Relationsship between chromosome races and species of Sorex of the araneus group in the western Alps

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Relationships between chromosome races and species of *Sorex* of the *araneus* group in the western Alps[1]

BY

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Summary.–HAUSSER J., BOSSHARD F., TABERLET P. and WÓJCIK J., 1991. Relationships between chromosome races and species of *Sorex* of the *araneus* group in the western Alps. *In*: J. HAUSSER, ed. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 79-95.

Five distinct karyotypic forms of the *S. araneus* group have been found in the western Alps and adjacent lowlands. Biochemical and morphometric studies confirm the relationships established on the karyotypic traits. *S. coronatus* is a well separated species and occupies the lowlands. *S. araneus* 'Vaud', 'Intermediate' and 'Acrocentric' forms differ only by the progressive diminution of Robertsonian metacentrics; they are morphologically and genetically very similar and succeed logically each other from North-East to South-West of the studied area. On the contrary, *S. araneus* 'Valais' is clearly differentiated genetically and morphologically, and occupies Valais, southern Alps and Italy. Some data suggest that this race was able to interbreed locally with the Acrocentric form, but not with the Vaud race.

Résumé.–HAUSSER J., BOSSHARD F., TABERLET P. et WÓJCIK J., 1991. Relations entre les races chromosomiques et les espèces de *Sorex* du groupe *araneus* dans les Alpes occidentales. *In*: J. HAUSSER, dir. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 79-95.

Cinq formes différant par leur caryotype se trouvent dans les Alpes occidentales et les plaines avoisinantes. Des études biochimiques et morphométriques confirment les

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relations établies sur la base des caractéristiques de leur caryotypes. *S. coronatus* est une espèce bien distincte et occupe les basses altitudes. *S. araneus* 'Vaud', 'Intermédiaire' et 'Acrocentrique' ne diffèrent que par une diminution progressive des métacentriques Robertsoniens. Elles sont morphologiquement et génétiquement très semblables et se succèdent logiquement du Nord-Est au Sud-Ouest de la région étudiée. Au contraire, *S. araneus* 'Valais' est bien différencié génétiquement et morphologiquement. Elle occupe le Valais, le sud des Alpes et l'Italie. Quelques données suggèrent que cette race a pu se croiser localement avec la forme Acrocentrique, mais pas avec la race Vaud.

INTRODUCTION

During the last glaciation, the Alps have been essentially a formidable ice barrier isolating Italy from central Europe. Today, their role in zoogeography is more complex. They act as a refugium for species adapted to cold climatic conditions, like *Marmotta marmotta*, as a maize of geographical traps which caught isolated populations into closed areas, like *Crocidura leucodon* in central Valais (MEYLAN 1967), as a limit of distribution for southern and northern species like *Pitymys multiplex* and *Pitymys subterraneus* (NIETHAMMER 1982, KRAPP 1982), and, still yet, as a barrier or a strong filter which isolate the Italian animal populations from their northern counterparts.

The shrews of the *Sorex araneus* group have not escaped the influence of the Alps in shaping their distribution areas and the genetic relationships of their local populations. In a previous paper (HAUSSER *et al.* 1986) we showed that the western Swiss Alps were occupied by two main karyotypic races of *S. araneus*, called 'Vaud' and 'Valais'; we suggested that they were issued from the introgression of a postulated primitive 'Acrocentric' population by two distinct sets of Robertsonian metacentrics coming respectively from the north-east and from the south. The Vaud race is a typical race of the WEPG (West European Phylogenetic Group, SEARLE 1984) while the Valais race is one of the most differentiated karyotypic race of *S. araneus* known so far. Data on populations with high 2Na in the western Alps (MEYLAN 1965) were intepreted as the present front of progression of Valais metacentrics into the primitive Acrocentric populations.

New karyotypic, electrophoretic and morphometric data now allow us to present a more detailed picture of the relationships of these shrews in the western Alps, and to correct somewhat our previous interpretation.

MATERIAL AND METHODS

Karyotypes

The karyotype of 293 individuals from 95 localities was analysed; for 220 of them, G-banded chromosomes were prepared after direct treatment of bone marrow or spleen cell suspensions, using a slightly modified method to that of

SEABRIGTH (1971). The remaining individuals, which came from previously known localities, have been studied by conventional staining only.

'Karyotypic distances' between the recorded taxa were computed as D = –ln S, where S is a Jaccard's similarity index (SNEATH and SOKAL 1973) based on the presence/absence of individual fusions or other karyotypic modifications of the ancestral karyotype, which is assumed to be analogous to the karyotype of *Sorex granarius* (WÓJCIK and SEARLE 1988, VOLOBOUEV and CATZEFLIS 1989). Individual characters were counted twice if homozygous, once if heterozygous (or in Y chromosomes) in the concerned taxon. This method is rather rough, but permits the computation of an UPGMA dendrogram and an easy comparison of the karyotypic data with the morphological and genetic ones.

Morphometry

A standard set of 26 orthogonal measurements (HAUSSER 1984) was recorded on the left jaw of 252 individuals, 150 of which were chosen for a discriminant analysis. They had been previously determined karyologically, except for 15 individuals which came from known localities or which were determined by biochemical methods (HAUSSER and ZUBER 1983). Statistical analysis were performed using SPSS^X package (44 North Michigan Avenue, Chicago, IL 60611) on a Digital Vax computer.

Morphometric distances between the karyologic taxa were computed as Mahalanobis distances, following the method described by HAUSSER (1984).

