Z. Säugetierkunde **60** (1995) 321–329

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allozymic variation and differentiation in moles (Genus *Talpa*, Insectivora) of the Val Bregaglia (Switzerland) and the Val Chiavenna (Italy)

By F. Suchentrunk, R. Maurizio, Anita Haiden, and G. B. Hart[illegible]

Forschungsinstitut für Wildtierkunde und Ökologie, Veterinärmedizinische Universität Wien, Wien, Austria and Institut für Haustierkunde, Universität Kiel, Kiel, Germany

Receipt of Ms. 19. 04. 1995
Acceptance of Ms. 02. 08. 1995

Abstract

Allozymic variation and differentiation of strictly parapatrically distributed European moles (*Talpa europaea*, n = 44) and Mediterranean moles (*T. caeca*, n = 34) were studied in the Val Bregaglia (Switzerland) and Val Chiavenna (Italy) to estimate interspecific separation and intraspecific gene pool structuring. Tissue samples were screened for allelic variation at 44 putative gene loci using horizontal starch gel electrophoresis. In *T. europaea* four and in *T. caeca* three regional samples separated from one another by water courses were discriminated. The proportion of polymorphic loci was 2.3 per cent in each regional sample, with polymorphisms at the Es-1 locus in *T. europaea* and at the Es-1 and the Es-D loci in *T. caeca*. Expected average heterozygosity ranged from 0.6 to 1.2 per cent in regional samples of *T. europaea* and from 0.9 to 1.2 per cent in *T. caeca*. In *T. caeca* one regional sample showed fixation of a unique allele ($Es\text{-}D^{143}$). This indicated paucity of migration across surrounding water courses. Inbreeding coefficients (F_{IS}) for the Es-1 locus ranged from 0.39 to 1.0 in regional samples. Significant deviations of genotype frequencies for the Es-1 locus due to deficiency of heterozygotes were found in one *T. europaea* and one *T. caeca* regional sample, respectively. The findings are discussed with respect to the parapatric pattern of distribution and the generally low gene pool variability of *Talpa* species found so far.

Introduction

In the Val Bregaglia (Bergell valley, Graubünden, Switzerland) the two mole species *Talpa europaea* and *T. caeca* show strict parapatric distribution. The river "Maira" ("Mera" in Italian) and two of its tributaries (Bondasca, Caroggia) form the parapatric contact line (Maurizio and Hausser 1990, see also Fig. 1). Maurizio and Hausser (1990) hypothesized that competition might be an explanation of this parapatric distribution. However, both species occupy diverse habitats on north and south slopes ranging from the bottom of the valley to an altitude of approximately 1 800 m. These habitats vary greater within each species range along the parapatric contact line than they do across this line. If competition did exert a strong influence on the distribution of the two species, we should note displacement of one species by the other at least in those habitats across the parapatric contact line, where the invading species was more successful.

The parapatric contact line does not appear to correlate with obvious climatic, vegetational or soil changes. This might suggest that the river system itself functions to a certain degree as a migratory barrier for the two species. In each species, the range of regional distribution is also split into several fragments by small mountain creeks (Fig. 1) with pos-

sible segregating effects on the intraspecific gene pools. The objective of the present study is to estimate the degree of gene pool structuring within each of the two species in relation to the local water courses. Occurrence of intraspecific gene pool segregation parallel to the creek system would indicate reduced migration across water courses. Thus it would foster the afore-mentioned hypothesis of the significance of the river system for maintenance of allopatry of these two species of moles in the Val Bregaglia.

Material and methods

Specimens of the European mole (*Talpa europaea* L., 1758, n = 44) and the Mediterranean mole (*Talpa caeca* Savi, 1822, n = 34) were collected in the Val Bregaglia, canton Graubünden, south-eastern Switzerland and in Valchiavenna, Province di Sondrio between June 1989–May 1994 (cf. also Maurizio and Hausser 1990). Individuals of both species were taken from different areas separated from one another by rivers and mountain creeks. Four regional samples were distinguished in *T. europaea* and three in *T. caeca*, in accordance with the areal fragmentation by the main water courses (Fig. 1). Regional sample sizes are given in table 1. Tissue samples of heart, kidney and liver were taken from each specimen and maintained at –20 C until processed.

