,7,9 |
| Non-specific hydrogenase | *NDH | H,K | 4 |
| Nucleoside phosphorylase | NP | K | 4 |
| Peptidase | *PEP | (3) H,K | 4,5,8,9 |
| Phosphoglucomutase | *PGM | (3) H,K,L | 2,3,4,5,7,8,9 |
| 6-phosphogluconate dehydrogenase | *6-PGD (PGD) | H,K | 2,3,4,5,8,9 |
| Phosphoglucose isomerase | *PGI (GPI) | H,K | 2,3,5,9 |
| Phosphoglycerate kinase | PGK | L | 4 |
| Sorbitol dehydrogenase | SDH | L | 9 |
| Superoxidase dismutase | *SOD | H,K | 4,5,8 |
| Transferrine | *TRF (TF) | L | 2,3, |
| Xanthine dehydrogenase | *XDH | H,K | 2,3,8,9 |
| Protein-A | *PROT-A | E | 6 |

[1] L=Liver, H=Heart, K=Kidney, P=Plasma, E=Erythrocytes. The number of loci in parenthesis.
[2] 1) Gebzynski & Jacek (1980), 2) Catzeflis et al. (1982), 3) Catzeflis (1984), 4) Frykman & Simonsen (1984), 5) George (1984), 6) Gebczynski (1985), 7) Searle (1985), 8) George (1988), 9) Heikkilä (unpubl.)

pears to be greater in England than in other parts of Europe, but this is probably because of the more sensitive method (cellulose acetate plates) used by Searle (1985) than most of the others (starch gels). In general, variation in the number of alleles in different loci is great in Europe. There are clear and sharp boundaries between some chromosomal races of *S. araneus* in Sweden, England and Finland, but whether there are true hybridization barriers between the chromosomal races cannot be settled without crossing experiments in the laboratory. The number of alleles can vary substantially between local populations even if there are no racial differencies (Frykman & Bengtson 1984, Searle 1985).

For species other than *S. araneus* there are little data for comparing the numbers of alleles in polymorphic loci, and only *S. caecutiens*, *S. minutus* and *Neomys fodiens* will be examined below.

According to Frykman (1984), *S. caecutiens* has three polymorphic loci out of 35: *EsB1*, *Mpi* and *Pgm*, all having two alleles. In the Finnish data (Heikkilä unpubl.), *S. caecutiens* had three alleles in *Ada* and *Est2* and two alleles in *Mpi* and *Pgi*. In Catzeflis' (1984) sample of Finnish *S. caecutiens* there were three alleles in *Est2* and *Pgm* and two in *Est1* and *Mod*. In George's (1988) sample, *S. caecutiens* had three alleles in *Pep-D* in Finland, two alleles in Honshu, but only one in Hokkaido, while *Pep-B* was monomorphic in Finland and Hokkaido but had two alleles in Honshu. Differences were found also in *Ab*, *Idh2*, *Ldh1* and *6-Pgd* between the Finnish and Japanese samples of *S. caecutiens*, the Finnish sample being monomorphic while the others had not more than two alleles (George 1988).

Turning to *Sorex minutus*, this had 9 polymorphic loci out of 35 in Sweden, all with two alleles (Frykman 1984): *Ada*, *Adh*, *Cat*, *EsB1*, *EsD*, *Idh2*, *LdhA*, *Mpi* and *Pgm*. In Finland *S. minutus* had two alleles in *Ada*, *Est2*, *Mpi* and *Pgi* (Heikkilä, unpubl.). In George's (1988) sample of *S. minutus*, *XDH*, *Hb* and *G-6-pdh* were polymorphic with 2, 2 and 3 alleles, respectively. In Switzerland *S. minutus* exhibits two alleles only in *Ldh-A*, the others (21 loci) being monomorphic (Catzeflis et al. 1982). According to Gebczynski (1985), *S. minutus* is polymorphic at 10 out of 22 loci in Poland, *Es-1*, *Es-6*, *Es-8*, *Ldh-1*, *Ldh-2*, *Lap-1*, *Lap-2* and *Prot.A* exhibiting two alleles while *Es-2* and *Mdh-1* had three alleles.