Electrophoresis

97 individuals were used in this study. 85 of them were determined karyologically. The remaining 12 individuals came from known localities and their determination was confirmed by the morphometrical analysis. 29 enzymatic loci (Table 1) were revealed after vertical starch gel electrophoresis (HILLIS and MORITZ 1990). Albumin was analysed on PAA gels following HAUSSER and ZUBER (1983). Genetic relationships were expressed as standard Nei's distance (NEI 1978).

RESULTS

Karyotypes

The analysed individuals have to be ranked into 5 different taxa, which karyotypes are described or redescribed here according to SEARLE *et al.* 1991. Their distribution is briefly mentionned. See also the map on Figure 4.

Sorex coronatus: n = 46.
Karyotype: XX/X ins(?,Y_1)Y_2, *af*, cms(*b*), *ci*, *gr*, cms(*h*), *jn*, *kq*, *lo*, *mp*, inv(*tu*)/*tu* (Fig. 1).

Table 1.–Results of the electrophoretic analysis.

Locus	EC	allele	allelic frequence in the studied taxa				
			coronatus N = 5	Valais 38	Vaud 25	Intermediate 22	Acrocentric 7
Aat-1	2.6.1.1	+100	1.00	0.99	1.00	1.00	1.00
		+150	0.00	0.01	0.00	0.00	0.00
Aat-2	2.6.1.1	-100	1.00	1.00	1.00	1.00	1.00
Acoh	4.3.1.3	+100	0.00	1.00	0.98	1.00	1.00
		+200	1.00	0.00	0.00	0.00	0.00
		+50	0.00	0.00	0.02	0.00	0.00
Acp	3.1.3.2	-100	1.00	1.00	1.00	0.95	1.00
		-180	0.00	0.00	0.00	0.05	0.00
Ada	3.5.4.4	+50	0.00	0.24	0.36	0.61	0.71
		+100	1.00	0.68	0.62	0.39	0.29
		+150	0.00	0.01	0.00	0.00	0.00
		+200	0.00	0.07	0.02	0.00	0.00
Adh	1.1.1.1	-85	0.00	0.05	0.00	0.02	0.21
		-100	0.80	0.95	1.00	0.98	0.79
		-110	0.20	0.00	0.00	0.00	0.00
Ak-1	2.7.4.3	-65	0.00	0.00	0.08	0.00	0.00
		-100	1.00	1.00	0.92	1.00	1.00
Ak-2	2.7.4.3	+100	1.00	1.00	1.00	1.00	1.00
Alb		+90	1.00	0.82	0.00	0.09	0.21
Ck-1	2.7.3.2	+100	1.00	1.00	1.00	1.00	1.00
CK-2	2.7.3.2	+100	1.00	1.00	1.00	1.00	1.00
Es-1	3.1.1.1	+80	0.20	0.14	0.00	0.00	0.00
		+100	0.80	0.86	1.00	1.00	1.00
Es-2	3.1.1.1	+88	0.20	0.04	0.00	0.00	0.00
		+95	0.00	0.30	0.00	0.09	0.14
		+100	0.80	0.66	1.00	0.91	0.86
Es-3	3.1.1.1	+97	0.00	0.05	0.00	0.00	0.00
		+100	1.00	0.90	0.99	0.98	0.93
		+110	0.00	0.05	0.01	0.02	0.07
G6pd	1.1.1.49	+100	1.00	1.00	1.00	1.00	1.00
Gpd	1.1.1.8	+50	0.00	0.00	0.04	0.00	0.00
		+100	1.00	1.00	0.96	0.00	0.00
Gpi	5.3.1.9	-50	0.00	0.01	0.00	0.00	0.00
		-100	1.00	0.99	1.00	1.00	1.00
Idh-1	1.1.1.42	+100	1.00	1.00	1.00	1.00	1.00
Idh-2	1.1.1.42	-85	1.00	0.00	0.00	0.00	0.00
		-100	0.00	1.00	0.96	1.00	1.00
		-120	0.00	0.00	0.04	0.00	0.00
Sod-1	1.15.1.1	-100	1.00	1.00	1.00	1.00	1.00
Sod-2	1.15.1.1	-100	1.00	1.00	1.00	1.00	1.00
Ldh-1	1.1.1.27	+100	1.00	1.00	0.96	1.00	1.00
		+130	0.00	0.00	0.04	0.00	0.00
Ldh-2	1.1.1.27	-100	1.00	1.00	1.00	1.00	1.00
Mdh-1	1.1.1.37	+100	1.00	1.00	1.00	1.00	1.00
Mdh-2	1.1.1.37	-100	1.00	1.00	1.00	1.00	1.00
Mpi	5.3.1.8	+100	0.90	1.00	0.56	0.89	0.64
		+120	0.10	0.00	0.44	0.11	0.36
Nadp	1.1.1.40	-100	1.00	1.00	1.00	1.00	1.00
Pgd	1.1.1.44	+100	0.90	1.00	0.96	1.00	1.00
		+110	0.10	0.00	0.04	0.00	0.00
Pgm	5.4.2.2	+80	0.00	0.03	0.00	0.02	0.00
		+100	1.00	0.97	1.00	0.98	1.00
Xdh	1.1.1.204	+100	1.00	1.00	1.00	1.00	1.00

EC : Enzyme commission numbers. Alleles are identified by their migration rate in percent of the most common one for the given locus. + and - indicate cathodic and anodic migration.

Figure 1.–G-banded karyogram of *S. coronatus* and *S. araneus*, Valais race. * : non-Robertsonian changes in *S. coronatus*.

