

Morphological clines across a karyotypic zone of house mice in Central Italy

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Abstract

Multivariate morphometric differentiation between chromosomal races of the mouse *Mus domesticus* in Central Italy was investigated using a population of $2n = 22$ "CB" karyotype, three populations of standard $2n = 40$ karyotype, five populations of $2n = 22$ "CD" karyotype and three populations from the hybrid zone between the latter two karyotypes. Whilst populations of different karyotype generally have significantly different morphometry, canonical analysis does not reveal that the populations ordinate into distinct aggregations based on karyotype, largely because the $2n = 22$ "CD" populations are so diverse. Nevertheless, canonical analysis does reveal a significant cline in morphology across the contact zone between the $2n = 40$ and $2n = 22$ "CD" mice. The nature of this transition, i. e. a cline 1. within the $2n = 40$ range, 2. within the hybrid range (but unrelated to chromosome number) and 3. within the $2n = 22$ "CD" range, tends to indicate that the morphometric divergence is due to adaptation to the different ecological regimes across which these mice are distributed rather than the phylogenetic divergence of the karyotypic races.

Introduction

Prolific speciation associated with chromosomal diversity in *Mus domesticus* (sensu Marshall and Sage, 1981) is thought to occur mainly at the ecological periphery of the species (Capanna, 1982) in contrast to the general karyotypic conservatism typical of the entire subgenus (Capanna, 1985). Centric fusions have

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reduced the common 40 "all-acroncentric" chromosome karyotype in many local populations, which has resulted in several chromosomal races, distributed from the Orkney islands (Adolph and Klein, 1981) to Marion island north of the Antarctic Convergence (Robinson, 1978).

However, the most intriguing pattern of chromosomal speciation in house mice occurs in Italy. In this region there is a high number (thirteen) of known chromosomal races (Corti et al., 1986), an extreme reduction in the diploid number (down to $2n = 22$; Capanna, 1982) and a complex phylogenetic relationship among populations with these chromosomal rearrangements (Corti et al., 1986). Meiotic abnormalities cause a postzygotic reproductive barrier that appears to completely inhibit gene flow between chromosomal races characterised by different centric fusions (Capanna et al., 1976). Although there appears to be no hybridization between these chromosomal races there is parapatric hybridization between chromosomal races and the surrounding 40-chromosome mice. Due to this restricted interbreeding, chromosomal races could be considered to be semispecies, but their systematic status is still open.

The subject of this paper is two of the chromosomal races that have a parapatric distribution in the Central Apennines, i. e. the $2n = 22$ "CB" and the $2n = 22$ "CD", and the hybrid between the latter race and the standard $2n = 40$ mice (Capanna et al., 1973, 1976, 1977) (Fig. 1). This hybrid zone between the $2n = 22$ "CD" and the $2n = 40$ populations has been extensively analysed in an area north-east of Rome since 1977 (Capanna et al., 1977; Spirito et al., 1980; Corti, 1987).

Both "CD" and "CB" chromosomal races show a diploid number reduced to $2n = 22$, but differ in 8 fusions out of 9 (Capanna et al., 1976). These 8 fusions show