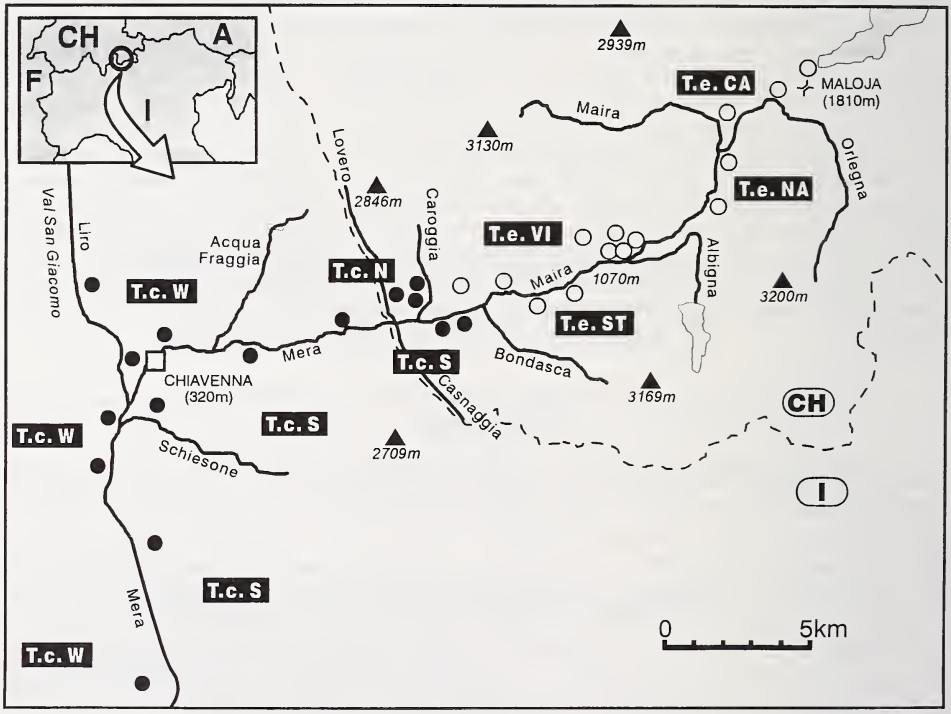

Fig. 1. Study area Val Bregaglia (Kanton Graubünden, Switzerland) and Val Chiavenna (Prov. di Sondrio, Italy). Sampling localities of *Talpa europaea* are indicated by open circles and *T. caeca* by full circles. Sample sizes are one or more individuals per circle. Regional samples for the study of gene pool structuring are as follows. *T. europaea*: *T. e.* CA = Casaccia, *T. e.* NA = Nasciarina, *T. e.* ST = Stampa, *T. e.* VI = Vicosoprano; *T. caeca*: *T. c.* N = North, *T. c.* S = South, *T. c.* W = West. For sample sizes of regional samples, see table 1.