*Neomys fodiens* in Sweden had only two polymorphic loci, *Mpi* and *Pgm*, with two alleles (Frykman 1984). In Poland this species had four alleles in *Es-3*, three alleles in *Lap-2*, *Mdh-1* and *Es-1*, and two alleles in *Ldh-1* *Ldh-2*, *Lap-1* and *Es-2* (Gebczynski & Jacek 1980). According to Catzeflis (1984), the number of polymorphic loci in *N. fodiens* vary from 4, 6 and 5 out of 32 in Finnish, French and Italian populations, respectively, to 11 out of 32 in Swiss populations. The total number of polymorphic loci in *N. fodiens* is 15 out of 32 (Catzeflis 1984). The allele numbers in *Mpi* and *Pgm* are two and four, respectively (Catzeflis 1984). In Poland *N. fodiens* exhibits two to four alleles in *esterases* (Gebczynski & Jacek 1980), but it is entirely monomorphic in Sweden (four different esterases; Frykman 1984).

From these data it is difficult to draw any general conclusions about the variation in the allele number in *S. caecutiens*, *S. minutus* and *N. fodiens*, because the results much depend on sample size and the loci scored (the sample sizes are generally small). Frykman & Simonsen (1984) conclude that the electrophoretically detectable genetic variation in *S. caecutiens*, *S. minutus* and *N. fodiens* is in general about the same as in *S. araneus*.

### 3.2. Average heterozygosity

Average heterozygosity and the number of polymorphic loci (generally scored at 1% level) are two widely used estimates of genetic variability in populations and species. Both of these parameters have their disadvantages related to small sample sizes and the loci scored (Nei & Graur 1984, Nevo 1978).

Average intraspecific heterozygosity values for mammals range generally from 0.008 to 0.085 (Nevo 1978). For subterranean insectivores Tolliver et al. (1985) give mean heterozygosity values from 0.000 to 0.024, for non-subterranean species from 0.026 to 0.034, and for insectivores in general the values range from 0.016 to 0.030. For three shrew species Nevo et al. (1984) give values from 0.011 to 0.026. Unfortunately, methodological differencies hamper direct comparisons between different studies. A case in point is the study of Gebczynski & Jacek (1980). Their extremely high average heterozygosity values are based on polymorphic loci only, and for this reason these cannot be used in comparisons.

In *S. araneus* the heterozygosity values range from 0.02 (George 1988) to 0.041 (Catzeflis 1984, Heikkilä unpubl.). These values agree closely with values reported by Nevo (1978) for mammals in general. If only data including one hundred or more individuals are considered, the picture changes only a little, and the values vary from 0.028 (Frykman & Simonsen 1984) to 0.041 (Catzeflis 1984, Heikkilä unpubl.; Table 1).

In *S. caecutiens* the mean heterozygosity varies from 0.02 (George 1988, Heikkilä unpubl.) to 0.054 (Catzeflis 1984), in *S. minutus* from 0.02 (George 1988, Heikkilä unpubl.) to 0.039 (Catzeflis 1984), and in *N. fodiens* the mean heterozygosity is about 0.03 (Catzeflis 1984, Frykman & Simonsen 1984; Table 1).

For *Sorex* species in general these studies give mean heterozygosity values ranging from 0.010 (*S. hoyi*, George 1984) to 0.054 (*S. caecutiens*, Catzeflis 1984), for *Neomys* species from 0.015 (*N. anomalus*, Catzeflis 1984) to about 0.03 (*N. fodiens*, Catzeflis 1984, Frykman & Simonsen 1984), and for *Crocidura suaveolens* 0.015 (Catzeflis 1984; Table 1). In the New World species the variation in heterozygosity is from 0.010 to 0.039 (George 1984), while

in the Old World species it is from 0.011 to 0.054 (Catzeflis 1984). The difference is not statistically significant (Mann-Whitney $U$, $z$=–1.53, $P>z$=0.13).