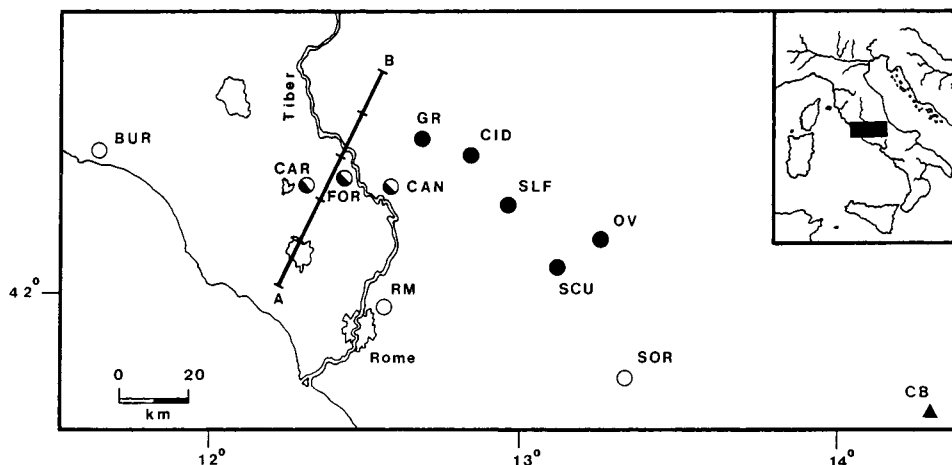


Fig. 1. Localities of Central Italian populations. The alphabetic codes are as for the table. Open circles denote $2n = 40$ populations, closed circles denote $2n = 22$ "CD" populations, half closed circles denote the hybrid populations between the former two karyotypes, and the triangle denote the $2n = 22$ "CB" population. Line AB is a geoclimatic transect across $2n = 40$ and $2n = 22$ "CD" contact zone.

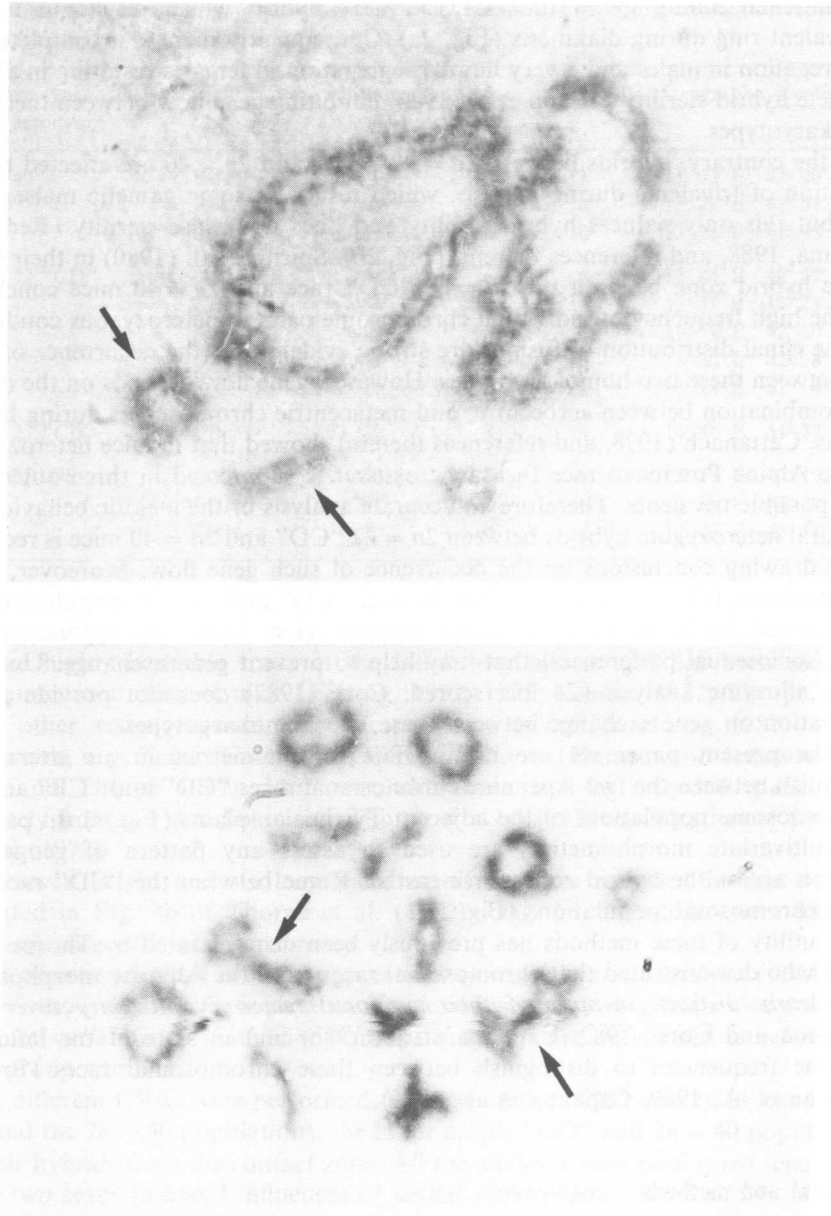


Fig. 2. (a) Diakinesis of a male hybrid between $2n = 22$ "CD" and $2n = 22$ "CB" illustrating a long multivalent chain formed by metacentrics showing monobrachial homology. The only bivalents (indicated by arrows) are the sex chromosomes and the only common metacentric (9.16). This results in hybrid sterility. (b) Diakinesis of a male structural heterozygote hybrid ($n_2 = 29$) from the contact zone between $2n = 22$ "CD" and $2n = 40$. 3 trivalent are formed (indicated by arrows) resulting in a reduction of fertility.

