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Key Word Index—*Arvicanthis niloticus*; *Mastomys erythroleucus*; *Mastomys huberti*; Muridae; Rodentia; electrophoretic variants; genetic polymorphism; inter-population differences.

Abstract—Electrophoretic patterns of blood proteins and enzymes have been analysed among 152 *Arvicanthis*, 75 *Mastomys huberti* and 13 *Mastomys erytholeucus* captured in 19 localities in Senegal. Individual variability (genetic polymorphism) was observed at four loci, while other loci appeared monomorphic. Differences in electrophoretic migration of some proteins were observed among populations originating from distant geographic areas. The overall trait in *Arvicanthis* is that individual variability is rather poorly developed while populations diverge first by the extent of polymorphism and the loci concerned and also by different electrophoretic behaviour of some proteins.

Introduction

Studies on electrophoretic patterns of some blood proteins of *Arvicanthis* from distant African countries suggested that all animals could not belong to the same species, *Arvicanthis niloticus* [1]. Concerning *Mastomys*, previous results obtained mainly on animals kept in Mammalian Department at the Paris Museum d'Histoire Naturelle (Dir. Prof. F. Petter) showed a relative genetic homogeneity of *Mastomys erythroleucus* and polymorphism at some loci for *M. huberti* [2].

The present investigation deals with population groups from various localities of one country, the Senegal. Although geographic distances are smaller than the ones considered previously, the present sampling corresponds to different environmental conditions. It was hoped to find populations diverging between them, the ones living along the riverside and the ones from coastal regions, those from the north and those from the south, the western and the eastern.

The studies were undertaken in cooperation with ORSTOM; the program of this institution was to obtain the overall pattern of a number of genetic markers in various areas during the prolonged periods of drought, to be compared to the pattern shown in the future, when the environmental conditions would become more favourable. Our interest was to continue investigations on the applicability of electrophoretic analysis to taxonomic and population studies.

(*Received for publication* 12 *June* 1986)

Result and Discussion

Arvicanthis

Homogeneity or variability of electrophoretic patterns differed according to analysed loci and the geographic origin. The occurrence (or not) of polymorphism in the populations studied is shown in Table 1; the chart (Fig. 1) indicates the localization of the captured animals.

The electrophoretic differences observed correspond to two causes: on the one hand, the individual variability at one locus, resulting from genetic segregation (i.e. true intra-specific polymorphism) occurs among litters of the families studied; on the other hand, populations can show different electrophoretic migration for the same protein, demonstrating inter-specific divergencies, past or in the making. These two levels of differences were discussed in previous reports [1, 2].

Albumin. Both kinds of the above differences

TABLE 1. DISTRIBUTION OF ELECTROPHORETIC PHENOTYPES AMONG POPULATIONS OF *ARVICANTHIS* FROM SENEGAL N 152

Locality of capture symbol of the region	Group composition	Albumin F	FS	S	Transferrin BF	BT	D	DS	F	FS	FT	S	T	Alkaline esterase F	FS	S
Savoigne, river Senegal	10 captured	5	4	1												
	2 litters of	(parents F × S)														
SAV	6 and 5 and	2	11	2												
	1 litter of 3	(parents FS × FS)														
		1	1	1	0	0	0	0	0	0	0	24	0	0	0	24
Savoigne SAV	35 captured	27	7	1	0	0	0	0	1	4	0	30	0	1	3	31
Dagana river Senegal	21 captured	17	4	0												
DAG	2 × 2 offspring	(parents F × ?)														
		4	0	0	0	0	0	0	0	4	0	21	0	3	13	9
Guede chantiers river Senegal GUC	13 captured 1 litter of 6	10	8	1	0	0	0	0	0	1	0	18	0	0	6	13
Diomandou river Senegal DIO	13 captured	10	2	1	0	0	0	0	0	2	0	7	0	1	7	5
Dogui Dombi river Senegal	6 captured	12	0	0	1	0	0	0	0	2	0	3	0	1	2	3
DOG	1 litter of 6				(parents BF × FS)									(parents FS × S)		
					1	0	0	0	2	3	0	0	0	0	5	1
Khar Yalla Green Cape	1 captured	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
KHY	1 litter of 6	(parents S × ?)			(parents S × ?)											
		0	0	0	0	0	0	0	0	2	0	4	0	0	6	0
Nyanga Green Cape NYA	5 captured	5	0	0	0	0	0	0	0	0	0	5	0	0	3	2
Ouest Lac Retba Green Cape OLR	1 captured	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Kedougou South East KED	2 captured	2	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Cape Skirring (Gambia)	2 captured	9	0	0	0	1	0	0	0	0	1	0	0	0	1	1
CSK					1	1	0	0	0	0	3	0	2	0	3	4
		103	43	6	3	2	1	3	3	18	4	116	2	6	51	95

were observed at albumin locus (Plate A, 1–3). Concerning the distribution of phenotypes four family cases could be examined:

(i) a female (presumed) homozygous S and a male (presumed) homozygous F, yielded two litters of six and five, showing all the heterozygous phenotype FS;

(ii) both parents FS yielded three offspring showing the three possible phenotypes: F, FS, S;

(iii) a female (presumed) homozygous F and a male FS yielded a litter of six, three being F and three FS;

(iv) both parents (presumed) homozygous F yielded two litters of six and seven all being F.

All results are in conformity with Mendelian inheritance rules.

Globally, among the 152 examined animals, 103 were F, 43 FS and six S; estimations of allelic frequencies are Al^F 0.819, Al^S 0.181. These figures reflect however only the predominance of the faster-migrating variant, the uneven distribution among populations introducing a bias.

Concerning populations, six groups were shown to be polymorphic for albumin and five were not; of course, negative results should always be taken with caution because of the low numbers of animals. The previous results on *Arvicanthis* from Senegal did not disclose individual variability of albumin [1, 2], which could have been either due to sampling effects or else to the fluctuating distribution of phenotypes between 1981 and 1984. The present data