The modifications of arms *b* and *h* have been attributed to centromeric shifts (cms) following VOLOBOUEV and CATZEFLIS (1989). The Y_1 is typically longer as in *S. araneus* and usually shows an additional subtelomeric dark band, which origin is difficult to assess. The metacentric *tu* sometime shows a clear central region tentatively attributed to an inversion in arm *t*. Due to the small sample they studied, VOLOBOUEV and CATZEFLIS (1989) have not mentionned these modifications comparing to *S. araneus*, whereas OLERT and SCHMID (1978) suggest a paracentric inversion for Y_2 and tiny deletions in *ut*. Further and detailed studies of the karyotype of this species are obviously needed.

Distribution: Northwestern Spain, France except mountain ranges, eastwards up to central Germany. In the studied area, this species is found in the lowlands and adjacent mountains slopes up to 900–1200 m. It occupies only the lowest part of the large alpine valleys.

Sorex araneus, Valais race: n = 94.
Karyotype: XX/XY_1Y_2, *af, bc, gi, hj, kn, l/o, m, p, q, r, tu* (Fig. 1).
Rb metacentrics *gi* and *hj* are typical for this race. The polymorphism of *lo* seems to be generalized throughout the studied area. 43 individuals showed to be homozygous for *lo*, 35 were heterozygous and 19 homozygous for *l,o*. This does not differ significantly from the Hardy-Weinberg expectation (χ^2 = 4.6658, $p > 0.05$).

Distribution: Valais, Southern Alps, Po valley and Italian mountains. This race was also found in the French Alps near Briançon. North of the Alps, it occupies the upper part of some valleys (Aar, Hinterrhein).

Sorex araneus, Vaud race: n = 100.
Karyotype: XX/XY_1Y_2, *af, bc, gm, hi, jl, kr, no, p, q, tu* (Fig. 2).
This race shows a polymorphism for Rb metacentric *no* in the Jura mountains, but it seems to be present in an homozygous state in the Alps and in the lowlands, where large samples were analysed (Jorat: 39 individuals, P. Gos and O. Rossier, personal communication; Champittet: 30 individuals, C. Neet, personal communication). Rare heterozygotes for the metacentric *jl* were found in the Alps.

Distribution: Northern slope of the Alps, Jura mountains; residual lowland populations along the lake of Neuchâtel and in the hills of the Jorat behind Lausanne. Related karyotypes, but without *no*, and with a polymorphic *kr*, have been found near Freiburg and Karlsruhe in Germany (BRÜNNER 1991).

Sorex araneus, Intermediate Vaud-Acrocentric form (hereafter: Intermediate): n = 24.
Karyotype: XX/XY_1Y_2, *af, bc, gm, h/i, j/l, k/r, n, o, p, q, tu* (Fig. 2).
This form, which cannot be called a race since it does not possesses characteristic fusions, shows a generalized polymorphism for Vaud metacentrics *hi, jl* and *kr*. The metacentric *gm* is always present in homozygous state, whereas *no* was never found. Unfortunately, our sample is