Horizontal starch gel electrophoresis was used to resolve variation in the following 33 isozyme systems encoded by 44 putative gene loci (abbreviation, EC number of enzymes and loci scored in parentheses): α-glycerophosphate dehydrogenase (GDC, EC 1.1.1.8, Gdc), sorbitol dehydrogenase (SDH, EC 1.1.1.14, Sdh), lactate dehydrogenase (LDH, EC 1.1.1.27, Ldh-1, -2), malate dehydrogenase (MOR, EC 1.1.1.37, Mor-1, -2), malic enzyme (MOD, EC 1.1.1.40, Mod-1, -2), isocitrate dehydrogenase (IDH, EC 1.1.1.42, Idh-1, -2), 6-phosphogluconate dehydrogenase, (PGD, EC 1.1.1.44, Pgd), glucose dehydrogenase (GDH, EC 1.1.1.47, Gdh), glucose-6-phosphate dehydrogenase (GPD, EC 1.1.1.49, Gpd), xanthine dehydrogenase (XDH, EC 1.2.3.2, Xdh), glutamate dehydrogenase (GLUD, EC 1.4.1.3, Glud), NADH-diaphorase (DIA, EC 1.6.2.2, Dia-1, -2), catalase (CAT, EC 1.11.1.6, Cat), superoxide dismutase (SOD, EC 1.15.1.1, Sod), purine nucleoside phosphorylase (NP, EC 2.4.2.1, Np), aspartate aminotransferase (AAT, EC 2.6.1.1, Aat-1, -2), hexokinase (HK, EC 2.7.1.1, Hk-1), pyruvate kinase (PK, EC 2.7.1.40, Pk-1), creatine kinase (CK, EC 2.7.3.2, Ck-1, -2), adenylate kinase (AK, EC 2.7.4.3, Ak-1, -2), phosphoglucomutase (PGM, EC 2.7.5.1, Pgm-1), esterases (ES, EC 3.1.1.1, Es-1, Es-D), acid phosphatase (ACP, EC 3.1.3.2, Acp-1), fructose-1,6-diphosphatase (FDP, EC 3.1.3.11, Fdp-1), β-galactosidase (β-GAL, EC 3.2.1.23, β-Gal), peptidases (PEP, EC 3.4.11, Pep-1, -2), guanine deaminase (GDA, EC 3.5.4.3, Gda), adenosine deaminase (ADA, EC 3.5.4.4, Ada-1, -2), aldolase (ALDO, EC 4.1.2.13, Aldo), fumarate hydratase (FH, EC 4.2.1.2, Fh), aconitase (ACO, EC 4.2.1.3, Aco-1), mannose phosphate isomerase (MPI, EC 5.3.1.8, Mpi), glucose phosphate isomerase (GPI, EC 5.3.1.9, Gpi-1).

Tissue preparation, electrophoresis and protein-specific staining were performed as described previously (Hartl and Höger 1986; Grillitsch et al. 1992). Genetic interpretation of band patterns was consistent with the principles outlined by Harris and Hopkinson (1976) and Hillis and Moritz (1990). For resolving allelic variants direct side-by-side comparison of migrating allozymes was carried out including samples of both species on the same gels, respectively. At each variable locus, the corresponding allele of the most common allozyme in *T. europaea* was designated 100 in case of anodal and –100 in case of cathodal migration. All other alleles were numbered as percentages of 100 and –100, respectively. In each specimen the genotypes at polymorphic loci were determined.

The following statistical analyses of population genetics were carried out using the BIOSYS-1 pc package, release 1.7 (Swofford and Selander 1989): allele frequencies, average heterozygosity (H), proportion of polymorphic loci (99% criterion) (P), exact tests of genotypes for deviations from Hardy-Weinberg equilibrium and F-statistics. F_{IS} values for the Es-1 locus were calculated for each regional sample. The same program package was used for calculation of genetic similarity and distance coefficients; Nei's (1978) unbiased D and modified Rogers distances (Wright 1978) were used for cluster analyses employing UPGMA and the distance Wagner procedure by midpoint rooting (Farris 1972). In each species, G-tests (Weber 1980) were carried out to prove homogeneity of allele frequencies at polymorphic loci across regional samples.