monobrachial homology in the "CD" × "CB" hybrid which results in a long multivalent ring during diakinesis (Fig. 2a). Consequently there is a complete lack of segregation in males and a very limited segregation in females resulting in almost complete hybrid sterility (Gropp et al., 1982) inhibiting gene flow between these two homokaryotypes.

On the contrary, hybrids between $2n = 22$ "CD" and $2n = 40$ are affected by the formation of trivalents during meiosis, which results in some gametic malsegregation, but this only reduces hybrid fertility and does not cause sterility (Redi and Capanna, 1988, and references therein) (Fig. 2b). Spirito et al. (1980) in their study on the hybrid zone between the $2n = 22$ "CD" race and $2n = 40$ mice concluded that the high frequency of individual chromosome pairs in heterozygous conditions and the clinal distribution of fusions are strong evidence for the occurrence of gene flow between these two homokaryotypes. However, gene flow depends on the degree of recombination between acrocentric and metacentric chromosomes during hybrid meiosis. Cattanaach (1978, and references therein) showed that in mice heterozygous for the Alpine Poschiavo race fusions, crossover is suppressed in three out of the seven possible trivalents. Therefore an accurate analysis of the meiotic behaviour of structural heterozygote hybrids between $2n = 22$ "CD" and $2n = 40$ mice is required before drawing conclusions on the occurrence of such gene flow. Moreover, there are indications (Corti et al., 1989) that $2n = 22$ "CD" and $2n = 40$ populations are characterised by different behavioural patterns (i.e. intermale aggression and female sociosexual preferences) that may help to prevent gene exchange. Unfortunately, allozyme analysis (24 loci scored; Corti, 1987) does not provide useful information on gene exchange between these two homokaryotypes.

In the present paper we use multivariate morphometrics in an attempt to distinguish between the two Apennine chromosomal races "CD" and "CB" and the 40 chromosome populations of the adjacent Tyrrhenian plains (Fig. 1). In particular, multivariate morphometrics are used to assess any pattern of geographic variation across the hybrid zone north-east of Rome between the "CD" race and the 40 chromosome populations (Fig. 1).

The utility of these methods has previously been demonstrated by Thorpe et al. (1982) who demonstrated that chromosomal races from the Alps are morphometrically clearly distinct, in spite of their supposed recent evolutionary divergence (Capanna and Corti, 1982; Capanna et al., 1985) and in spite of the failure of allozyme frequencies to distinguish between these chromosomal races (Britton-Davidian et al., 1980; Capanna et al., 1985).

Material and methods

Two hundred and twenty one individuals representing three $2n = 40$ populations, five "CD" populations, one "CB" population and three populations from the $2n = 40$ × "CD" hybrid zone were used in this study (Table 1). All the specimens used in this morphometric study had been previously karyotyped (Corti, 1987) and the chromosome arm constitutions identified by G-banding (Seabright, 1971).

Table 1. Chromosomal races, populations' locality codes, samples of males and females, altitude above sea level (m.) and geographic location.

Karyotype and acronym	Locality Code	Altitude a.s.l. (m.)	M	F	Geographic location
$2n = 40$	BUR	0	10	11	11° 33' E 42° 20' N
	RM	40	14	14	12° 29' E 41° 53' N
	SOR	281	12	10	13° 36' E 41° 43' N
$2n = 22$ "CD"	GR	705	6	6	12° 44' E 42° 27' N
	CID	484	12	14	12° 57' E 42° 23' N
	SLF	980	6	5	13° 7' E 42° 10' N
	OV	1,400	12	12	13° 30' E 42° 8' N
	SCU	730	8	6	13° 14' E 42° 4' N
$2n = 22$ "CB"	CB	320	8	14	14° 46' E 41° 37' N
HYBRIDS	CAR	400	8	9	12° 14' E 42° 19' N
	FOR	208	7	6	12° 19' E 42° 20' N
	CAN	150	10	8	12° 36' E 42° 18' N