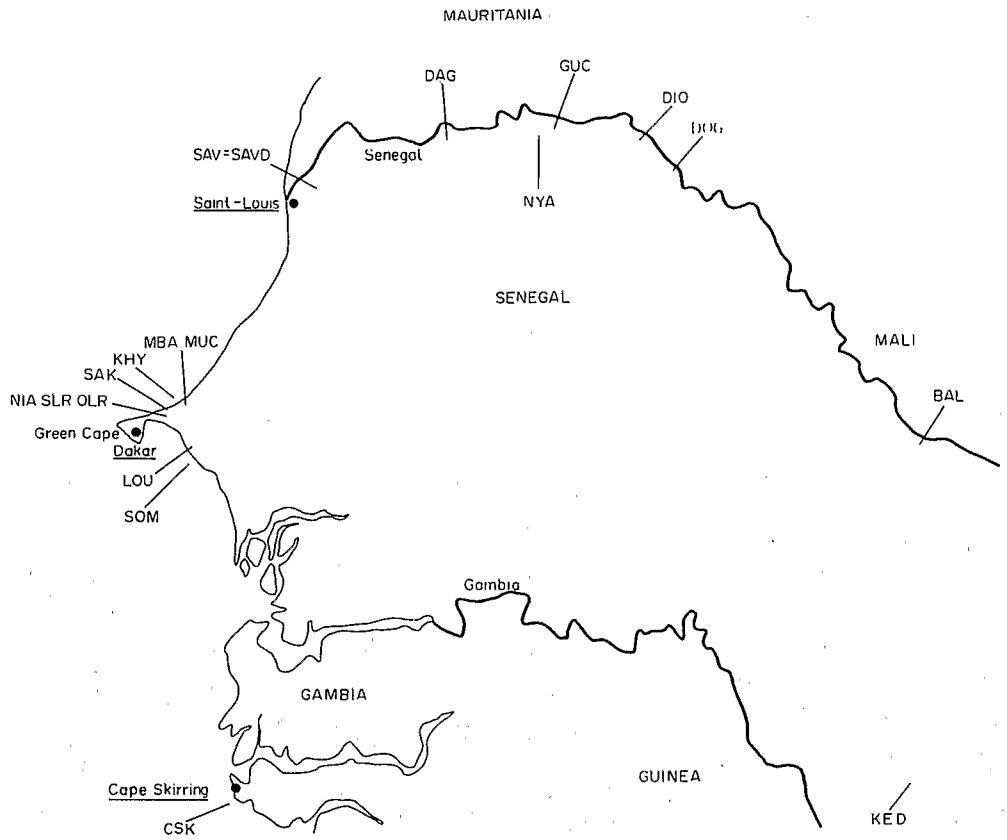

FIG. 1. DISTRIBUTON CHART OF POPULATION SAMPLES STUDIED.

establish, firmly, however that genetic polymorphism occurs at the albumin locus in *Arvicanthis* from Senegal.

Differences of electrophoretic migration with geographic localization. Variation in albumin migration was noted in the experimental conditions used between populations issued from different localities. Thus the variant designated F (fast migrating as compared with S in polymorphic populations, the same symbol being used by analogy for monomorphic groups) is found at the same position on the gel for all individuals from groups SAV, SAVD, DIO, DAG, DOG, GUC, KHY and NYA (Figure 1), i.e. from regions along the river Senegal and those around the Green Cape. The migration is slower for animals from south west and south east, CSK and KED (Plate A; 1). The variant S encountered in homozygous state in SAV, SAVD, DIO, GUC and KHY groups showed identical migration.

The migration differences observed among populations of Senegal are smaller than those reported between *Arvicanthis* from Egypt, Senegal and Haute Volta [1, 2]. However they already demonstrate divergencies between populations of *Arvicanthis* from various areas of a region.

Transferrin. Polymorphism at transferrin locus has previously been described [1, 2]; in the present study one of the electrophoretic techniques has been modified by introduction of polyacrylamide sheets. The overall results obtained on starch (pH 7.4) and on acrylamide sheets (pH 8.5) are equivalent, but the second technique yields bands sharper and better defined (Plate A; 3 and 4).

The allelic variants form two bands, the main

one intense, slower than secondary, lighter band; heterozygous individuals display generally four-band patterns but in some cases only three are distinctly observed, when the secondary band of the slower allelic variant overlaps the main band of the faster variant (Fig. 2).

Some population groups appeared monomorphic, others were weakly polymorphic with preponderance of the variant S, as for example the group SAV, where most of the individuals are presumed homozygotes S but one animal shows the phenotype F (Plate A; 2) (Table 1). Among *Arvicanthis* from DAG and GUC groups polymorphism was observed, but besides the main phenotype S only FS were present. No family segregation could be studied. Among KHY group a female S mated to an unknown male yielded 4S and 2FS. Other groups showed polymorphism richer in transferrin variants. Thus DIO disclosed bands, D, F and S, distributed in four phenotypes; there was no family in this group (Fig. 2 and Plate A; 4) (Table 1).

The group DOG also contains three bands of transferrin but not the same as DIO, band B being faster than D. This group presents a nice family case: the female FS mated to a male BF yielded a litter comprising phenotypes F, FS and BF. Therefore, B, F, and S qualify as allelic variants, not only as electrophoretic bands (Fig. 2 and Plate A; 4) (Table 1).

The B band is shared by *Arvicanthis* from Cape Skirring; this last group, however, in contrast with all the others, did not display the main band S, showing instead an even slower band designated T (Plate A, 4). In this group it was also possible to observe genetic segregation of phenotypes, a female FT mated to a male BT yielded BF, BT, FT and T (Fig. 2) (Table 1).

Global phenotype distribution. With the restrictions already noted for albumin system, a globalization of phenotypes yields 3BF, 2BT, 1D, 3DS, 3F, 17FS, 4FT, 117S, 2T. The estimation of frequences would be greatly biased, therefore it is omitted. The locus of transferrin in *Arvicanthis* from Senegal is certainly polymorphic, family data leading to consider the four following allelic variants: B, F, S, and T; as to D there is a presumption, since it was observed in a heterozygous phenotype DS. The variant S was the most frequent among the animals analysed.

Geographic distribution of transferrin variants. As shown in Table 1, the polymorphic system of transferrin is characterized, among *Arvicanthis* of Senegal, by a common 'thread', the slowly migrating variant S; it is present in all groups, except in the sole CSK population. The main polymorphism of S and F was encountered in populations SAV from Green Cape and in DAG and GUC groups, both from the river borders. Two other groups from areas along the river, DIO and DOG contain, besides S and F, other fast migrating variants, different in each group.

The occurrence of variant D exclusively among 13 animals from Diomandou (four

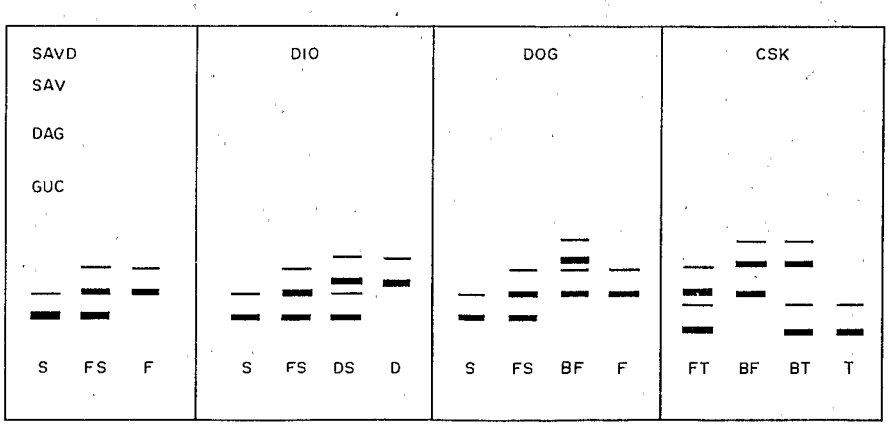

FIG. 2. DIAGRAM OF TRANSFERRIN BANDS IN POPULATIONS OF *ARVICATNHIS.*

individuals carried it), localized between other groups lacking of this variant raised the question of its origin. The studied individuals were all captured, so the genetic segregation could not be analyzed. It would be of interest to examine more animals of this and adjacent regions, in order to clarify if there could have occurred a local mutation leading to this variant, or a more trivial event such as admixion of unknown group of *Arvicanthis* carrying it. Other transferrin bands present in this group are identical to those of the majority of studied animals.

Concerning the variant B, the results are even more surprising, since it is shared by DOG and CSK, two groups from distant areas. More data are needed to clarify this point. The group CSK, although small, contains besides B another rare band, slowly migrating, T, which probably takes the place of S. The analysis of the litter indicates that T is an allelic variant of transferring in *Arvicanthis.* The presence of two rare variants of transferrin in *Arvicanthis* from CSK could be interpreted as a sign of the beginning of a divergence. On the other hand however, the sharing of B by DOG and CSK populations appears as a link between them and might be taken as indication that both belong to the same species. These considerations deserve complementary data.