Results

Of the 44 loci analysed nine exhibited allelic variation. Seven loci (Mod-2, Pgd, Gpd, Xdh, Np, Aco-1, Mpi) had alleles alternatively fixed in the two species. Variation was detected only at two loci (Es-1, Es-D) in at least one species (Tab. 1). An allelic polymorphism was found only in Es-1 within each regional sample. Es-D showed a fixed allele ($Es\text{-}D^{143}$) in one of the *T. caeca* regional samples (*T. c.* N; cf. Fig. 1, Tab. 1). G-tests for homogeneity of frequencies of Es-1 alleles across regional samples (cf. Tab. 1) revealed heterogeneity in *T. europaea* ($G = 8.02$, $p < 0.05$, d. f. = 3) and homogeneity in *T. caeca* ($G = 2.9$, $p > 0.05$, d. f. = 2). Mean observed/expected heterozygosity (calculated over 44 loci) was 0.003/0.01 for *T. europaea* and 0.005/0.01 for *T. caeca*. The mean proportion of polymorphic loci was 2.3% in both species. Allele frequencies in the *T. europaea* and *T. caeca* regional samples are given in table 1 along with heterozygosity values and rates of polymorphism. Significant deviations of observed genotype frequencies from Hardy-Weinberg expectations at the Es-1 locus were found in one of the *T. e.* regional samples and one of the *T. c.* regional samples (Tab. 1). All these deviations were due to heterozygote deficiency (Tab. 2). The F_{IS} values for the Es-1 locus of each regional sample are given in table 1. The matrices of Nei's (1978) unbiased genetic distances and modified Rogers

distances are presented in table 3. A Wagner tree produced by rooting at midpoint of longest path (cophenetic correlation = 1 000) using modified Rogers distances is displayed in figure 2. The UPGMA dendrogram based on Nei's (1978) D genetic distances revealed essentially the same relationships of the concerned gene pools as the Wagner tree.

Table 1. Allele frequencies at variable loci, heterozygosity (H_0 – observed, over 44 loci, H – expected, over 44 loci), proportion of polymorphic loci (P) and inbreeding coefficients (F_{IS}) for the Es-1 locus of the regional samples of *Talpa europaea* and *T. caeca* from the Val Bregaglia and environs. For acronyms of regional samples, see Fig. 1. Significant deviation of genotype frequencies from Hardy-Weinberg expectations are indicated by asterisks with the most common allele at the affected locus (* – $p < 0.05$, ** – $p < 0.001$), n – sample size.

Locus/Allel		regional samples						
		Talpa europaea (T. e.)				*Talpa caeca (T. c.)*		
n		*T. e.* CA 10	*T. e.* NA 12	*T. e.* VI 18	*T. e.* ST 4	*T. c.* N 9	*T. c.* S 15	*T. c.* W 10
Mod-2	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	80	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Pgd	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	59	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Gpd	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	93	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Xdh	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	83	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Np	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	64	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Aco-1	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	110	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Mpi	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	61	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Es-1	100	0.550	0.542	0.833**	0.750	0.500	0.700	0.750*
	82	0.450	0.458	0.167	0.250	0.500	0.300	0.250
Es-D	100	1.0	1.0	1.0	1.0	0.0	1.0	1.0
	143	0.0	0.0	0.0	0.0	1.0	0.0	0.0
H_0(%)		0.7	0.6	0.0	0.0	0.8	0.5	0.2
H(%)		1.2	1.2	0.6	1.0	1.2	1.0	0.9
P(%)		2.3	2.3	2.3	2.3	2.3	2.3	2.3
F_{IS} (Es-1)		0.39	0.50	1.0	1.0	0.33	0.52	0.73

Table 2. Observed (o) and expected (e) genotype frequencies at the Es-1 locus for all regional samples of *Talpa europaea* (*T. e.*) and *Talpa caeca* (*T. c.*). For acronyms of regional samples, see Fig. 1. For significance of deviations from Hardy-Weinberg expectations see, table 1.

genotype	regional sample						
	Talpa europaea (T. e.)				*Talpa caeca (T. c.)*		
	T. e. CA o/e	*T. e.* NA o/e	*T. e.* VI o/e	*T. e.* ST o/e	*T. c.* N o/e	*T. c.* S o/e	*T. c.* W o/e
82/82	3/1.9	4/2.4	3/0.4	1/0.1	3/2.1	3/1.2	2/0.5
82/100	3/5.2	3/6.2	0/5.1	0/1.7	3/4.8	3/6.5	1/3.9
100/100	4/2.9	5/3.4	15/12.4	3/2.1	3/2.1	9/7.2	7/5.5