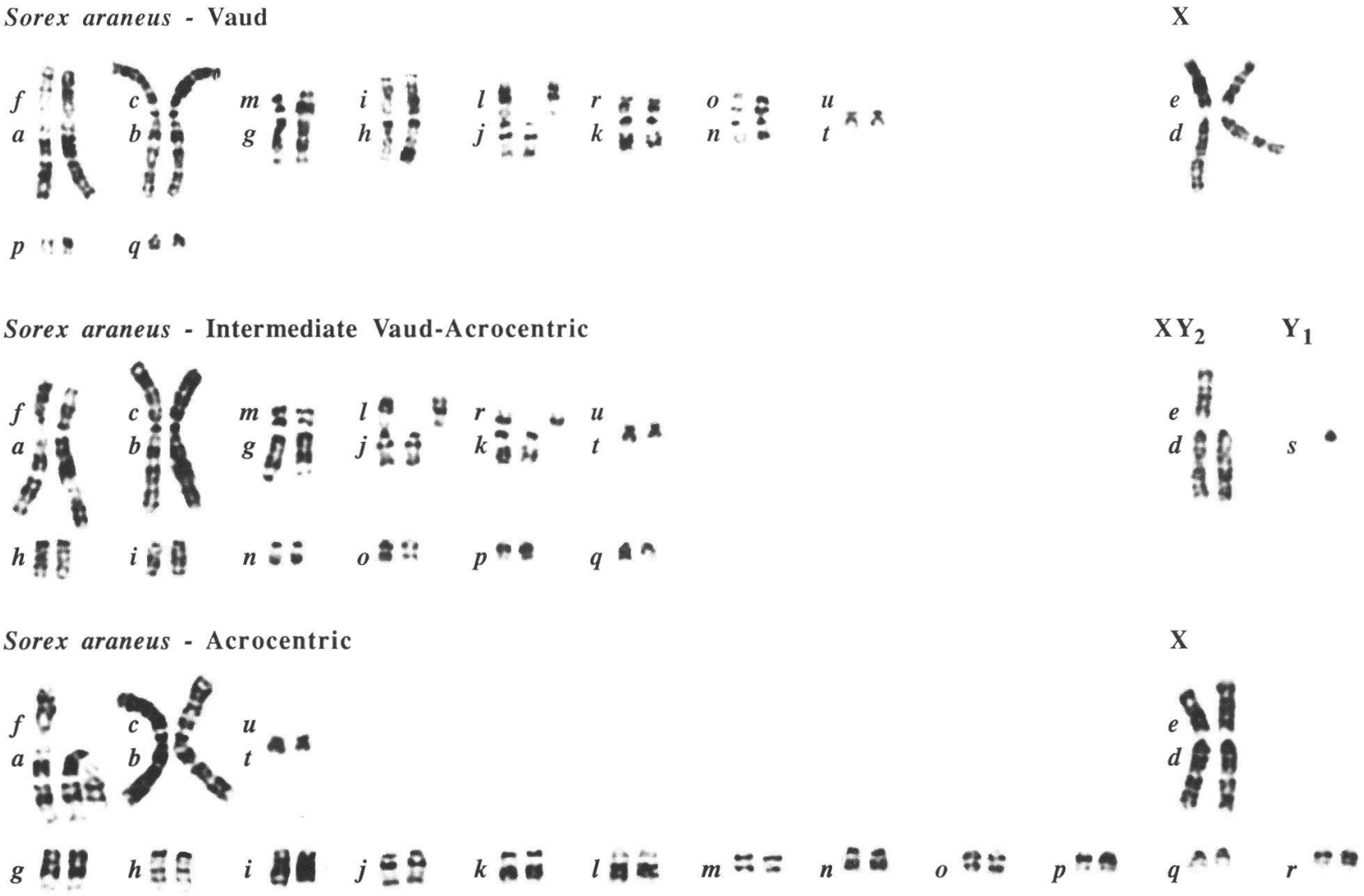

Figure 2.–G-banded karyograms of *S. araneus* Vaud race, Intermediate Vaud-Acrocentric and Acrocentric forms. For additional variations, see text.

too small to detect any logical pattern in the geographical distribution of the polymorphic metacentrics. *jl* is the most frequent of them (50 % of the genomes), whereas *hi* and *kr* are present in 4% of the genomes and were never found in homozygous state.

Distribution: mountains between Rhone and Arve valleys, limited eastward by the chain of the Dents du Midi.

Sorex araneus, Acrocentric form: n = 26.
Karyotype: XX/XY_1Y_2, *af, bc, g, h, i, j/l, k, m, n, o, p, q, r, tu* (Fig. 2).
This form represents the most primitive karyotype yet observed in *Sorex araneus*. On the 12 autosomic arms involved in the Robertsonian polymorphism of this species, only *j* and *l* are present as a polymorphic metacentric. The frequency distribution of *jl* does not differ significantly from the Hardy-Weinberg expectation (*jl*: N = 6; *j/l*: N = 10; *j,l*: N = 10; $\chi^2 = 1.39$, $p << 0.05$). Again, this form cannot be called a race, if we define them by the presence of mutually incompatible fusions. The presence of *jl* clearly links this form to the Intermediate form and Vaud race rather than to the Valais race.

Distribution: French Alps south of the Arve valley; prealpine ranges of Savoy. Similar karyotypes were also observed in the Massif Central (HAUSSER 1976).

As a whole, the distribution of these forms shows a generalized parapatry, except for *S. coronatus* and *S. araneus* in the Jorat, where both species present relatively intermixed populations, depending of microclimatic conditions (P. Gos and O. Rossier, personal communication). We had the opportunity to find a contact zone between the Vaud and Valais races in the Haslital, and another one between the Acrocentric form and the Valais race at les Houches, near Chamonix (Fig. 5). In each case, the contact zone is extremely sharp (about one km), and only one mixed locality was found. No hybrids were found either in the vicinity of the Acrocentric–Valais contact zone (25 individuals analysed along a transect of five km) or between Vaud and Valais races (13 individuals analysed on a similar transect). In the last case, the arms *g*, *h*, *i* and *k*, which are implied in monobrachial homologies between Vaud and Valais races, were never found in an acrocentric condition.

The karyotypic distances betwen the five taxa were computed using the characteristic fusions of each of them, as well as the four non-Robertsonian differences mentionned for *S. coronatus*. Their distance matrix is shown in Table 2, and a UPGMA dendrogram (Fig. 6) illustrates their karyologic relationships: *S.coronatus* is the most isolated, and the Vaud, Intermediate and Acrocentric forms appear closely related.

Morphometry

The results of the discriminant analysis are shown in Figure 3. Whereas *S. coronatus* and Valais race of *S. araneus* are perfectly individualized by the analysis, the Vaud, Intermediate and Acrocentric forms (VIA group) remain