Tolliver & Robbins (1987) observed statistically significant differences in average heterozygosity between males and females of *Blarina carolinensis*, but they could not give any explanation for the difference. Unfortunately, this kind of work has not been conducted on other shrew species or on small mammals in general.

In general, the number of loci studied in these studies ranges from 22 to 35 (Gebczynski & Jacek 1980 excluded). The sample sizes, excluding *S. araneus*, are small, ranging from a few individuals to tens of individuals. Nonetheless, the observed variation in mean heterozygosity between populations is extensive, and in *S. araneus*, *S. caecutiens* and *S. minutus* the values observed in different populations vary by even two orders of magnitude.

### 3.3. The number of polymorphic loci

The number of polymorphic loci (at 1% level) ranges from 72% (*S. araneus*, Gebczynski & Jacek 1980, based on 11 loci) to 4% (*S. hoyi*, George 1984, 1988, based on 25 loci; Table 1). Variation is also large within species but between studies. For instance in *S. araneus*, the observed variation is from 72 to 11% (Gebzynski & Jacek 1980, George 1984, 1988).

Another view to variation in the number of polymorphic loci can be obtained by considering whether or not individual loci are polymorphic in different areas. In *S. araneus*, *Ak* is polymorphic in mixed samples from Finland, England (George 1988) and Switzerland (Catzeflis et al. 1982), but it seems to be monomorphic in four other populations in Switzerland and Italy (Catzeflis et al. 1982). In the *Ldh* loci, there seems to be little variation in Sweden (Frykman et al. 1983), Switzerland (Catzeflis et al. 1982) and England (Searle 1985), but in Poland *Ldh-1* varies more substantially (Gebczynski & Jacek 1980). *Mdh* seems to be monomorphic in Sweden (Frykman et al. 1983) and in large parts of Europe, except in Hungary (Catzeflis 1984). In Poland *Mdh-1* is highly polymorphic (Gebczynski & Jacek 1980). In general, there are no obvious trends in the number of polymorphic loci in *S. araneus* on a large spatial scale, but variation on smaller areas can be substantial (e.g. Catzeflis 1984, Frykman et al. 1983, Heikkilä unpubl.).

In different species, the percentage of polymorphic loci ranges from 15 (*S. caecutiens*) to 63% (*S. araneus*; Catzeflis 1984) in the European *Sorex* species, whereas in the New World *Sorex* the values range from 4 (*S. hoyi*) to 42% (*S. vagrans*; George 1984, 1988).

### 3.4. Temporal patterns

Very little data are available on temporal genetic variation in shrews. Gebczynski (1985) has recently published a study on seasonal variation in biochemical polymorphism in *S. minutus*. According to him, 10 out of 22 loci were polymorphic. There seemed to be differences, but not uniform ones, in allele frequencies in different loci between samples of individuals of different ages. The average heterozygosity values changed slightly throughout the year, being lowest in autumn and winter and highest in the oldest, ower-wintered shrews. A possible explanation for such variation in heterozygosity is a higher rate of mortality of homozygotes during winter and early spring (Gebczynski 1985). Unfortunately, Gebczynski (1985) did not analyse possible differences between the sexes, as did Tolliver & Robbins (1987), who found statistically significant differences in mean heterozygosity between the sexes of *Blarina carolinensis*. For the reliability of certain enzymes in general as genetic markers see Mihok & Ewing (1983) and McGovern & Tracy (1981).

### 3.5. Intraspecific variation

Using the standard genetic distances of Nei (1972, 1978), there are differences of an order of magnitude between populations of *S. araneus* in Central and southern Europe and northern Europe (Catzeflis 1984). The genetic distances between Swiss and Italian populations range from 0.003 to 0.052, while between Hungarian and Austrian populations the distance is 0.001. The distances between North and South European populations range from 0.068 to 0.210, between Danish and Finnish populations from 0.091 to 0.102, and among Finnish populations the standard genetic distance is 0.005 (Fig 1).