Table 3. Matrix of genetic distance coefficients. Above diagonal Nei's (1978) unbiased genetic distances and below diagonal modified Rogers distances (Wright 1978) among samples of *Talpa europaea* (*T. e.*) and *T. caeca* (*T. c.*) of the Val Bregaglia and environs. For acronyms, see figure 1.

regional sample	1	2	3	4	5	6	7
1 *T. e.* CA	****	.000	.001	.000	.203	.175	.176
2 *T. e.* NA	.001	****	.002	.000	.203	.176	.176
3 *T. e.* VI	.043	.044	****	.000	.205	.175	.175
4 *T. e.* ST	.030	.031	.013	****	.204	.174	.174
5 *T. c.* N	.426	.426	.429	.428	****	.024	.024
6 *T. c.* S	.400	.400	.399	.399	.154	****	.000
7 *T. c.* W	.400	.400	.399	.399	.155	.008	****

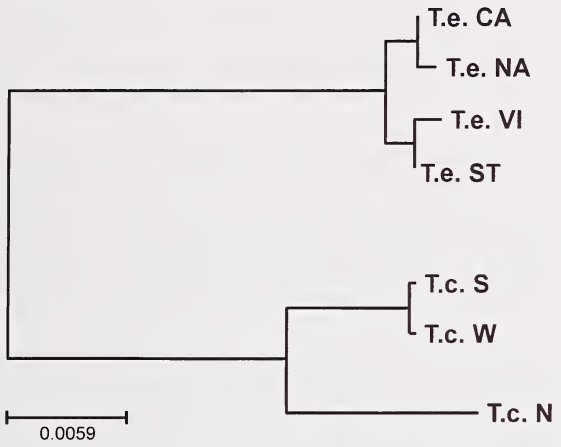

Fig. 2. Wagner dendrogram (midpoint rooting of longest path) using modified Rogers distances (Tab. 3) and displaying differentiation of gene pools of *Talpa europaea* (*T. e.*) and *T. caeca* (*T. c.*) regional samples of the Val Bregaglia (Switzerland) and Valchiavenna (Italy). For acronyms of regional samples, see Fig. 1.

Discussion

In the present study on gene pool structuring of *Talpa europaea* and *T. caeca* of the Val Bregaglia we found indication for reduced or even interrupted gene flow across the river Maira and another water course in both species. This corresponds to the hypothesis of the significance of the river Maira and two of its tributaries for maintenance of parapatry of the two mole species in this region.

Regarding gene flow across rivers and creeks the most striking result was found in *T. caeca* regional samples from north and south of the river Maira. The *T. c.* N. regional sample shows fixation for the Es-D^{143} allele, an allele which has not been found elsewhere in *T. caeca*. Just across the river Maira, south of *T. c.* N, all *T. caeca* individuals harbour the Es-D^{100} allele and no other allele has been detected at this locus in the study area. In *T. caeca* from north of the river Maira the Es-D^{143} allele also does not occur anywhere west of the Aqua Fraggia creek; it occurs, however, on both sides of the Lovero creek. Since we have examined only one individual from the area between Aqua Fraggia and Lovero we cannot exclude introgression of the Es-D^{100} allele in this area by crossing the Aqua Fraggia from west to east.