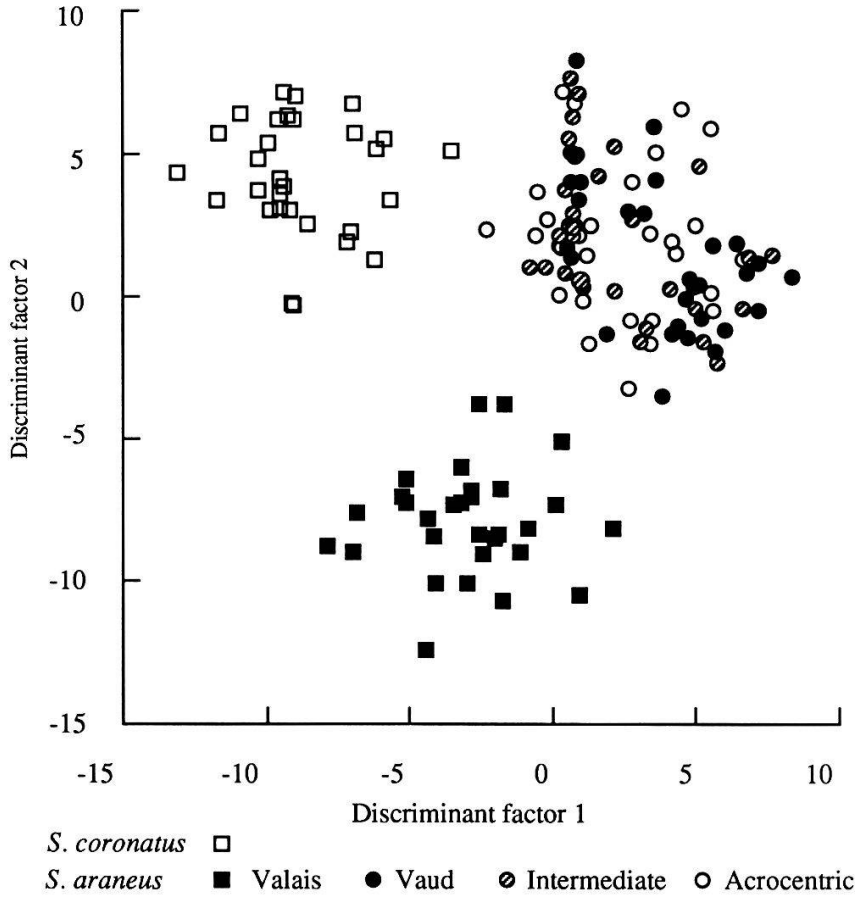

Figure 3.–Discriminant analysis: distribution of the analysed animals on the two first discriminant factors, representing 95.7 % of the variance between taxa.

Table 2.–Matrices of karyotypic, morphometric and genetic distances. C: *Sorex coronatus*; VS: *S. araneus* Valais race; VD: *S. araneus* Vaud race; I: *S. araneus* Intermediate; A: *S. araneus* Acrocentric. See text for further details.

		C	VS	VD	I
Karyotypic distances					
	VS	2.234			
	VD	2.741	1.609		
	I	2.603	1.386	0.368	
	A	2.442	1.099	0.956	0.588
Morphometric distances					
	VS	13.469			
	VD	14.113	11.677		
	I	12.866	11.536	2.202	
	A	12.054	11.277	3.131	1.140
Nei's genetic distances					
	VS	0.082369			
	VD	0.121744	0.036663		
	I	0.123114	0.025717	0.007673	
	A	0.114504	0.022026	0.008587	0.005429

intermixed and cannot be identified with a sufficient security for practical purposes. Morphological distances are given in Table 2, and the same results are shown as an UPGMA tree in Figure 6. This analysis was also used to classify the remaining measured animals. The definitive attribution of VIA individuals to Vaud, Intermediate or Acrocentric taxon was eventually decided on the basis of other (karyotypic) data from the same locality or according to the known, allopatric distribution of these three forms. As a whole, the results showed perfectly conguent with the karyotypic data and allowed us to complete our distribution map (Fig. 4).

Electrophoresis

The results are listed in Table 1. 17 of the 30 studied loci were shown to be polymorphic. Genetic distances between taxa are shown in Table 2 and Figure 6. The pattern obtained is the same as for karyotypic or morphologic distances, but the group Vaud–Intermediate–Acrocentric (VIA group) is more distinctly clustered, and can be considered as genetically homogeneous. *S. coronatus* is clearly distinct of the 3 *S. araneus* taxa. As we took small samples in each locality, no attempt was made to analyse each of them in detail; it proved nevertheless interesting to examine the geographical distribution of the albumin's alleles. As already published (HAUSSER and ZUBER 1983, NEET and HAUSSER 1989), *Sorex araneus* Vaud race is characterized by a fast migrating allele (+100), whereas *S. coronatus* and *S. araneus* Valais possess a slow allele (+90). Our data (Fig. 7) indicate that the western populations of Valais race also present the +100 albumin, whereas the +90 allele was found in two Intermediate and two Acrocentric individuals. These results suggest present or past genetic flow between Acrocentric, Intermediate and Valais populations.

DISCUSSION

The consistency of the results obtained by morphometric and electrophoretic methods with the karyotypic data clearly confirms the validity of the model of chromosomal divergence of this group based mainly on Robertsonian fusions, which was suggested by many authors (see for instance SEARLE 1984, 1986, HAUSSER *et al.* 1985, ZIMA *et al.* 1988, VOLOBOUEV and CATZEFLIS 1989). This consistency is nevertheless puzzling: it was shown that, at least in southern Europe, the morphological differentiation of these shrews is linked to their geographical origin and to their habitat conditions, which masks their genetic relationships (HAUSSER 1984). The selective effect of habitat had to be removed in order to detect the morphologic differentiation related to their phylogeny. In the present study, this was not necessary and the relation of the morphological differentiation with the genetical one is immediatly obvious (Fig. 6). This apparent contradiction is possibly due to the far smaller and more homogeneous area studied here, and also to the recentness of the recolonization of this area, which was almost entirely covered by ice during