Genetic distances vary in the same manner in *N. fodiens*. The Finnish sample differs from Swiss, Italian and French samples at genetic distances ranging from 0.061 to 0.146. Interestingly, the genetic distance between two Swiss populations was as high as 0.94 (Catzeflis 1984). Genetic distances between Swedish *S. araneus* chromosomal races vary from

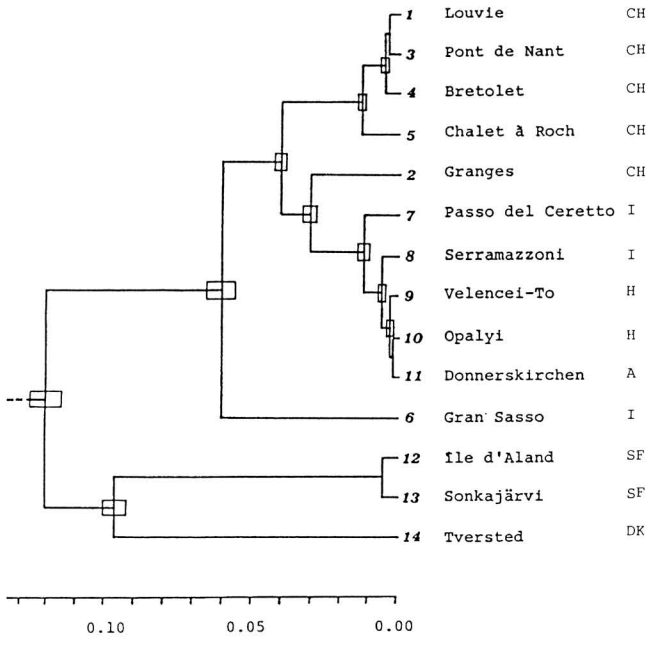


Fig 1. Phenetic dendrogram (UPGMA) constructed from standard genetic distances (Nei 1978) according to Catzeflis (1984). Boxes represent standard errors. Fourteen populations of *Sorex araneus* from different parts of Europe. Abbreviations: CH = Switzerland, I = Italy, H = Hungary, A = Austria, SF = Finland and DK = Denmark.

0.004 to 0.019, being largest between the northern and southern races (Frykman & Simonsen 1984). The results of Frykman & Simonsen (1984) and Catzeflis (1984) are based on variation in 27 loci, analysed with Nei's formula (1978).

### 3.6. Intrageneric and intergeneric variation

The standard genetic distances in the *araneus* species group (*S. araneus*, *S. coronatus* and *S. granarius*) vary from 0.038 to 0.184 (0.057–0.111) and 0.006 to 0.165 (0.009–0.057) between *S. araneus* and *S. coronatus* and *S. araneus* and *S. granarius* respectively. The distance between *S. coronatus* and *S. granarius* varies from 0.043 to 0.116 (0.057–0.065) (Catzeflis 1984; values in parenthesis are from Catzeflis et al. 1982). This group consists of morphologically very similar species, which form a phyletic unit with relatively low genetic distances between the members.

A similar situation occurs amongst some Nearctic species, for instance *S. monticolus* and *S. vagrans*, which species George (1984) included in one group, referred to as *S. vagrans*. Within the *cinereus* species group, *S. cinereus*, *S. haydeni* and *S. fontinalis* were found to have a very high overall similarity value ($S$=0.959) (George 1984, 1988). George (1984, 1988), unlike the other authors, has used Roger's (1972) genetic similarity index ($S$).