Esterases. The activity demonstrated by the reaction with α-napthyl acetate was studied in two different electrophoretic conditions, on alkaline polyacrylamide or acid starch gels.

The bands of activity are located at pH 8.5 little behind of albumin zone. While the previously reported results [1, 2] failed to demonstrate polymorphism of alkaline esterase, with a modified technique the individual variation could be observed. The patterns were formed of two or three bands, and interpreted as phenotypes F, FS and S (Plate B; 1 and 2).

Groups of *Arvicanthis* from regions alongside the river Senegal, i.e. SAVD, SAV, DAG, NYA, GUC, DIO and DOG, showed very similar patterns; the group GUC seems however to be slightly different. The observed polymorphism shows the predominance of variant S, homozygous phenotypes F are infrequent. Patterns shown by groups KHY, KED and CSK differ from the previous by localization of bands (Plate B, 3).

Altogether, there is a separation of populations into a large group living alongside the river Senegal, showing a continuous esterase pattern with individual polymorphism while the three remaining small groups, largely distant geographically, differ from the previous and also between them.

Acid esterase. The patterns of bands are more complex than those of alkaline esterases as is generally the case, acid buffers favorize the multiplication of bands. Acid esterase patterns of *Arvicanthis* are spread over a large portion of the gel, no other proteins migrating anodically in these conditions. On the whole, the patterns appear roughly similar between groups SAVD, SAV, DAG, NYA, GUC, DIO and DOG on the one hand and KHY on the other while groups KED and CSK display patterns completely different (Plate C, 1–6). The correspondence between acid esterase patterns and geographical localization differs therefore from that of alkaline esterases, where the group KHY appeared separated from the river populations.

Three sets of bands were tentatively individualized as expression of allelic variants A, B and C (Plate C; 1 and 3), but in general, the complexity of observed patterns prevented a close analysis of phenotypes. In any case, individual variability was certain in groups SAV and SAVD, DIO, DAG, DOG, GUC, KHY and NYA; in contrast, groups CSK and KED showed non-variable patterns.

The geographic distribution of patterns, different for alkaline and acid esterases and the fact that groups showing polymorphism or monomorphism are not the same in the two cases, are arguments to state that patterns displayed in alkaline and acid conditions of electrophoretic separation do not corresond to the same allelic variants. They could however belong to the same locus, in which case one or the other, instead of being unique, are overlapping expression of two or more not visualized variants. An analogous situation was described previously for transferrin locus [1].

The enzymes of haemolysate. All specimens could be analysed, which enlarges and completes previous observations [1, 2].

PGD. As is the case for all tested mammalian species, this enzyme forms one or three bands, depending on the state of homo- or heterozygosity. Populations were tested at first separately, to detect possible individual

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Among SAV and SAVD one animal showed a phenotype considered as FS, all the others were F; the groups DAG, GUC, DOG were uniformly F. In the group DIO were found two presumed FS; the groups KHY and NYA were monomorphic (Plate D; 1 and 2). All these populations shared the same electrophoretic migration of variant F of PGD, while groups CSK and KED diverged in this respect. The PGD of these two groups showed a notably faster migration than that of the seven other groups (Plate D; 3). On the other hand no individual variation was found among CSK and KED.

The PGD locus shows therefore a clear divergence between *Arvicanthis* from northern areas of Senegal and the southern, western or eastern. These results establish a similarity with the previously described differences between *Arvicanthis* from Senegal and those from Haute Volta. In the latter case the migration zone of the southern group appeared much faster (more anodic) than the present material, but there was, in addition, marked individual polymorphism [2] not observed now among CSK and KED animals. To ascertain whether the PGD of *Arvicanthis* from Haute Volta is identical with that of CSK or KED the animals should be compared directly, which was not realizable. At least electrophoretic data disclose that a divergence exists separating the *Arvicanthis* from north of Senegal and those from south.

Hemoglobin. No individual polymorphism was observed but different groups showed different localization of red spots. In general hemoglobin of *Arvicanthis* forms diffuse spots cathodically with respect to the origin of migration. CSK and KED yielded more condensed spots remaining at the insertion point (Plate D; 4), their hemoglobin appears to be at the isoelectric equilibrium at pH 7.2. The groups CSK and KED diverge at this locus from other *Arvicanthis* examined.

PGM. This enzyme usually forms two-banded patterns for each allelic variant but the faster band can be very weak. No individual polymorphism was detected in the studied material, but one sample from DIO group and one from DAO disclosed very strong activity, as compared with others (Plate D; 7 and 8). Inter-group differences were demonstrated by the faster migration of PGM from CSK and KED group, again confirming the divergence between northern and southern populations.

PHI. This locus showed monomorphic within groups, and the localization of the band was identical between populations. The migration was neutral or slightly cathodic. The absence of differences between groups confirms previous findings concerning *Arvicanthis* from Senegal and from Haute Volta which yielded the same localization of PHI bands [2].

MDH. No polymorphism was demonstrated at that locus, but the migration was different in different groups. The migration of MDH of *Arvicanthis* from CSK and KED was faster than that of SAV, GUC, OLR, DIO, DAG or NYA, similarly to the difference between MDH of *Arvicanthis* from Senegal and from Haute Volta (Plate D; 5 and 6). These differences again show a separation between *Arvicanthis* from northern and southern areas.

Concluding remarks for Arvicanthis. Studies of groups originating from different areas disclosed two levels of variability: (a) individual polymorphism genetically determined was observed at loci of albumin, transferrin, esterase and PGD; (b) divergencies between groups of different geographical origin documented by different electrophoretic migration were noted at a small degree for albumin and transferrin and at a marked degree for acid asterase, PGD, PGM, Hb and MDH. The populations that can be separated by the latter criterion are, on the one hand, the group of northern located groups, those from along the river Senegal and around the Green Cape, and on the other hand, the southern located groups, from around Cape Skirring or Kedougou; it seems probable that these latter two are closely similar or identical to *Arvicanthis* from Haute Volta, studied previously [1, 2].

Mastomys

Two species of *Mastomys* have been studied, captured often in the same areas, such as OLR, SLR and KED. The majority of *M. huberti* came