The mandible was chosen as the morphological character system because it has a series of highly heritable traits in the laboratory mouse and has been useful in morphometric studies of mice (Festing, 1972, 1973; Leamy, 1977; Thorpe et al., 1982), other rodent species, e. g. Vesper mice (Corti et al., in 1987) and in Insectivores, e. g. *Talpa* (Corti et al., 1985) and *Sorex* (Hausser and Jammot, 1974; Searle and Thorpe 1987). Moreover, characters can be recorded quickly and accurately from the mandible using Thorpe et al.'s (1982) modification of Festing's method (1972).

The seven height and six length characters that are recorded in this way are illustrated in Fig. 3b of Thorpe et al. (1982). Only left mandibles were used, to avoid influence of lateral asymmetry.

To assess the affinities between populations canonical variate analysis (CVA) was used (Thorpe, 1983a). Canonical variate analysis ordines groups along axes of maximum variation so that among-groups distances are maximised in relation to within-group variance.

Two different CVAs were performed, the first on the "CD" and "CB" chromosomal races and the $2n = 40$ populations, the latter on the "CD" and $2n = 40$ populations and their hybrids from the contact zone. All the analyses were performed separately for the two sexes to avoid influences of sexual dimorphism.

Since there could be a bias in the growth stage of our samples (which comprise sub-adults and adults) all the data were initially tested by multiple group principal component analysis (MGPCA) (Thorpe et al., 1982; Thorpe, 1983a, b, 1988) to test whether there was a "growth" component due to ontogenetic variation. The MGPCA could not detect any sign of ontogenetic variation in our sample. Therefore all CVAs were performed on the raw data.

All the specimens are deposited at the Museum of the Department of Animal and Human Biology, University of Rome "La Sapienza".

Results and discussion

Morphological differentiation between "CD", "CB" and 2n = 40 karyotypic populations

On the basis of CVA performed on the populations of the "CD" (GR, CID, SLF, SCU, OV), the "CB" chromosomal race and the 2n = 40 populations (RM, SOR, BUR) (Fig. 1, Table 1), any given pair of populations are significantly different if they are of a different karyotype with only one exception (i. e. BUR 2n = 40 and OV 2n = 22 are not significantly different). The significance level of between-population discrimination is shown by the values of the F-matrix (Table 2). The single 2n = 22 "CB" population is significantly different from all other karyotypic populations (Table 2). This is consistent with the finding that 2n = 22 "CB" is also the only race to show different fixed alleles at two loci (Idh-1 and Me-2) (Corti, 1987) in contrast to the general low genetic differentiation estimated between chromosomal races and standard 2n = 40 mice through multi-locus electrophoretic analysis (Britton-Davidian et al., 1980; Capanna et al., 1985).

Table 2. Upper row: the matrix of the F-values between the three 2n = 40 populations (BUR, RM, SOR), the five 2n = 22 "CD" populations (GR, CID, SLF, OV, SCU), and the 2n = 22 "CB" race; *p < 0.05, **p < 0.01. Lower row: the matrix of Mahalanobis distances between centroids of the 2n = 40 and the 2n = 22 "CD" populations.

	BUR	RM	SOR	GR	CID	SLF	OV	SCU	CB
BUR	—								
RM	1.67 2.77	—							
SOR	0.98 2.54	2.55** 2.67	—						
GR	1.71* 3.35	3.49** 3.34	2.10* 2.92	—					
CID	2.09* 3.36	4.62** 3.35	2.77** 2.91	3.15** 3.55	—				
SLF	2.06* 4.08	3.15** 3.80	2.22** 3.38	0.94 2.36	1.59 2.95	—			
OV	1.31 2.99	4.79** 3.60	3.15** 3.81	3.82** 4.33	4.55** 3.72	3.85** 4.77	—		
SCU	2.25** 4.87	3.47** 4.73	2.16* 3.94	0.58 2.28	3.12** 4.82	1.41 3.35	3.80** 5.77	—	
CB	1.81* 5.55**	5.55** 4.44**	4.44** 3.41**	3.41** 6.94**	6.94** 4.01**	4.01** 2.31**	2.31** 2.85**	2.85**	—