Differentiation between the members of the *araneus* species group and *S. samniticus*, *S. alpinus*, *S. isodon*, *S. caecutiens* and *S. minutus* is much greater than within the *araneus* group, ranging from 0.229 between *S. araneus* and *S. minutus* to 0.714 between *S. isodon* and *S. alpinus* (Catzeflis 1984; Fig 2). The distance between *S. araneus* and *S. caecutiens* is 0.51 (0.27), between *S. araneus* and *S. minutus* 0.32 (0.23), and between *S. caecutiens* and *S. minutus* 0.52 (0.35); Frykman & Simonsen 1984; values in parenthesis are from Catzeflis 1984). These values are based on 35 (Frykman & Simonsen 1984) and 26 loci (Catzeflis 1984), respectively. According to George (1984) the similarity (Roger's $S$) between *S. araneus* and *S. caecutiens* is highest, 0.740, between *S. araneus* and *S. minutus* $S$=0.708, and between *S. caecutiens* and *S. minutus* $S$ was lowest, 0.683.

The genetic distances between the genera *Sorex*, *Neomys*, *Crocidura* and *Suncus* are as follows (Catzeflis 1984): *Sorex-Neomys* from 2.67 to 3.24, *Sorex-Crocidura* from 2.14 to 3.09, *Sorex-Suncus* from 1.63 to 3.05, *Neomys-Crocidura* from 1.61 to 2.40, *Neomys-Suncus* 1.89 to 1.98, and *Crocidura-Suncus* from 0.55 to 1.00. The values are based on 22 loci.

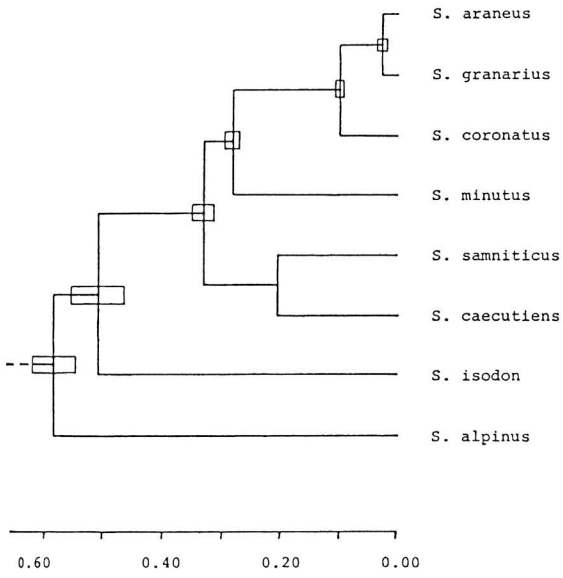


Fig 2. Standard genetic distance (Nei 1978) dendrogram (UPGMA) of eight species of *Sorex* according to Catzeflis (1984). Boxes represent standard errors.

## 4. Conclusions

In *Sorex araneus*, the allelic variation in polymorphic loci is quite extensive and the average heterozygosity and the number of polymorphic loci are high. Keeping in mind the extensive chromosomal polymorphism in this species, one might expect the chromosomal variation and the overall genetic variation to be correlated (Cothran & Smith (1983). However, Frykman & Simonsen (1984) found no relationship between chromosomal variation and variation in structural genes in *S. araneus*, but they found genetic variation to be about the same in *S. araneus* as in the other shrew species, and generally similar to that found in other small mammals. On the other hand, Searle (1985) suggests that the chromosomal races have diverged to some extent in England. Although none of the alleles detected was diagnostic for a karyotypic race, in certain loci there was variation both in allele frequency and mean heterozygosity, suggesting divergence (Searle 1985). Searle (1985) also suggests that because genetic heterogeneity in certain loci did not show any regularity with regard to site, date or habitat quality, such variability might be due to reduction in gene flow and to genetic drift.

Small-scale genetic variation between populations, commonly observed in shrews, may be due to genetic subdivisions of populations for reasons other than chromosomal races (Searle 1985). Temporal variation in allele frequencies, as observed by Gebczynski (1985) in *S. minutus*, may have something to do with the relationships between heterozygosity and fitness (Gebczynski 1985), or it may reflect changes in the viability of the sexes and differences in the variability between sexes, as observed by Tolliver & Robbins (1987) for *B. carolinensis*.

The population genetic work conducted so far on shrews points to certain interesting patterns in ecology and population genetics, but much more work is needed before any definite conclusions can be drawn.

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