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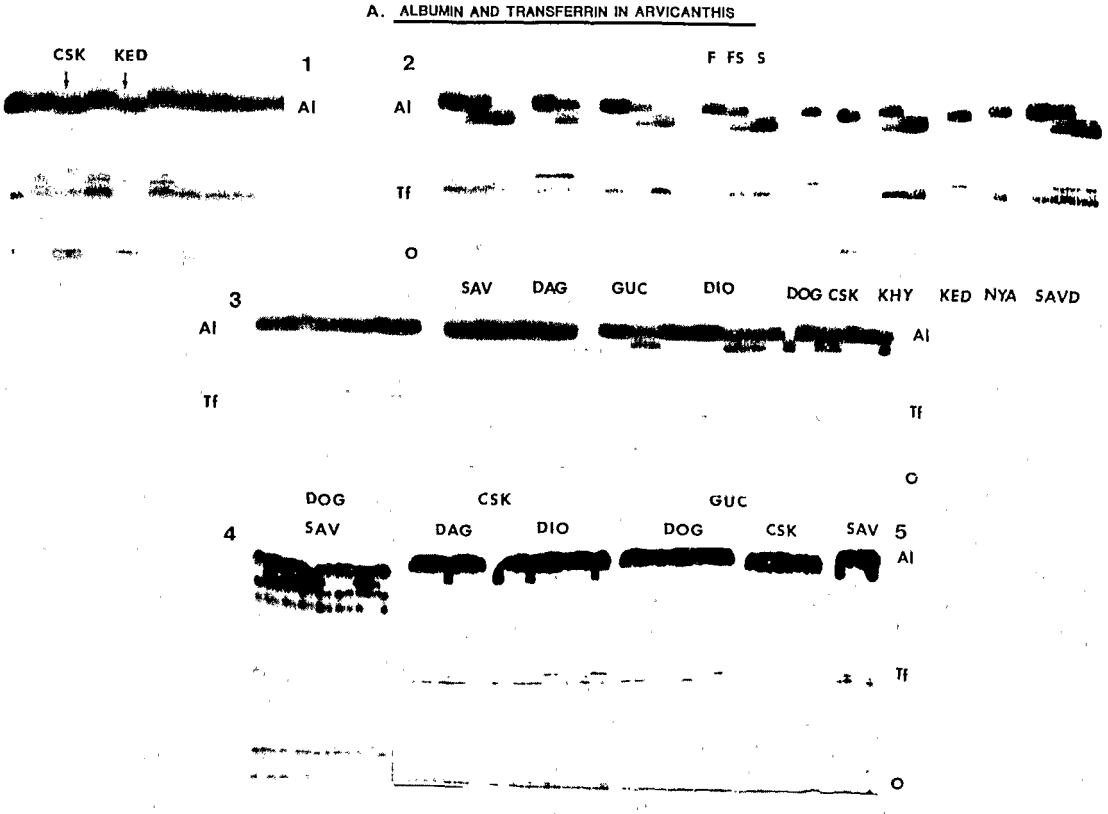

PLATE A. ALBUMIN AND TRANSFERRIN PATTERNS IN *ARVICANTHIS*. INDIVIDUAL POLYMORPHISM AND INTER-POPULATION DIFFERENCES. 1, 2 and 3: starch gels pH 7.4, 4: acrylamide gel pH 8.5. 1: Different migration of band F of albumin in *Arvicanthis* from CSK and KED. 2: Representative polymorphic patterns of albumin in various populations. 3: Polymorphism of transferrin in DOG and CSK groups and of albumin in GUC. 4: Patterns of transferrin in various populations (see Fig. 2).

B. ALKALINE ESTERASES IN ARVICANTHIS AND MASTOMYS

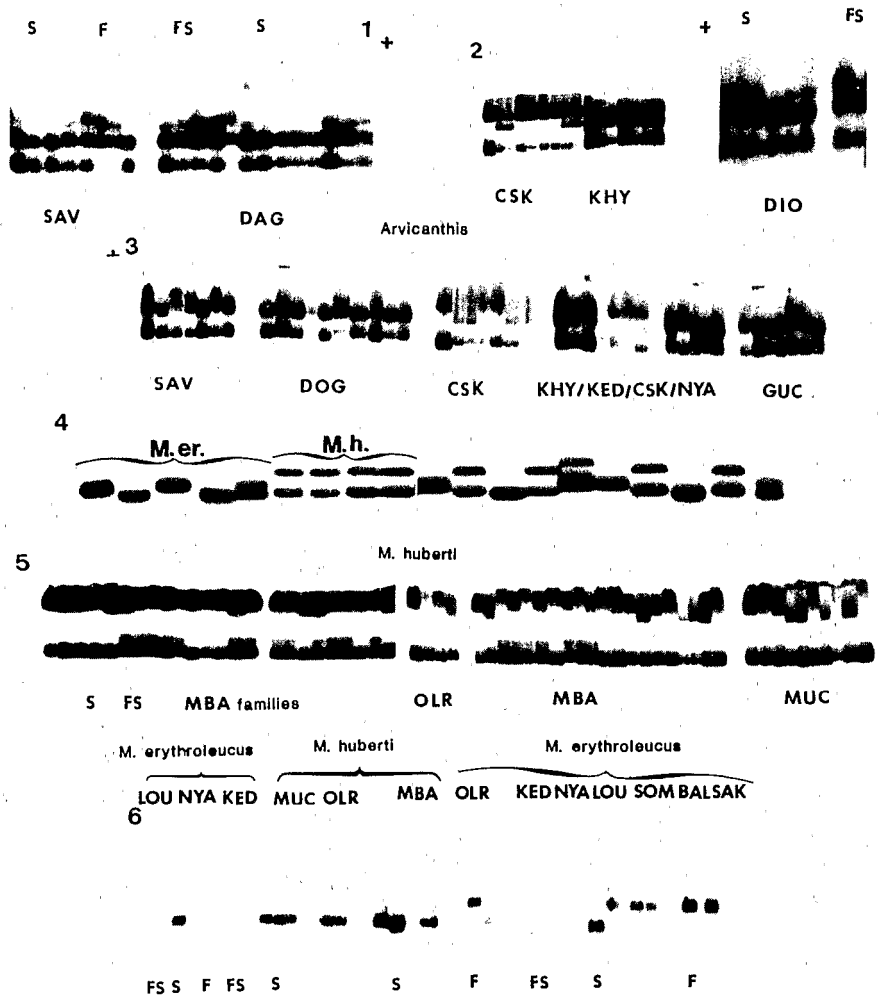

PLATE B. ALKALINE ESTERASES IN *ARVICANTHIS* AND *MASTOMYS*. INDIVIDUAL POLYMORPHISM AND INTER-POPULATION DIFFERENCES. 1, 2, and 3: acrylamide gel; various patterns in *Arvicanthis*. 4: starch gel; compared patterns of *Mastomys erythroleucus* and *huberti*. The first five animals are a family (see Plate C; 7); the last 10 shows various patterns encountered (results obtained in 1982 on animal stock furnished by Prof. F. Petter). 5: Acrylamide patterns of *M. huberti*. Individual polymorphism in families of MBA. Comparison of some population. 6: Acrylamide gel. Compared migration of esterase in *M. huberti* and *M. erythroleucus*. Only the slower component is apparent, the faster has lost its activity upon storage of samples.