The Es-D^{143} allele is autapomorphic to the *T. c.N* regional sample and it also does not occur in the other mole species *T. europaea* of the Val Bregaglia. Thus, we interpret this allele as phylogenetically younger than the Es-D^{100} allele. Concerning the origin, aggregation and fixation of the Es-D^{143} allele in the *T. c.* N regional sample, it could be selectively preferred over the Es-D^{100} allele under the particular conditions of habitat of the *T. c.* N regional sample. This is, however, very unlikely because all individuals of *T. europaea* and *T. caeca* with the alternative Es-D^{100} allele live in a variety of habitats reaching from the bottom of the valley to an altitude of approximately 1 800 m. Obviously, this variety of habitats is far greater than that of habitats at the bottom of the valley where both alleles are separated only by the river Maira. Moreover, within the *T. c.* N. regional sample, moles occur also in various habitats, again from the bottom of the valley to an altitude of approximately 1 800 m, but all have exclusively the Es-D^{143} allele. If there was some selection preferring the Es-D^{143} allele, this allele should occur rather in a specific habitat than in a region covering probably as many habitat types as the other regions where the Es-D^{100} allele occurs exclusively. Alternatively, the Es-D^{143} allele could also occur at very low frequencies in other *T. caeca* regional samples and the fixation of it in the *T. c.* N regional sample could be due to a founder effect. Also, the autapomorphic Es-D^{143} allele could have evolved in the *T. c.* N. regional sample and its fixation could be due to genetic drift. Finally, the *T. c.* N. regional sample could represent a relic population of moles which invaded that area in the postglacial phase. Repeated catastrophies (floods, avalanches etc.) could have eradicated all other mole populations in the Val Bregaglia and reinvasions of moles carrying only the Es-D^{100} allele began later on. This would mean that the *T. c.* N. regional sample was an "ancient population" although it carried a phylogenetically younger allele than the other mole populations which immigrated into the Val Bregaglia at a later time.

In view of the remarkably scarce migration that is generally required to prevent genetic divergence under selectively neutral conditions (Hartl 1988), we interpret the occurrence of the Es-D^{143} allele exclusively in *T. c.* N and the absence of the Es-D^{100} allele in this regional sample as resulting from an already longer-lasting lack of migration across the river Maira and probably also across the Aqua Fraggia.

In *T. europaea* of the Val Bregaglia only the Es-1 locus is polymorphic with two alleles. The significant variation of allele frequencies across the regional samples indicates somewhat separated gene pools. In particular, the *T. e.* VI regional sample is separated from the *T. e.* CA and *T. e.* NA regional samples. This indicates reduced gene flow across the river Maira. However, no such reduction of migration obviously occurs across the Orlegna creek, separating the *T. e.* CA and the *T. e.* NA regional samples in the eastern part of the Val Bregaglia. Regarding the situation with the *T. e.* ST regional sample we were not able to finalize our conclusions because of the rather low sample size. Although *T. e.* ST clusters with *T. e.* VI, which would suggest gene flow across the river Maira in this part of the valley, it could equally well be associated with the *T. e.* NA regional sample.

The second important finding of this study concerns the statistically significant deviations of genotye frequencies at the Es-1 locus from the Hardy-Weinberg expectations in two regional samples due to heterozygote deficiency. In the remaining five regional samples we observed the same tendency toward heterozygote deficiency. Although based on low sample sizes, we consider these findings as being reliable, because of the generally rather low population densities of moles in the study area. Thus, the proportion of animals sampled is quite high and this fact increases the reliability of the population genetic estimators. The general uniform excess of homozygous genotypes in all regional samples might either result from respective low effective population sizes and high tendencies toward inbreeding or be due to substructuring of gene pools within regional samples (Wahlund effect). This accords to the above-cited interpretation of little or interrupted migration across water courses.

Values of observed heterozygosity and rates of polymorphism found presently in the moles are very low. They correspond to those of many other subterranean talpids (Yates and Greenbaum 1982; Tolliver et al. 1985; Filippucci et al. 1987; Nevo et al. 1990; Yates and Moore 1990). Among others Nevo (1978, 1979) and Nevo et al. (1990) argued that subterranean mammals living in fairly constant and homogeneous environments should harbour lower allozymic variability than above-ground dwelling mammals that are exposed to more fluctuating and unstable environments. Tolliver et al. (1985), however, could not confirm this "niche-width hypothesis of genetic diversity" in a series of subterranean and above-ground living insectivores. They suggested that there might be other aspects of the biology of insectivores that contribute to the reduction of their genetic diversity. We found indications for reduced or even interrupted gene flow among regional samples and quite high rates of inbreeding within regional samples of moles. Thus, little genetic exchange between local populations in connection with low effective population sizes and inbreeding could have also contributed to the erosion of allelic variability in the course of the evolutionary history of both species (see also Yates and Moore 1990). However, we emphasize that Nevo's (Nevo et al. 1990) niche-width hypothesis of low allozymic diversity in subterranean mammals and the present hypothesis are not mutually exclusive.

