orbit (Bryant, 1988*b*:297, fig.
r the Carnivora. 2) In *Sansa-*
ep dorsoventrally (Fig. 2). In
lorsally. 3) In *Sansanosmilus*
arge, deep fossa on the lateral
, but to a lesser degree, in the
Sansanosmilus, the distance
ical of nimravines and other
to the facial region and the
e buccal displacement of the
rkedly concave diastema give
unique among carnivorans. 6)
margin of the flange is usually
ontrast, in barbourofelines the
s and terminates as a dorsopos-
ers are extremely compressed
ingual surfaces (Martin, 1984).
ie parastyle. This cusp is absent
posterior width of the diaphysis
greater than the width of the
donts, the anteroposterior width
) In *Barbourofelis*, and probably
rally and thicker mediolaterally
corner of the medial surface of
et that is contiguous with the
ivorans surveyed. Identification

GENETIC VARIABILITY AND BIOCHEMICAL SYSTEMATICS OF DOMESTIC AND WILD CAT POPULATIONS (*FELIS SILVESTRIS*: FELIDAE)

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ABSTRACT.—Genetic variability and phylogenetic relationships among domestic and wild populations of cats were studied by allozyme electrophoresis. Tissues were obtained from 67 specimens of European wild cats (*Felis silvestris silvestris*), African wild cats (*F. s. libyca*), and domestic cats from Italy; 54 presumptive loci were resolved. The average proportion of polymorphic loci and heterozygosity were $\bar{P} = 0.11$, $\bar{H} = 0.042$ in the wild cat, and $\bar{P} = 0.20$, $\bar{H} = 0.066$ in the domestic cat. Despite reduced genetic variability, local populations of wild cats were not inbred, as indicated by nonsignificant F_{IS} values. Both F_{ST} and Nei's genetic distances between domestic and wild populations were low ($\bar{F}_{ST} = 0.04$; $\bar{D} = 0.0082$). Dendrograms indicate that the domestic cat belongs to the African wild cat lineage, which supports current hypotheses on cat domestication. Based on the genetic evidence, we suggest that the European wild cat, the African wild cat, and the domestic cat belong to the same polytypic species (*Felis silvestris* Schreber, 1777), and that the European and African wild cats diverged approximately 20,000 years ago.

Felis silvestris, the wild cat of the Old World, is distributed widely throughout the Palearctic Region, from Scotland to South Africa and from Morocco to central and southern China (Corbet, 1978; Haltenorth, 1953). It has followed a typical geographic radiation (Rassenkreis—Mayr, 1963), with populations at the extremes of the distribution showing clearly distinguishable phenotypes (Haltenorth, 1953; Hemmer, 1978; Pocock, 1951; Weigel, 1961). Its distribution in the major Mediterranean Islands is a consequence of human colonization during prehistorical times (Davis, 1984; Ragni, 1981; Vigne and Alcover, 1985), and several local isolates are on the verge of extinction because of human activities (Ragni, 1988; Smit and van Wijngaarden, 1976).

The domestic cat, one of the most widespread mammals in the world, originated from *Felis silvestris* (Lever, 1985; Pocock, 1951). The means of and reasons for its domestication remain under discussion (Clutton-Brock, 1981; Todd, 1977). Following domestication, artificial selection has led to phenotypic and genotypic differentiation. There have been extensive studies of *Felis* genetics and population dynamics, and of the geographic diffusion of the species brought about by international trade (Blumenberg, 1978–1979; Todd, 1977).

Systematic relationships between the different wild forms of *Felis* and the domestic cat are controversial; some regard them as different species, whereas others consider them subspecies of *F. silvestris* (Ragni and Randi, 1986). The Italian populations of *Felis* include the European wild cat (*F. silvestris*), the African wild cat (*F. libyca*), and the domestic cat (*F. catus*). Multivariate analyses of skull characters from Italian populations of *F. silvestris*, *F. libyca*, and *F. catus* (Ragni and Randi, 1986) showed phenotypic continuity among them and supported the hypothesis of conspecificity. This evidence showed the domestic cat to be more similar to the African wild cat than to the European wild cat (Ragni and Randi, 1986).

Because of the high heritability of allozyme variability, multilocus protein electrophoresis can be used to obtain reliable information on phylogenetic relationships among organisms. In addition, these data can be used to analyze the genetic structure of populations, which may have special importance in the conservation of populations of endangered carnivores (O'Brien et al., 1985).