Patterns of variation across $2n = 22$ "CD" and $2n = 40$ hybrid zone

The CVA of the "CD" and $2n = 40$ populations and their hybrids shows a very incomplete segregation of the $2n = 40$ and "CD" races, with their hybrids tending to be intermediate along the second and third canonical variates (Fig. 3). Whilst the $2n = 40$ populations are all quite similar, the $2n = 22$ "CD" populations are very diverse (see also Mahalanobis distances in Table 2). The second canonical variate (CV II) tends to contrast the height measurements with the posterior projection of



Fig. 3. Three dimensional scatter diagram of group centroids on canonical variates for the $2n = 40$ populations, $2n = 22$ "CD" populations and their hybrid populations. Third axis represents the first canonical variate. First, second and third canonical variates absorb 49.57, 16.55, and 14.4% of the total dispersion, respectively, to explain cumulatively 80.52% of the total variation. Units along axes represent pooled within-group standard deviations. Karyotypic codes are as for Fig. 1. Dotted lines enclose homokaryotypes and hybrids.

the coronoid process (with $2n = 40$ mice having a relatively low profile mandible with a posteriorly projecting coronoid), and the third canonical variate tends to contrast the height of the coronoid process with the expansion of the posterior of the mandible (with $2n = 40$ mice having a relatively low coronoid process and an expanded posterior mandible).

When the populations are projected onto a geoclimatic transect (Fig. 1) across the contact zone and their CV II scores are plotted against this transect (Fig. 4) a significant cline in morphology across the zone is revealed ($r = -0.32$, $d.f. = 86$, $p < 0.01$). The $2n = 40$ mice tend to have high CV II scores, the hybrids tend to have intermediate scores and the $2n = 22$ "CD" mice tend to have, on average, low scores although there is considerable variation in CV II scores between $2n = 22$ "CD" populations. The geoclimatic transect has been selected in such a way that it reflects progressive changes in altitude (Table 1), climate, seasonality, and ecology in the ranges of $2n = 40$, hybrids, and $2n = 22$ "CD" (for example, mice from the BUR population live feral in the Mediterranean maquis, whereas OV mice are strictly commensal).

This cline could be due to separate, morphologically distinct, phylogenetic lineages for each karyotype (i. e. $2n = 22$ "CD" and $2n = 40$) meeting parapatrically and partially introgressing, to produce a gradual transition in karyotype matched with a transition in morphology. An alternative explanation is that the transition is caused by natural selection for current conditions as the various populations are

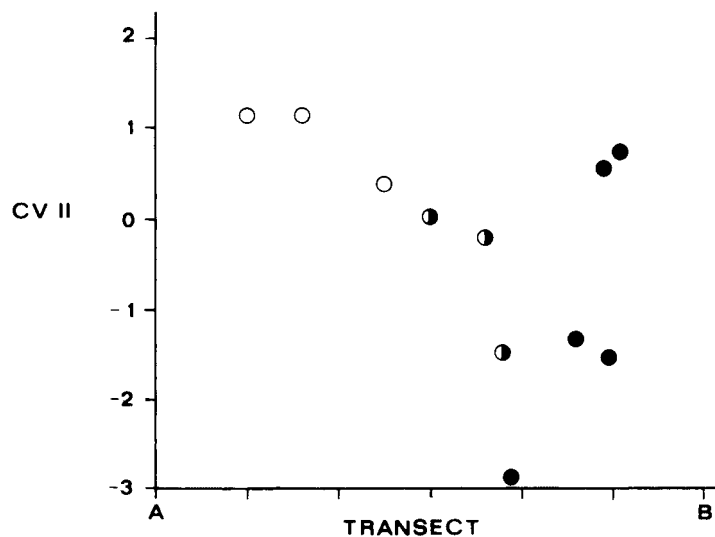


Fig. 4. Geoclimatic transect across the contact zone between $2n = 22$ "CD" and $2n = 40$ populations. The transect line (AB) and symbols for the karyotypes are as in Fig. 1 and the vertical axis (CV II) is from the canonical variate analysis illustrated in Fig. 3. There is a significant correlation between the canonical variate 2 scores and the projection of populations onto the transect ($r = -0.32$, $d.f. = 86$, $p < 0.01$).