C. ACID ESTERASES OF ARVICANTHIS AND MASTOMYS

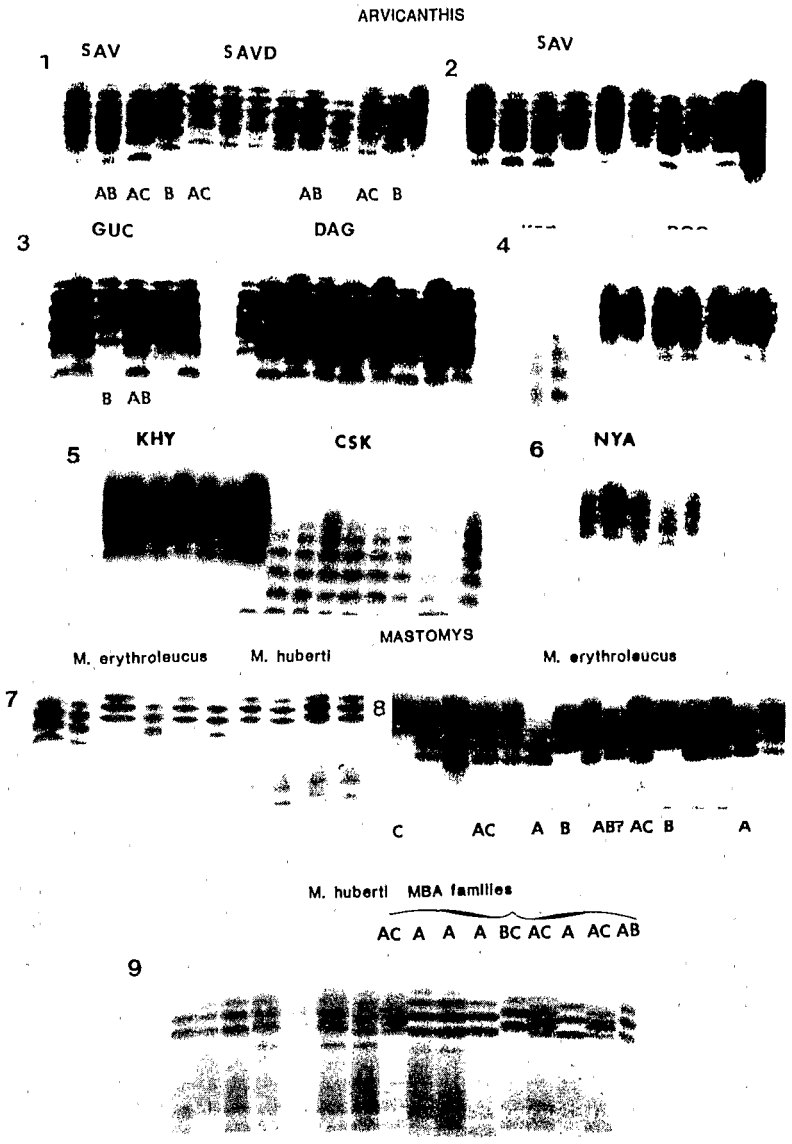

PLATE C. ACID ESTERASES IN *ARVICANTHIS* AND *MASTOMYS*. 1–6: Individual polymorphism and inter-population differences in *Arvicanthis*. 7: Compared patterns of *M. erythroleucus* and *huberti*. The animals are the same as on Fig. 4, Plate B. 8: Patterns observed in a litter; the coexistence of presumed homozygotes A and B and of heterozygotes AC appears non-compatible. 9: Patterns in families of *M. huberti* (MBA).

D. ERYTHROCYTE ENZYMES OF ARVICANTHIS

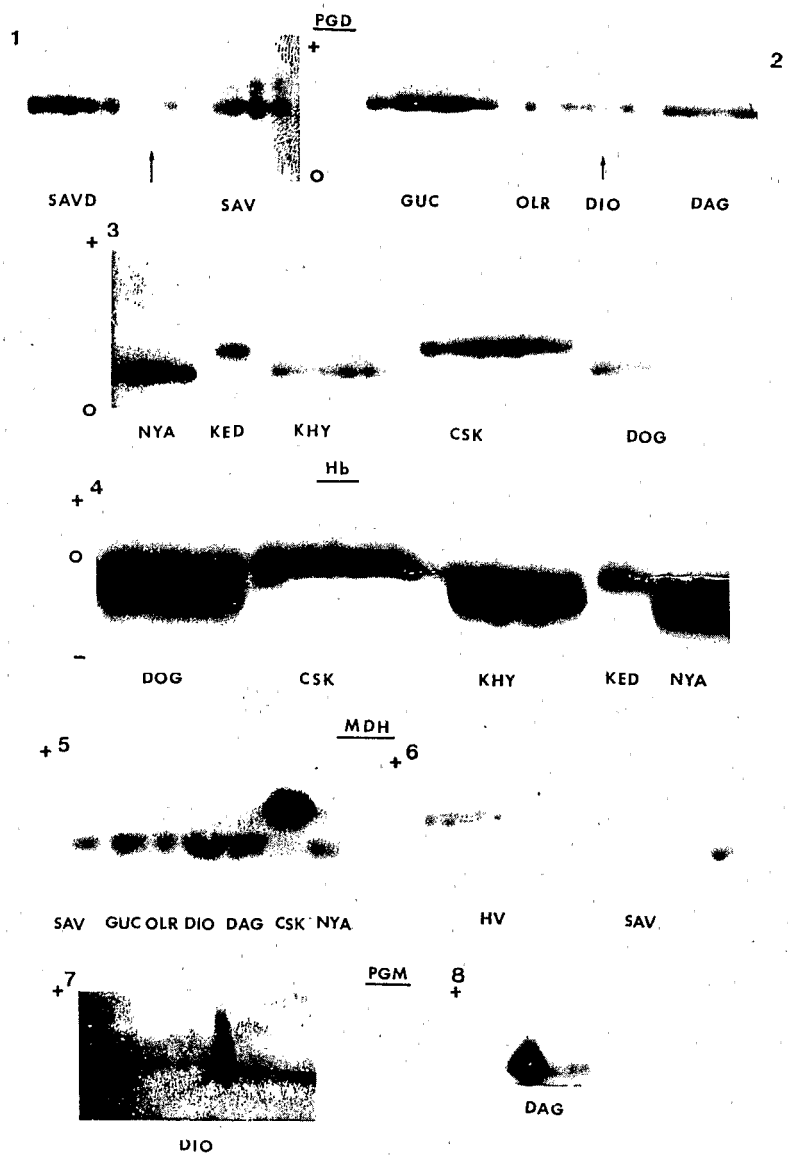

PLATE D. ERYTHROCYTE ENZYMES OF *ARVICANTHIS*. INDIVIDUAL POLYMORPHISM AND POPULATION DIFFERENCES. 1, 2 and 3: PGD. Two animals in SAV and DIO groups disclose phenotypes interpreted as FS heterozygotes. Groups KED and CSK exhibit faster migration of the unique band of activity than other group (the spots seen between patterns of KHY and CSK are artifactual). 4: Hemoglobin spots migrate less cathodically for CSK and KED. 5 and 6: MDH. Different migration is shown for CSK group and for animals from Haute Volta. 7 and 8: PGM. Two animals in DIO and DAG groups showed very intense reaction.