Despite the very low allozymic variation in both species, distinct separation between the gene pools of the two mole species is presently indicated by seven diagnostic loci. This is in good accordance with previous data of the two species (Filippucci et al. 1987). Contrary to this pronounced interspecific divergence, absolute genetic differentiation of the four regional samples of *T. europaea* is negligible. Similar results have been found for various *T. europaea* populations from northern Italy (Filippucci et al. 1987). However, the latter authors found a quite clear separation between *T. europaea* from the Austrian Alps and some populations from northern Italy due to a very high frequency of the Mpi^{108} allele in the Austrian sample and the absence of this allele in all the Italian *T. europaea* samples. In *T. caeca* from Italy, the genetic distance between a population of *T. c. caeca* from Tuscony and one from Abruzzo was low, whereas genetic differentiation between these two populations and one of *T. c. augustana* from Aosta (northwestern Italy) was quite high (Filippucci et al. 1987). This significant divergence of gene pools of two conventional *T. caeca* subspecies was predominantly due to alternatively fixed alleles at one locus (Gpd). Similarily, the presently found isolation of the *T. c.* N gene pool from those of the two other *T. c.* regional samples in the Val Bregaglia is also due to alternative fixation of alleles at one locus (Es-D). All these findings suggest that the rate of gene pool divergence in both mole species might be occasionally accelerated by random isolation of particular genomic variants and their subsequent fixation due to genetic drift in small populations.

Acknowledgements

We are indepted to Miss Dina Maurizio (Vicosoprano) for her help with catching the moles. Dr. M. Giacometti (Vienna) transferred some mole samples to our laboratory, dissected some specimens and helped with questions on the local geography of the study area.We would like to thank Dipl-Ing. Dr. K. Bauer (Vienna), Prof. E. Nevo (Haifa) and Dr. Friederike Spitzenberger (Vienna) for valuable discussions and providing access to the literature. Doz. W. Pinsker (Vienna) commented on the manuscript. A. Körber (Vienna) carried out graphical work. M. Palaschke (Vienna) translated the French literature.

Zusammenfassung

Allozymvariabilität und -differenzierung bei Maulwürfen (Genus Talpa, Insectivora) aus dem Bergell (Schweiz) und dem Val Chiavenna (Italien).

Untersucht wurden Genpoolvariabilität, -strukturierung und -differenzierung bei zwei Maulwurfarten (*Talpa europaea*, n = 44) und *Talpa caeca*, n = 34), die im Untersuchungsgebiet strikte parapatrische Verbreitung zeigen, anhand der allelischen Variation an 44 hypothetischen Strukturgenloci mittles Stärkegelelektrophorese. Bei *T. europaea* wurden vier und bei *T. caeca* drei regionale, durch Wasserläufe voneinander getrennte, Subpopulationen analysiert. Die Polymorphierate betrug für jede Subpopulation 2,3%. Bei *T. europaea* war nur ein Locus (Es-1) polymorph; bei *T. caeca* lag allelische Variation an zwei Loci (Es-1, Es-D) vor. Die erwarteten durchschnittlichen Heterozygotiewerte waren generell sehr niedrig (*T. europaea*: 0,6–1,2%; *T. caeca*: 0,9–1,2%). Bei *T. caeca* zeigte sich in einer Subpopulation ein fixiertes Allel am Es-D Locus. Die Inzuchtskoeffizienten (F_{IS}) für den Es-1 Locus lagen bei den einzelnen Subpopulationen zwischen 0,39–1,0. Am Es-1 Locus wurden signifikante Abweichungen der Genotypenhäufigkeiten zu Ungunsten der Heterozygoten festgestellt. Die Ergebnisse werden in Hinblick auf das örtliche parapatrische Verbreitungsmuster der Arten und die allgemeine Verarmung der Genpoolvariabilität bei Maulwürfen diskutiert.