Although there have been several studies of the biochemical genetics of the domestic cat (Auer and Bell, 1981; Kohn and Tamarin, 1973; Thuline et al., 1967; Van de Weghe et al., 1981), population studies have been scarce (Allan et al., 1981; Nozawa et al., 1985; O'Brien, 1980). Only preliminary biochemical data are available for the European wild cat. Herein, we report

on electrophoretic analyses of tissue and erythrocyte proteins from European and African wild and domestic cat populations from Italy.

Materials and Methods

Blood and tissue samples were obtained from 67 specimens (Fig. 1) of *Felis silvestris*, including: *F. s. silvestris*, the European wild cat; *F. s. libyca*, the African wild cat; and *F. s. catus*, the domestic cat. Samples of the European wild cat were collected in the Central Apennine region (Fig. 1, sample 1, $n = 7$), in Sicily (sample 2, $n = 10$), and in a northeastern alpine-prealpine region (sample 3, $n = 7$). The African wild cats were collected in Sardinia (sample 4, $n = 3$). All blood and tissue samples were taken from captive or road-killed specimens. The cranial index (Shauenberg, 1969) and coat-color pattern (Haltenorth, 1953; Pocock, 1951; Ragni, 1981; Weigel, 1961) were used to identify wild forms. Specimens of domestic cat were taken from two locations in the central Apennine region: Umbria (sample 5; $n = 13$); and Bologna, Emilia Romagna (sample 6, $n = 27$). These specimens were obtained by authorized collectors.

Erythrocytes, muscle, heart, and kidney tissues were collected and stored at −80°C. Vertical polyacrylamide-gel electrophoresis (7.5% acrylamide concentration) was used to resolve 54 presumptive loci encoding 43 enzymes and 11 nonenzymatic proteins. Electrophoretic conditions were as follows (erythrocytes = R, heart = H, liver = L): Discontinuous tris-glycine, pH 8.3 (Davis, 1964): lactate dehydrogenase (LDH-1, LDH-2; Enzyme Commission No. 1.1.1.27; L, H, R); malate dehydrogenase (MDH-1, MDH-2; 1.1.1.37; H, R); malic enzyme (ME-1; 1.1.1.40; H); diaphorase (DIA-1; 1.6.2.2; H, L), superoxide dismutase (SOD-1, SOD-2; 1.15.1.1; L); hexokinase (HK-1; 2.7.1.1; L); adenylate kinase (AK; 2.7.4.3; H); alkaline phosphatase (ALP; 3.1.3.1; L); acid phosphatase (ACP-1, ACP-2; 3.1.3.2; L); amylase (AMY; 3.2.1.1; L); adenosine deaminase (ADA; 3.5.4.4; L); pyrophosphatase (PP; 3.6.1.1; H, L); fumarase (FUM-1, FUM-2; 4.2.1.2; H); mannose-phosphate isomerase (MPI; 5.3.1.8; H); peroxidase (POX-1, POX-2, POX-3; 1.11.1.9; L); hemoglobin (HB-1, HB-2; R); albumin (ALB; L); general proteins (PT-1 through PT-8; H). Discontinuous tris-glycine, pH 8.5 (Jolley and Allen, 1965): glucose dehydrogenase (GDH-1, GDH-2, GDH-3; 1.1.1.47; H); glucose-6-phosphate dehydrogenase (G-6-PDH; 1.1.1.49; H, L); aspartate aminotransferase (AAT-1; 2.6.1.1; H); phosphoglucomutase (PGM-1, PGM-2, PGM-3; 2.5.7.1; H, L); glucosephosphate isomerase (GPI; 5.3.1.9; H). Citrate-phosphate, pH 5.9 (Harris and Hopkinson, 1976): isocitrate dehydrogenase (IDH-1, IDH-2, 1.1.1.42; H, R). Tris-borate, pH 8.2 (Studier, 1973): xanthine dehydrogenase (XDH; 1.2.3.2; H, L); esterase (EST-1, EST-2, EST-3, EST-4; 3.1.1.1; L); peptidase (PEP-A, PEP-B, PEP-C, PEP-D; 3.4.11; L). Phosphate, pH 7.0 (Harris and Hopkinson, 1976): 6-phosphogluconate dehydrogenase (6-PGD; 1.1.1.44; L, H, R).