E. ALBUMIN AND TRANSFERRIN PATTERNS OF MASTOMYS

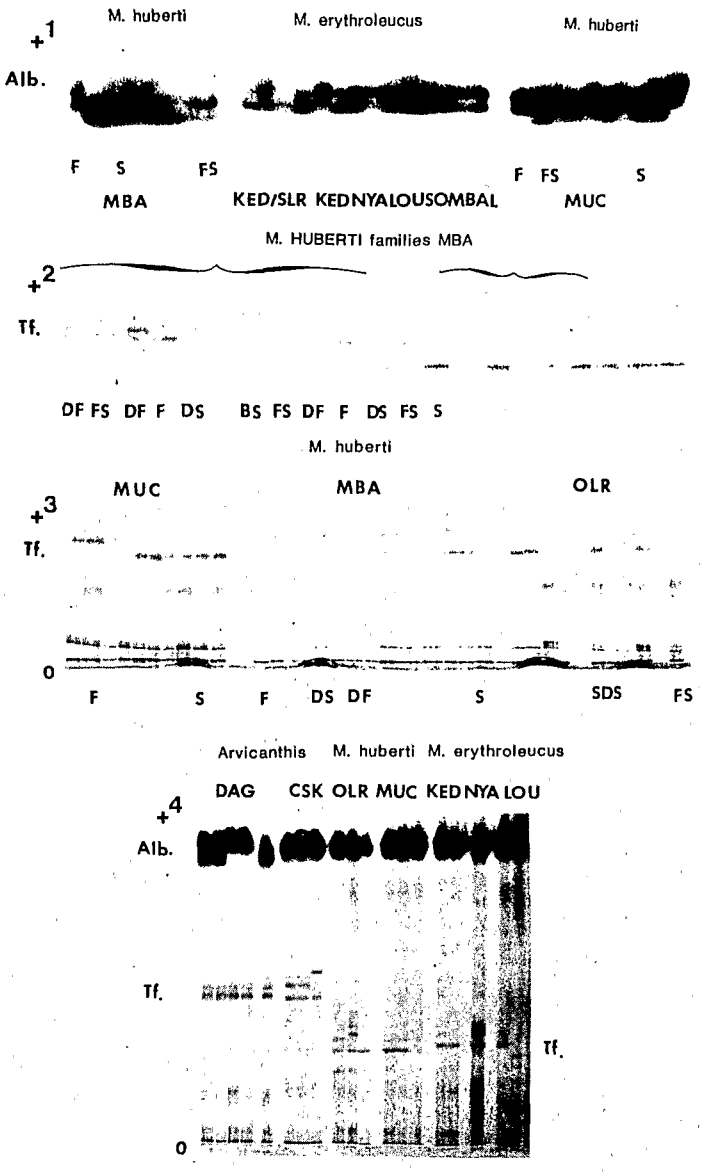

PLATE E. ALBUMIN AND TRANSFERRIN PATTERNS OF *MASTOMYS*. INDIVIDUAL POLYMORPHISM AND INTER-SPECIES DIFFERENCES. 1: Albumin phenotypes in populations of *M. huberti* and *M. erythroleucus*. Starch gel pH 7.4. 2: Transferrin phenotypes segregating in families of *M. huberti* (MBA) acrylamide gel. 3: Compared migration of transferrin in populations of *M. huberti* (the same sheet as in Plate B, 5). Acrylamide gel. 4: Compared migration of transferrin in *M. huberti* and *M. erythroleucus*.

F. ERYTHROCYTE ENZYMES IN 2 SPECIES OF MASTOMYS

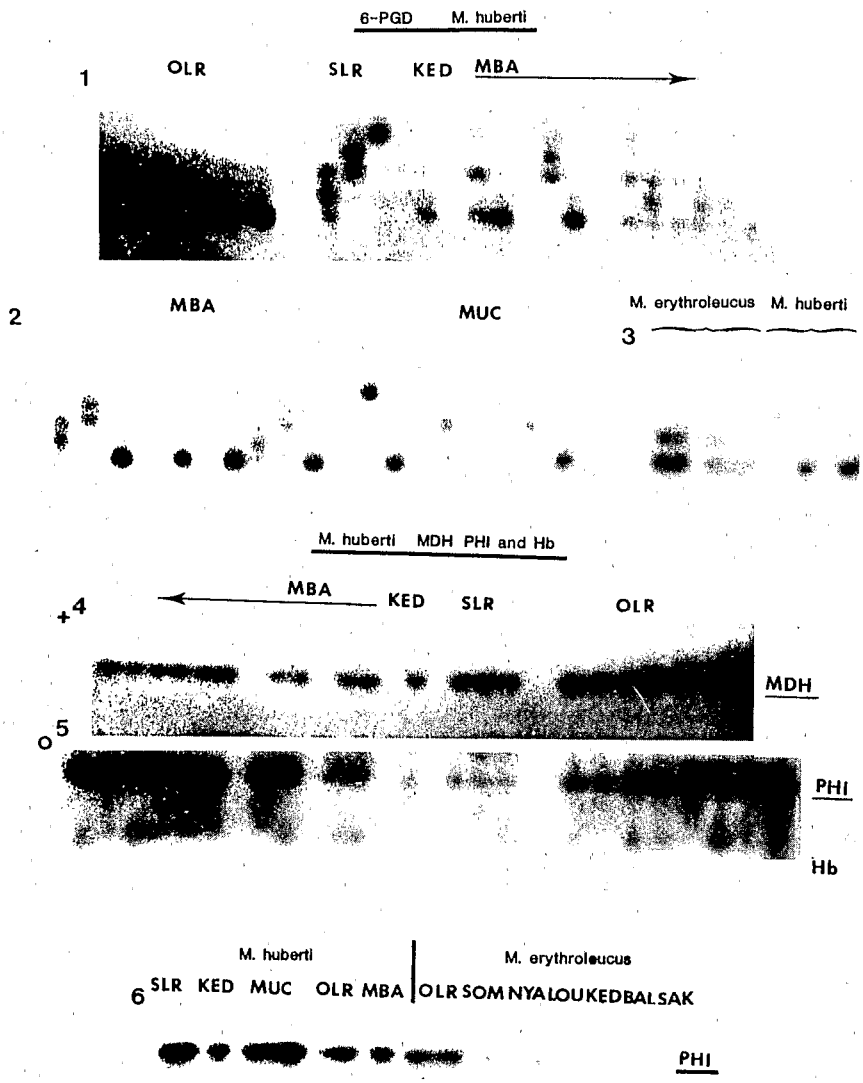

PLATE F. ERYTHROCYTE ENZYMES OF *MASTOMYS*. 1 and 2: PGD. Individual polymorphism (see Fig. 4) and comparison of population groups of *M. huberti*. 4 and 5: Compared migration of MDH, PHI and Hb in populations of *M. huberti*. 6: Compared migration of PHI in *M. huberti* and *M. erythroleucus*.

from localities in Green Cape; these animals constituted six families comprising one or two litters each. Only a few *M. huberti* came from other areas, therefore there is less evidence for comparing populations between them than was the case for *Arvicanthis*. As only 13 *M. erythroleucus* were collected for the present study, some unpublished results obtained on animals previously provided by Prof. F. Petter of Mammalian Department at the Museum d'Histoire Naturelle are given, to complete the data.

M. huberti: *albumin and transferrin.* At albumin locus two variants were recognized (Plate E; 1) having the same electrophoretic migration for all analyzed samples. The segregtion of phenotypes in litters conformed to Mendelian scheme (Table 2), therefore frequencies could be estimated, roughly equal (Table 3) for the two alleles.

Patterns of transferrin obtained on acrylamide sheets permitted to discriminate easily four different bands. The commonest band was designated S, the others, migrating faster, were named F, D and B. Phenotype distribution in four family groups led to consider these bands as allelic variants (Table 2), out of which D was found in two populations, OLR and MBA, while B was observed only once, among the MBA.

As example of phenotypic segregation let us consider the litter of eight displaying five various phenotypes (Table 2, Fig. 3 and Plate E; 2). The mother was DF, the father was not available for analysis; one of the offspring carried a unique phenotype BS (Plate E; 2) which raised the question of its father's genotype. It could neither be BD, BF nor BS if a regular pattern of inheritance were expected. The four phenotypes of other members of the litter were all compatible with a presumed paternal genotype FS. Since at other loci examined the individual having transferrin BS showed phenotypes entirely alignated on those of its presumed brothers and sisters, only transferrin locus would raise the suspicion that it does not belong to the litter considered.