References

Farris, J. S. (1972): Estimating phylogenetic trees from distance matrices. Am. Nat. **106**, 645–668.

Filippucci, M. G.; Nascetti, G.; Capanna, E; Bullini, L. (1987): Allozyme variation and systematics of European moles of the genus *Talpa* (Mammalia, Insectivora). J. Mammalogy **68**, 487–499.

Grillitsch, M.; Hartl, G. B.; Suchentrunk, F.; Willing R. (1992): Allozyme evolution and the molecular clock in the Lagomorpha. Acta theriol. **37**, 1–13.

Harris, H.; Hopkinson, D. A. (1976): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North-Holland Publ. Co.

Hartl, D. L. (1988): A primer of population genetics. 2nd ed. Sunderland, Massachusetts: Sinaur Associates, Inc. Publishers.

Hartl, G. B.; Höger, H. (1986): Biochemical variation in purebred and crossbred strains of domestic rabbits (*Oryctolagus cuniculus* L). Genet. Res. **48**, 27–34.

Hillis, D. M.; Moritz, C. (1990): Molecular Systematics. Sunderland, Massachusetts: Sinauer Associates, Inc. Publ.

Maurizio, R.; Hausser, J. (1990): Différenciation morphologique et répartition en zone de contact de *Talpa europaea* L. et *Talpa caeca* Savi au Val Bregaglia. Bull. Soc. Vaud. Sc. Nat. **80**, 221–233.

Nei, M. (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583–590.

Nevo, E. (1978): Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. **13**, 121–177.

Nevo, E. (1979): Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. **10**, 269–308.

Nevo, E.; Filippucci, M. G.; Beiles, A. (1990): Genetic diversity and its ecological correlates in nature: comparisons between subterranean, fossorial, and aboveground small mammals. In: Evolution of subterranean mammals at the organismal and molecular levels. Ed. by E. Nevo and O. A. Reig. New York: Allan R. Liss, Inc. Pp. 347–366.

Swofford, D. L.; Selander, R. B. (1989): BIOSYS-1. A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. Champaign, IL: Centre for Biodiversity, Illinois Natural History Survey.

Tolliver, D. K.; Smith, M. H.; Leftwich, R. H. (1985): Genetic variability in Insectivora. J. Mammalogy **62**, 405–410.

Weber, E. (1980): Grundriß der biologischen Statistik. Stuttgart, New York: G. Fischer.

Wright, S. (1978): Evolution and genetics of populations. Vol. IV. Variability within and among natural populations. Chicago: Univ. Chicago Press.

Yates, T. L.; Greenbaum, I. F. (1982): Biochemical systematics of North American moles (Insectivora: Talpidae). J. Mammalogy **63**, 368–374.

Yates, T. L.; Moore, D. W. (1990): Speciation and evolution in the family Talpidae (Mammalia: Insectivora). In: Evoultion of subterranean mammals at the organismal and molecular levels. Ed. by E. Nevo and O. A. Reig. New York: Alan R. Liss Inc. Pp. 1–22.

Authors' addresses: Dr. Franz Suchentrunk, Anita Haiden, Forschungsinstitut für Wildtierkunde und Ökologie, Veterinärmedizinische Universität Wien, Savoyenstr. 1, A-1160 Wien, Österreich, Dr. h. c. Remo Maurizio, CH-7603 Vicosoprano/GR., Schweiz, Prof. Dr. Günther B. Hartl, Institut für Haustierkunde, Christian-Albrechts-Universität Kiel, Olshausenstr. 40, D-24118 Kiel, BRD.