Estimates of mean heterozygosity ($\bar{H}$) and percent polymorphic loci (P) were calculated for each sample, and observed and expected Hardy-Weinberg genotype frequencies were compared by chi-square tests (Li and Horvitz, 1953). Single locus chi-square tests of heterogeneity between samples (Workman and Niswander, 1970) also were computed. F-statistics were calculated by a procedure that corrects for sampling biases, including small number of populations and small or unequal samples (Weir and Cockerham, 1984). F_{ST} is an estimate of the proportion of the total genetic variability distributed among samples. F_{IS} is a measure of deviation of the genotypic frequencies from Hardy-Weinberg expectations. Significant positive F_{IS} values could indicate inbreeding in the samples. The FORTRAN programs GENDIS (Nei, 1978) and PHYLAL (Rogers, 1984) were used for computation of genetic distances. Dendrograms were constructed by use of the KITSCH, FITCH, and CONTML computer programs (PHYLIP package—Felsenstein, 1989). KITSCH and FITCH use Nei's (1978) genetic distance matrix to generate dendrograms; KITSCH assumes a molecular clock, whereas FITCH does not. Dendrograms also were constructed by use of the unweighted pair-group method (UPGMA—Sneath and Sokal, 1973) and the Fitch and Margoliash (1967) method. CONTML (Felsenstein, 1989) generates dendrograms with confidence limits for each branch length under the assumption that divergence between lineages results from genetic drift in the absence of new mutations. PHYLAL (Rogers, 1984) was used to construct dendrograms from the Rogers' (1984) genetic-distance matrix.

Results

Thirteen of 54 loci were polymorphic in at least one population (Table 1). Electrophoretic variation at the G-6-PDH and AAT-1 loci (Table 1) has not been reported previously in *F. silvestris*. Single-locus chi-square tests for agreement with Hardy-Weinberg expectations were significant at the ADA, ME-1, PEP-B, and PT-8 loci in the domestic cat samples. Nonrandom sampling could account for this, as siblings may have been included in the samples inadvertently.

Domestic cat populations ($\bar{H} = 0.066$; $P = 0.20$) appear to harbor approximately 30% more genetic variability than wild populations ($\bar{H} = 0.040$; $P = 0.11$). PGM-3, ME-1, and PEP-B