distributed across an environmentally heterogeneous area. For example, the $2n = 40$ populations are from the coastal plain, the $2n = 22$ populations are from the Apennine mountains whilst the hybrid populations are geographically intermediate. The first explanation hypothesizes a 'phylogenetic' cause for the geographic variation whilst the second hypothesizes an 'ecological' cause (Endler, 1983; Thorpe, 1984, 1987).

These two hypotheses result in slightly different expectations and consequently one can attempt to test them to decide which is the most likely. If the 'phylogenetic' hypothesis is correct then, although one would expect a correlation between geographic position and morphology when the transect is considered in its entirety (i. e. between karyotypic forms), one does not expect a correlation between morphology and transect position within either the $2n = 40$ or $2n = 22$ karyotypes. One would expect a gradual transition in morphology within the hybrid belt if it were linked to a gradual transition in the karyotype. On the other hand, if the ecological hypothesis is correct there could be indications of a correlation between geographic position and morphology within the karyotypic groups.

The results favour the 'ecological' explanation rather than the 'phylogenetic' explanation. There is a significant correlation within the $2n = 40$ karyotypic group ($r = -0.38$, $d.f. = 28$, $p < 0.05$) and also within the hybrid karyotypic group ($r = -0.58$, $d.f. = 23$, $p < 0.01$) even though there is no transition in the karyotype itself (e. g. $2n$) across the 'hybrid' section of the transect (Corti, 1987). There is also a significant correlation in morphology and transect position within the $2n = 22$ "CD" karyotype although in this case it is positive ($r = 0.51$, $d.f. = 38$, $p < 0.001$). The fact that the trend in morphology can change direction over such a short distance tends to indicate that within the 'ecological' category of causes it is natural selection rather than gene flow that is the predominant force. This is compatible with the conclusion (Capanna et al., 1976, 1985; Fig. 2b) that gene flow between $2n = 22$ and $2n = 40$ mice must be restricted to a certain degree because of hypofertility and limited recombination of hybrids between these homokaryotypes (see Introduction). However, some gene flow between $2n = 40$ and $2n = 22$ "CD" mice could occur for the loci that are located in the area of the chromosomes with recombination. Consequently we cannot entirely reject the 'phylogenetic' hypothesis even though it is less probable than the 'ecological' hypothesis.

Although there is no comparable karyological restriction of gene flow between the $2n = 22$ "CD" populations, these valley populations are separated by mountains and this may restrict gene flow between them. There is clearly more divergence between $2n = 22$ "CD" populations than between the $2n = 40$ populations (Fig. 3, Table 2), even though the latter have a wider distribution. Therefore, drift and local, microgeographic adaptation (Via and Lande, 1985) may be the important factors influencing the divergence between $2n = 22$ "CD" populations.

It can be difficult, if not impossible, to separate the 'ecological' and 'historical (phylogenetic)' causes of geographic variation (Endler, 1983). The former cause, i. e. selection in natural populations, has a large and diverse literature which has recently been reviewed by Endler (1986). When a character set is dominated by phylogeny then it can be possible to indicate this by an analysis of the anagenic

patterns in a phylogenetic tree (Thorpe, 1984). However, in many cases both of these factors make a substantial contribution to the differentiation of the populations. In this situation the specific 'ecological' effects can be regressed out if they are known, as in Hausser's (1984) study of shrews. In this study the specific selection effects are not known. Nevertheless, the balance of probability is in favour of 'ecology' rather than 'phylogeny' as the primary causative factor.

These results contrast with our previous study of morphometric divergence of Robertsonian populations of mice (Thorpe et al., 1982) where we interpreted the divergence phylogenetically. Indeed, the divergence of the karyotypic races of mice has generally not considered the effects of ecological adaptation (Capanna et al., 1977, 1985; Capanna, 1982; Corti et al., 1986), although natural selection for current ecological conditions is implicated in the morphological divergence of this commensal species in several cases (references in Thorpe, 1981).

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