The bands, S, F and D have the same electrophoretic migration in various populations of *M. huberti* (Plate E; 3 and 4), it is therefore possible to estimate globally their allelic frequencies (Table 3).

Mostomys erythroleucus: *albumin and transferrin.* Two-band patterns of albumin formed in

TABLE 2. DISTRIBUTION OF ELECTROPHORETIC PHENOTYPES AMONG *MASTOMYS HUBERTI* FROM SENEGAL N 75

Locality of capture symbol of the region	Group composition	Albumin			Transferrin						6-PGD				
		F	FS	S	BS	DF	DS	F	FS	S	1	1–2	1–3	2–3	3
Ouest Lac Retba Green Cape OLR	8 individuals captured	0	0	8	0	0	1	1	2	4	8	0	0	0	0
Sud Lac Retba Green Cape SLR	3 captured	2	1	0	0	0	0	0	0	3	0	1	0	1	1
M'Bouane Green Cape MBA	17 captured (1 serum lacking)	4	9	2	0	1	2	0	4	9	5	3	5	2	2
	7 families	parents FS × FS			parents FS × S						parents 1 × 2–3				
	litters of 7, 5, 4 and	2	3	2	0	0	0	0	2	2	0	3	3	0	0
	4 from 3 matings	parents FS × S			parents S × S						parents 1-2 × ?				
	both parents analyzed	0	0	4	0	0	0	0	0	17	3	5	0	0	0
	litters of 8, 4, and 2	parents FS × ?			parents DF × ?						parents 3 × ?				
	from analyzed females	5	7	2	(1)	2	1	2	2	0	0	0	6	0	0
	mated to unknown males	parents F × ?			parents S × ?						1–2 × 1–3				
		5	5	0	0	0	0		0	6	4	2	1	2	0
											parents 1 × 1–3				
M'Bouane Green Cape MUC	11 captured	2	8	0	0	0	0	3	1	6	4	0	7	0	0
Kedougou South East KED	1 captured	1	0	0	0	0	0	0	1	0	1	0	0	0	0
		21	33	18	1	3	4	5	12	47	26	14	25	3	3
			(3 n.d.)					(2 n.d.)					(2 n.d.)		

TABLE 3. ALLELLIC FREQUENCIES IN *MASTOMYS HUBERTI*

Al^a	0.52
Al^b	0.48
Tf^B	0.007
Tf^D	0.048
Tf^F	0.185
Tf^S	0.760
PGD^1	0.623
PGD^2	0.130
PGD^3	0.247

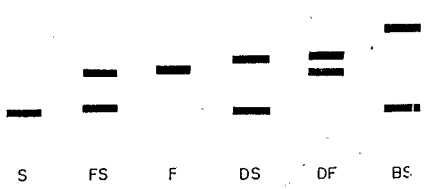

FIG. 3. DIAGRAM OF TRANSFERRIN BANDS IN *MASTOMYS HUBERTI.*

starch gels at pH 7.4 were interpreted as phenotypes S or FS (Plate E; 1). Comparison between two species showed a difference in migration, the lower band of albumin S of *M. erythroleucus* having the same localization as the upper S band of *M. huberti.*

Transferrin patterns of *M. erythroleucus* from various areas showed differences in migration; however, as the total number of examined animals was small, it seems not adequate to interpret these differences in terms either of individual or population differences (Plate E; 3 and 4).

Esterases. The observed patterns of activity were different according to pH and the nature of the gelified medium for the two species of *Mastomys.*

Alkaline esterases. M. erythroleucus formed in starch gels shows variable patterns of one or two intense spots; in some sera the faster spot was a weak and fine band (Plate B; 4). Previous families studies permitted to recognize three allelic variants, F, I and S for the main, lower band. Compared with these variable patterns, alkaline esterases of *M. huberti* appeared rather uniform, showing two intense bands (Plate B; 4). On acrylamide sheets both species formed two rows of esterase spots, both showing variability and suggesting two separate loci. The more anodic row was poorly resolved and will not be analysed here. The lower row (Esl) showed patterns of one single or two spots, corresponding to two variants forming phenotypes FS and S (Plate B; 5).

For *M. huberti* this variation was analysed in the available family material in MBA population yielding the following phenotypes:

parents FS × FS offspring	12 FS + 5 S
FS × S	1 FS + 3 S
FS X ?	3 FS + 3 S
S × ?	8 S,

which gives globally 16 FS + 19 S while the adults were 8 FS and 8 S. The estimated allelic frequencies, would be Es 1^F 0.23 and Es 1^S 0.77 for MBA population alone. In fact, since other groups showed uniformly the phenotype S, globally then Es $1^F = 0.16$ and Es $1^S = 0.84$ in *M. huberti.*

Similar variability at the level of the slower rate of esterase spots was observed for *M. erythroleucus.* The migration of the faster band corresponds to that of variant S of *M. huberti.* Among the 13 animals analysed there were 7 F, 4 FS and 2 S, distribution contrasting with the lack of phenotypes F among *M. huberti.*

Acid esterases. In general the pattern of acid esterases in *Mastomys* comprises less bands than that of *Arvicanthis,* three to five. There is a marked difference between the two species of *Mastomys, M. erythroleucus* yields bands in the middle of the gel while *M. huberti* also shows slower migrating bands, near the origin; these latter probably belong to another locus (Plate C; 7).

Family studies disclosed for *M. erythroleucus* at least three sets of bands, tentatively assignated to variants designated A, B, C from the slower to the faster. However, attempts to establish correspondence between alkaline F, I and S and the acid series of bands were not entirely successful. Thus, for one family, F (or F1) corresponded to AC, S or IS to C and FS to C (or BC?); in a second family, FS corresponded to B or BC, IS to AC and I to A. Only this last pair appears confirmed in population analyses; the discrepancies are due to the uneasy discrimination between complex patterns 'heterozygotes' AB, BC or AC; the simpler 'homozygous' phenotypes A, B, and C are typed more easily (Plate C, 7 and 8).

In *M. huberti* only the faster bands were analysed disclosing three distinct sets of bands. Family studies led to identify the allelic variants designated A, B and C, the heterozygotes AB and BC being poorly resolved while the heterozygotes AC showed nicely separated six or seven bands (Plate C; 9). Phenotype segregation analysis in families yielded:

parents	AB × ?	offspring 4 A + 3 AC + 1 BC
	AB × AB	2 A + 5 AB
	AC × ?	3 A + 3 AC.

Erythrocyte enzymes. Data reported previously [2] were confirmed for both species of *Mastomys* concerning monomorphic loci such as PGM, PHI, Hb and MDH (Plate F; 4, 5, and 6). Concerning PGD, its three allelic polymorphism in *M. huberti* contrasts with monomorphism observed for *M. erythroleucus* (Fig. 4 and Plate F; 1, 2, and 3). This latter species appears therefore much less diversified individually than the former.

Summarizing Remarks and Conclusions

The variability of electrophoretic patterns can occur at individual level, that is intra-species or intra-populations; this is generally due to a genetic segregation, qualified currently by the term of polymorphism. It can also differentiate between the groups of individuals. If such groups are distinct population entities, then differences of physico-chemical parameters evidenced by different electrophoretic migration could constitute marks of some evolutionary events.