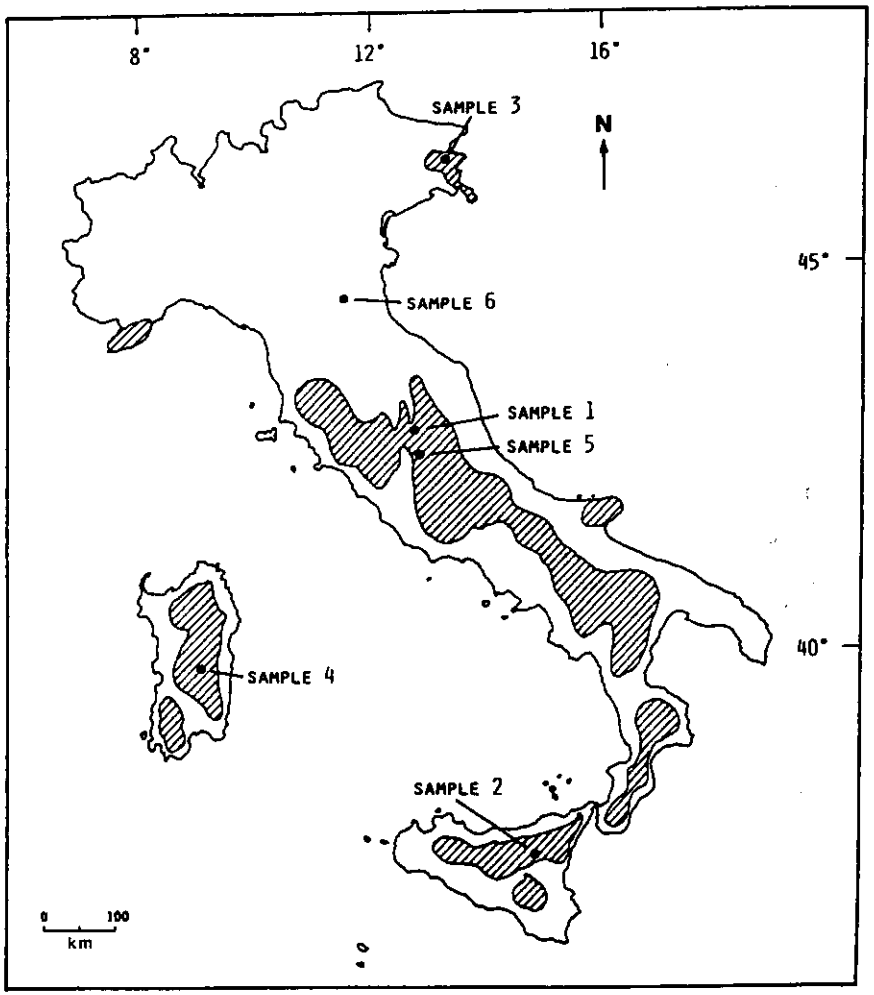

FIG. 1.—Collecting localities of *Felis silvestris* in Italy. Samples 1, 2, and 3 are the European wild cat (*F. s. silvestris*); sample 4 is the African wild cat (*F. s. libyca*); samples 5 and 6 are the domestic cat *F. s. catus*). The approximate distribution of European and African wild cats in Italy is indicated by the shaded areas.

showed allelic variation only among the domestic cats (Table 1). Three loci (GPI, ME-1, and EST-1) showed significant chi-square tests of heterogeneity in allele frequency between wild and domestic cat samples, and F_{ST} values were significant at four loci (GPI, ME-1, EST-1, and 6-PDG). Among the wild cat samples, only GPI showed a significant F_{ST} value, and ADA and PEP-D showed significant positive F_{IS} values. F_{ST} was significant at PEP-D and ME-1 in domestic cat samples, and ADA, ME-1, PEP-B and PEP-D showed significant F_{IS} values. The average F_{ST} values for all polymorphic loci were 0.05 among all samples, 0.04 among wild cats only, and 0.03 among domestic cats only.

Genetic distances (Table 2) were short, and their standard errors were large because of small sample sizes. The greatest distance, $D = 0.0167$, was observed between the Sicily and Sardinia

TABLE 1.—*Allele frequencies (±1 SE) for 13 polymorphic loci in six Italian populations of* Felis silvestris.

Locus	Allele	*F. s. silvestris*			*F. s. libyca*	*F. s. catus*	
		Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
n		7	10	7	3	13	27
GDH-2	a	0.33	0.20	0.12	0.33	0.56	0.35
	b	0.67 ± 0.14	0.80 ± 0.13	0.88 ± 0.12	0.67 ± 0.19	0.44 ± 0.12	0.65 ± 0.06
PGM-3	a						
	b	1.0	1.0	1.0	1.0	1.0	1.0
AAT-1	a		0.05				
	b	1.0	0.95 ± 0.06	1.0	1.0	1.0	1.0
G6PDH	a	0.17			0.50	0.30	0.26
	b	0.83 ± 0.11	1.0	1.0	0.50 ± 0.20	0.70 ± 0.14	0.74 ± 0.06
GPI	a		0.42	0.12		0.08	0.06
	b	1.0	0.58 ± 0.14	0.88 ± 0.12	1.0	0.92 ± 0.05	0.94 ± 0.03
ADA	a		0.36	0.33		0.19	0.09
	b	1.0	0.64 ± 0.13	0.67 ± 0.14	1.0	0.81 ± 0.08	0.91 ± 0.04
ME-1	a					0.23	0.02
	b	1.0	1.0	1.0	1.0	0.77 ± 0.08	0.98 ± 0.02
PEP-B	a					0.11	
	b	1.0	1.0	1.0	1.0	0.89 ± 0.06	1.0
PEP-C	a	0.71	0.92	0.83	1.0	0.71	0.59
	b	0.29 ± 0.12	0.08 ± 0.08	0.17 ± 0.11		0.29 ± 0.09	0.14 ± 0.07
PEP-D	a	1.0	0.86	1.0	0.83	0.81	0.72
	b		0.14 ± 0.09		0.17 ± 0.15	0.19 ± 0.08	0.28 ± 0.06
PT8	a	0.75	0.50	1.0	1.0	0.86	0.75
	b	0.25 ± 0.12	0.50 ± 0.20			0.14 ± 0.09	0.25 ± 0.06
6-PGD	a				0.67	0.21	0.22
	b	1.0	1.0	1.0	0.33 ± 0.19	0.79 ± 0.08	0.78 ± 0.06
EST-1	a		0.08 ± 0.08	0.12			0.13 ± 0.04
	b	0.29	0.42 ± 0.14		0.50	0.64	0.63 ± 0.06
	c	0.71 ± 0.12	0.50 ± 0.14	0.88 ± 0.12	0.50 ± 0.25	0.36 ± 0.13	0.24 ± 0.06

TABLE 2.—*Values of Nei's (1978) genetic identity (above the diagonal) and unbiased standard genetic distance (±1 SE) (below the diagonal) among populations of* Felis silvestris.