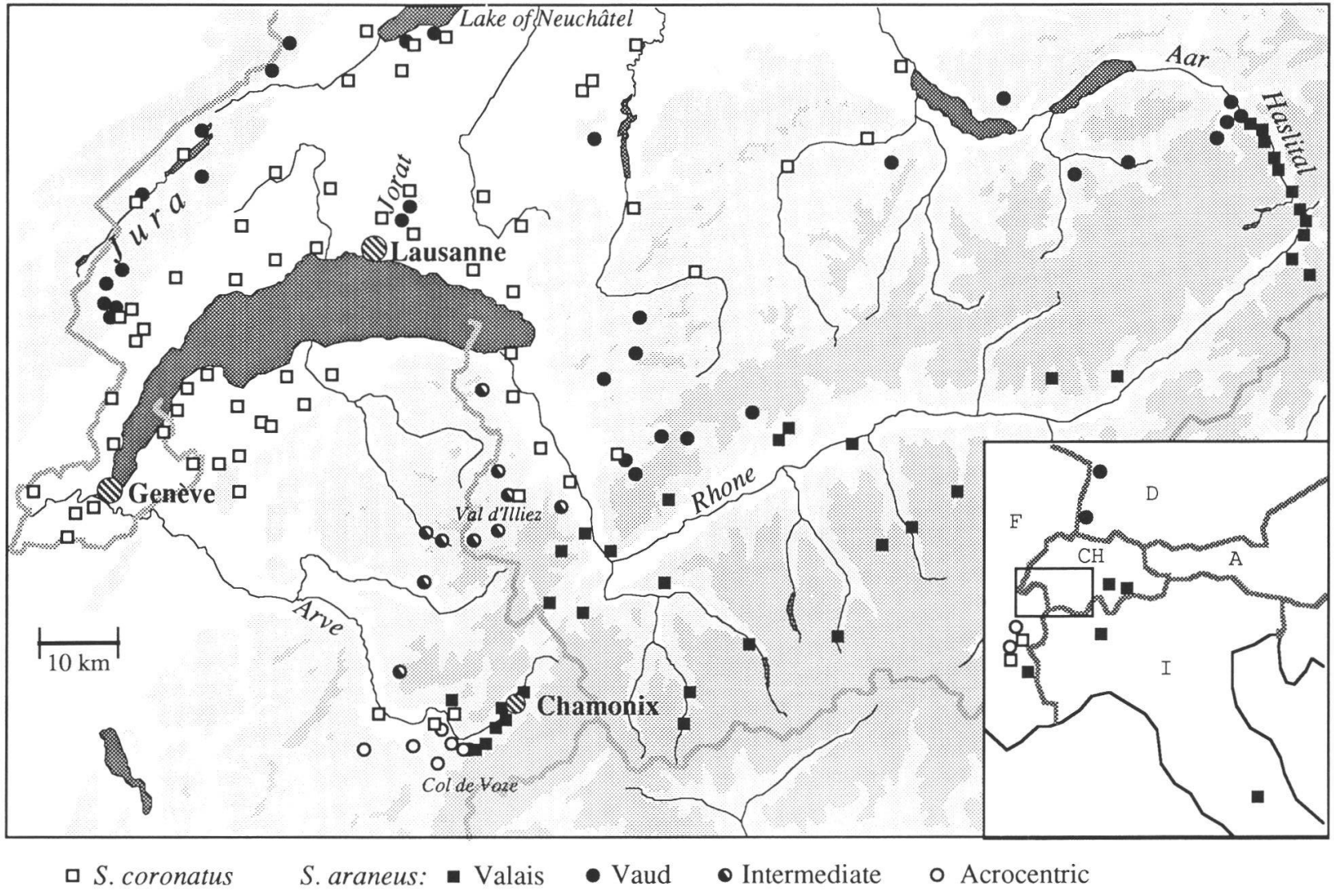

Figure 4.–Distribution map of the five taxa of shrews in the studied area. For *S. coronatus* and *S. araneus* Vaud race, additional data were taken from HAUSSER (1978), TABERLET (1982) and BRÜNNER (1991). On the small map, only recent karyotypic data are shown.

the last glaciation. In this hypothesis, the local populations of different taxa did not have time enough to converge morphologically, even when living in similar conditions. For instance, the large morphological distance between the Valais race of *S. araneus* and the VIA group is possibly due to a recent 'importation' of morphological characteristics developped in populations isolated for a long time in Italy. Note however than syntopic populations of *S. coronatus* and *S. araneus* Vaud race appear more similar than allotopic ones (NEET 1989), what shows that the process of selective convergence is in action.

In a previous publication (HAUSSER *et al.* 1986) we supposed that the karyotypes with high 2Na numbers previously described by MEYLAN (1964, 1965) from the Val d'Illiez in western Valais, and by FORD and HAMERTON (1970) from the Col de Voze in Savoy (See Fig. 4) marked the present front of introgression of the Valais Rb metacentric into postulated primitive acrocentric populations. Even if we have eventually found acrocentric individuals, we know now that this interpretation was erroneous, and that, instead of Valais metacentrics, these populations (Intermediate in the Val d'Illiez and Acrocentric at Col de Voze) bear Vaud metacentrics and can be grouped with the Vaud race in a genetically and morphologically homogeneous VIA group. From the karyotypic point of view, the Vaud, Intermediate and Acrocentric taxa form a logical sequence, since each Rb metacentric of the Intermediate group is typical of the Vaud race, from which only *jl* was found in the Acrocentric group (which was named before this observation).

Our previous interpretation was based on the fact that Vaud populations are isolated from the Intermediate ones by the presence of *S. coronatus* in the lowest part of the Rhône valley. This species also separates Intermediate and Acrocentric populations in the Arve valley. Thus, the Intermediate and Acrocentric populations have an easier contact with the Valais race of *S. araneus* than with their Vaud relatives. However, this situation may be very recent: we know that *S. araneus* Vaud still occupies marshy areas in the lowlands of Switzerland, for example along the lake of Neuchâtel (HAUSSER 1976, NEET 1989). It is quite possible that the species replacement in the Alpine valleys occured as late as the end of the 19th. century, when the big marshes of the low Rhône and Arve valleys were drained. Thus we can admit that, until recently, there was a progressive and continuous increase of acrocentrics in the VIA populations towards the South, and that the situation was 'fossilized' by the progression of *S. coronatus*.