Previous data on *Arvicanthis* [1, 2] demonstrated differences, notably for PGD, between a southern group of animals (from Haute Volta) and the northern ones (from Senegal and Egypt). In spite of this divergence, lack of information on the eventual reproductive barrier in natural environment* prevented formulation of a conclusion that *Arvicanthis* from Haute Volta belongs to a species other than *Arvicanthis niloticus.*

The present results again disclose significant differences, this time at various loci, between groups from the north and from the south of Senegal. Yet none of the studied groups contained individuals showing polymorphic patterns of PGD comparable to the ones of *Arvicanthis* from Haute Volta. Was this due only to a sampling effect, or to a real difference between the studied populations from Guinea and from the south east of Senegal and the population from Haute Volta? The direct comparison could not be carried out due to lack of fresh material. Nor is information available concerning the eventual reproductive barriers between all these groups.

Therefore to postulate that all the southern *Arvicanthis,* CSK, KED and Haute Volta, constitute one species which is not *Arvicanthis niloticus* remains at present a hypothesis, yet it appears probable.

*A personal communication from Prof. F. Petter discloses that mating attempts in cages between *Arvicanthis* from Senegal and from Haute Volta were unsuccessful.

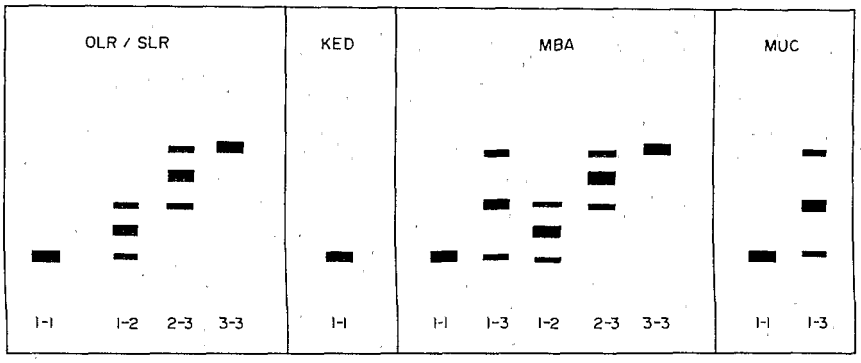

FIG. 4. DIAGRAM OF 6-PGD BANDS IN *MASTOMYS HUBERTI.*

Concerning now the extent of individual variation among *Arvicanthis,* polymorphism was present in a few groups, but was not evident in others. The reported results are indeed subject to re-evaluation when more numerous groups from some areas will be available. However, the overall picture is the poor development of individual polymorphism in this genus. It should be noted that the observed variation concerned different loci in different groups, therefore further data are highly desirable to complete the picture.

If differences in the distribution and the extent of individual polymorphism in various local populations of *Arvicanthis* are confirmed in future studies, then this mechanism could represent one of the first steps towards inter-population divergencies. The presence of different formes of one protein in various groups, as was observed, would correspond then to the ultimate phase of the processus, the different allelic variations predominating in different populations becoming eventually 'fixed'.

Concerning *Mastomys* the situation appears somewhat different, the present results confirm the previous ones [2] as to the individual variation more frequent in *M. huberti* than in *M. erythroleucus.* These species appear homogeneous over the whole area studied, only very small differences between local populations being observed; of course, the numbers of individuals from some localities were so low that again more data are needed to complete the conclusions. Anyway, it seems interesting that environmental parameters show less influence on *Mastomys* than on *Arvicanthis,* in not inducing population differences.

Concerning now the span of electrophoretic variability, there can be less objective difference between analogous bands of two species of the same genus (for example, the main transferrin bands of *M. huberti* and *M. erythroleucus* are distant by 2 mm in the experimental conditions used) than between bands formed by two extreme allelic variants in a single population group (for example the distance of 5 mm between bands D and S of transferrin, observed among members of one family of *M. huberti*). Similar facts were found for other loci or other species; in general, the extent of migration differences is variable and appears actually unpredictable.

Therefore, as pointed out previously [2], application of electrophoretic methods to taxonomic studies requires caution in interpretation of experimental data. Information on the precise correspondence between genetically determined variation of base sequences and the electrophoretic behaviour of resulting allelic proteins is lacking for a great many of polymorphic proteins. It is not easy to assign limits to the electrophoretic variability disclosed experimentally in relation to biological criteria used in differentiation between species.

Experimental

Materials. Animals were captured in traps in various localities and areas of Senegal during spring 1984. The points of capture can be grouped in three major regions: (a) along the river: Sahel, (b) Green Cape area: Sahelo-Soudanese and (c) the south: Guinea (Fig. 1).

The trapped animals have been identified as *Arvicanthis niloticus* (64), *Mastomys huberti* (39) and *Mastomys erythroleucus* (13). Other genera comprised *Taterillus, Myomys daltoni* and *Tatera gambiana*; they were analysed together with others, but the number of animals being too low, the results are not reported here. Certain females were gravid at the moment of capture; their offspring were born in the trap or a few days later, in cages. Other females have been mated to arbitrarily chosen males and yielded litters that are part of the studied material.

Blood and tissue extracts were taken from parents and offspring available at the ORSTOM laboratory at Dakar. Frozen samples of plasma and erythrocyte suspension (in saline–heparin) arrived in our laboratory in June 1984; they have been distributed in several aliquots stored at −20° and analysed in repeated runs over a period of 18 months.

Methods. Electrophoretic separation in starch gel was used for albumin (pH 7.4) and acid esterase (pH 4.5) in serum and for erythrocyte enzymes (pH 7.2). Alkaline esterases and transferrin were analysed simultaneously on acrylamide sheets (pH 8.5). Up to 40 samples can be run on one gel at 7.2 or 7.4, 16 at 4.5 and 60 at 8.5.

The buffer composition and the electrophoresis parameters were the following. pH 4.5 details as reported [3] gel buffer Tris–citrate, starch concentration 11.6%, electrode buffer sodium borate; 300 V for 20 min, then 400 V for 1 h and 500 V until the boundary migrates 7 cm, on a cooling plate at −5°. pH 7.4 gel buffer Tris 0.095 M, cacodylic acid 0.008 M, starch concentration 14.4%, electrode buffer sodium borate 0.3 M borate; 40 mA and 145 V for 6.5 cm of migration at room temperature. pH 7.2 (method currently used for horse blood typing) modified from [4]; gel and electrode buffer sodium phosphate, starch concentration 13%; 100 mA and 100 V during 16 to 18 h at +4°. pH 8.5 modified by AM Scott from [5] adapted in our laboratory. A steep gradient of acrylamide concentration was 8, 5 and 12%; gel buffer Tris 0.09375 M sulphate; electrode buffer Tris–borate. The run is carried out

at −5° on a cooling plate; the current is first 60 mA for 6 min then 60 W constant during 5 to 6 h.

The starch gels at pH 4.5 were exclusively revealed for esterase activity, since no other proteins appeared to migrate in these conditions; those at pH 7.4 although cut in 2 slices were coloured for proteins only, the esterases being poorly resolved. The acrylamide sheets were either revealed first for esterases and next for proteins or run in duplicate and coloured separately. The starch gels at pH 7.2 for erythrocyte enzymes were of 9 mm thick and were cut in 3 slices; each gel could be revealed for four different enzymes, however the middle slices showed better separation and were reserved for polymorphic or variable enzymes.

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