This geographical succession Vaud–Intermediate–Acrocentric could be explained by a selection pressure against Vaud metacentrics, where they meet the Valais race, who's metacentrics show monobrachial homologies with the Vaud ones. SEARLE (1986, 1988) has clearly illustrated such a mechanism for the contact zone between Oxford and Hermitage karyotypic races. However, in our case, they are strong arguments against this hypothesis:

1.–The Rb metacentrics of the Valais race do not show a similar decrease, and it is difficult to see why this pattern should not be symmetrical. For example, the Valais race is sharply replaced by Acrocentric populations in the

contact zones at Les Houches (Fig. 5); "Valais–Acrocentric" Intermediate populations or individuals have not been found, although the distribution of albumin alleles suggests that hybridation may occasionally occur and be successful.

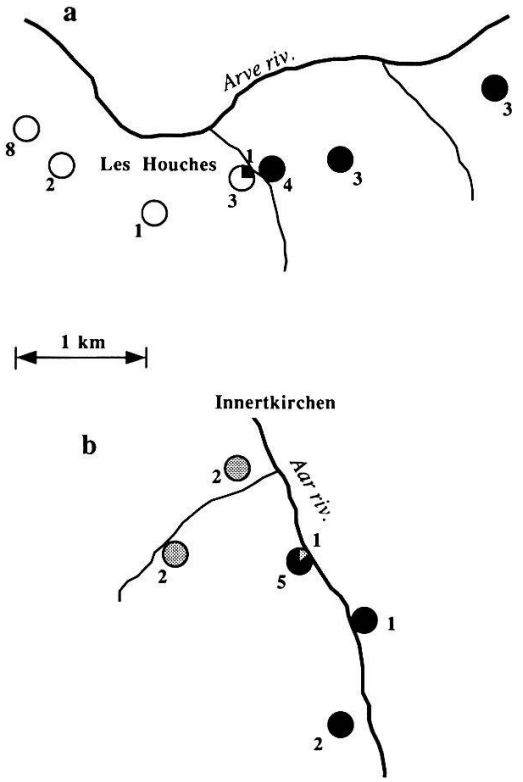

Figure 5.–Contact zones between (a) *S. araneus* Valais race (black circles) and the Acrocentric form (white circles) and between *S. araneus* Valais and Vaud races (grey circles). Figures indicate the numbers of individuals analysed in each population.

2.–In the contact zone between Vaud and Valais races in the Haslital (Fig. 4), neither an increase of acrocentrics nor hybrids have been found. Here too, the contact zone seems to be extremely sharp (see also NEET and HAUSSER 1991, TABERLET *et al.* 1991).

Thus, if we were wrong with the origin of the metacentrics of the Intermediate populations, the hypothesis of a progressive introgression of (Vaud instead of Valais) metacentrics southwards into primitive acrocentric populations remains the most acceptable one, and is reinforced by the genetic homogeneity of the VIA group compared with the Valais race. Metacentrics should be favoured in different degrees by meiotic drive (see discussion in HAUSSER *et al.* 1985). Therefore, they should progress at individual paces, which can be evaluated thanks to the fragmentation of the geographic distribution of the VIA group by *S. coronatus*. At this time *jl* had already colonized the southern French Alps, whereas *on* –which is still polymorph in Jura– had not attained the Rhône valley. *gm*, *hi* and *kr* had time to spread

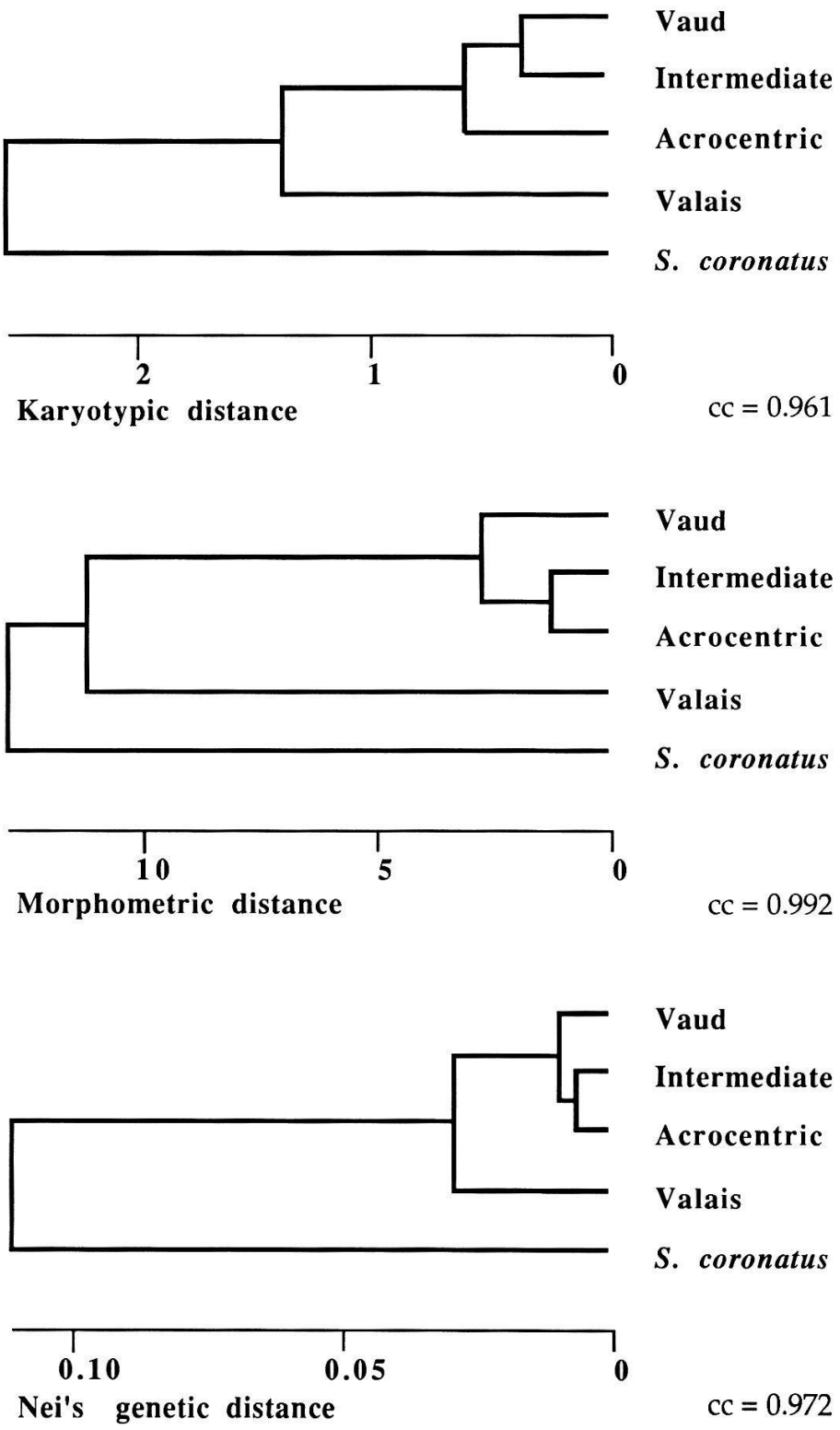

Figure 6.–UPGMA dendrograms of the karyotypic, morphometric and genetic distances between the five studied taxa. cc: cophenetic correlations with the corresponding distance matrix (Table 2).

south of the Rhône, but were stopped at the Arve valley. As for *jl*, it is worthwile to note that karyotypes analogous to the Acrocentric ones, with only one polymorphic Rb metacentric, have been reported in the Massif Central (HAUSSER 1976). If this metacentric actually corresponds to *jl*, one can suppose than the first populations invading the Alps after the glaciation already bore this metacentric, which is present in every *Sorex araneus* race except the Valais one.

Well differentiated by its karyotype, its morphology and its genetics, the Valais race evolved certainly during a long isolation in Italy, from where it had no other possibility than the Simplon pass (2005 m) to colonize the Valais. It is quite possible that for some time these populations remained isolated in the medium Rhône valley by the retreating glaciers (M. Burri pers. comm.). Our biochemical results suggest that the contact was realized first in the western part of the Valais, a long time before Vaud metacentrics reached the Rhône region. The Valais populations (maybe still polymorphic for *gi*, *jh* and *kn*) should have met Acrocentric populations without serious problems of chromosome incompatibility –and thus hybridize with them. This hypothesis could explain the polymorphism of albumin encountered in this region. On the contrary, the contact of Valais with Vaud populations needed some more time, to allow the large glaciers of the Bernese alps to retreat and open the passes. When they met, their respective metacentrics with monobracial homologies were probably already homozygous. As hypothetic F1 hybrids would usually present a multivalent of eleven elements at metaphase I, it is almost certain that they should be sterile (but see MERCER *et al.* 1991). As a matter of fact, neither hybrids nor indirect indications of hybridization between Vaud and Valais races have been found so far (see NEET and HAUSSER 1991), except the presence of albumin +100 allele in a Valais population of northern Ticino (Fig. 7). This could be explained by the delayed introgression of Vaud metacentrics in some remote valleys of the northern Alps, were Acrocentric or polymorphic populations could maybe still exist.

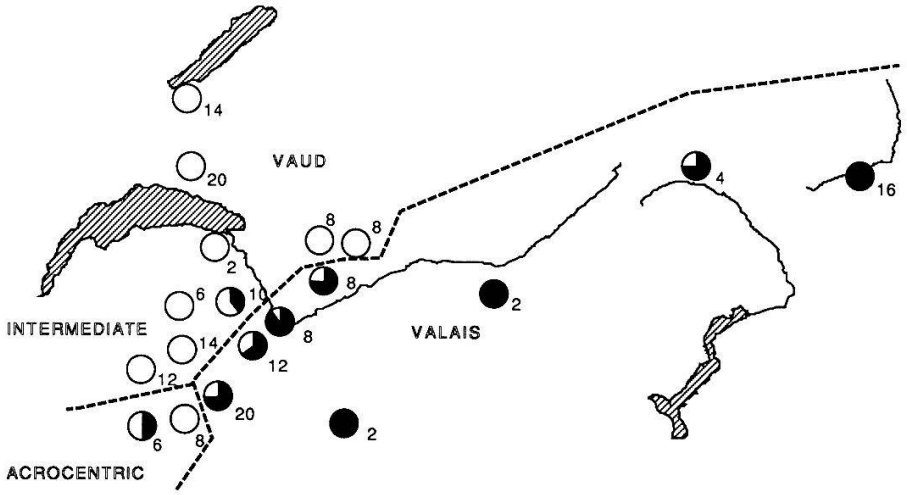

Figure 7.–Proportion of albumin allele +90 in studied populations of *S. araneus*. Small samples from the same geographical region have been pooled. Figures indicate the number of individuals analysed.

Thus, Valais populations have possibly interbred with Acrocentric ones, but not with bearers of the full set of Vaud chromosomes. Vaud and Acrocentric populations are genetically almost identical, the only difference between them lying in the presence or absence of metacentrics incompatible with the Valais ones. Contrary to the opinion of BENGTSSON and FRYKMAN (1990), it seems therefore quite possible that Robertsonian fusions are in some cases sufficient to cut gene flow between chromosome races.

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