Sample	*F. s. silvestris*			*F. s. libyca*	*F. s. catus*	
	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
1		0.9949	0.9968	0.9918	0.9962	0.9958
2	0.0051 ± 0.0035		0.9946	0.9835	0.9919	0.9924
3	0.0032 ± 0.0020	0.0054 ± 0.0044		0.9853	0.9881	0.9868
4	0.0083 ± 0.0079	0.0167 ± 0.0102	0.0148 ± 0.0087		0.9967	0.9947
5	0.0038 ± 0.0023	0.0081 ± 0.0033	0.0119 ± 0.0068	0.0033 ± 0.0039		0.9996
6	0.0042 ± 0.0034	0.0076 ± 0.0032	0.0133 ± 0.0075	0.0053 ± 0.0043	0.0004 ± 0.0010	

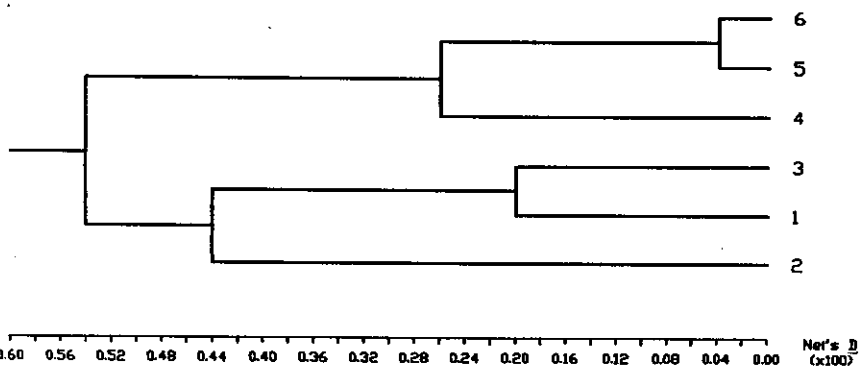

FIG. 2.—Best-fit tree (sum of squares = 0.0) for six *F. silvestris* populations (numbered as in Fig. 1). Tree constructed by the KITSCH program (Felsenstein, 1989) with Nei's (1978) unbiased standard genetic distances and with option $P = 0.0$.

wild cat samples; the shortest, 0.0004, was measured between the two domestic cat samples. The average genetic distance among wild cat populations was 0.0046, among domestic cat populations was 0.0004, between domestic and wild cat populations, 0.0082.

The best-fit dendrogram (KITSCH program—Felsenstein, 1989) divided the samples into two main lineages (Fig. 2): the African wild cat, which includes the domestic cat, and the European wild cat. Trees produced by FITCH, CONTML, and PHYLAL procedures (Fig. 3) are unrooted because of the absence of an outgroup. Short genetic distances with large standard errors produce two branches of zero length in the FITCH dendrogram (Fig. 3a), causing samples 3 and 5 to be placed on the internodes. In the tree produced by CONTML (Fig. 3b), the branches leading to samples 1, 5, and 6 are not significantly different from zero.

DISCUSSION

No fixed allelic differences were found between wild and domestic cat samples, although certain alleles were unique to domestic cats (Table 1). The 6-PGD enzyme was polymorphic in both African wild cats and domestic cats, suggesting possible common ancestry of these forms. The single AAT-1 heterozygote in the Sicily sample suggests an ancient isolation of this wild cat population.

Populations of wild cats had consistently lower genetic variability than populations of domestic cats; this may result from population bottlenecks that reduced genetic variability in wild cats. Nevo et al. (1984) argued that mammalian habitat specialists have lower levels of heterozygosity than generalists; the European wild cat is known to be a habitat specialist sensitive to environmental fluctuations (Ragni et al., 1987). Heterozygosity and polymorphism estimates for Italian domestic cats are similar to those measured in cat populations from Japan (Nozawa et al., 1985), North America (O'Brien, 1980), and England (Allan et al., 1981). Large effective population sizes and high levels of genetic variability in domestic cats may result from the relatively recent diffusion of the domestic cat (during the last 3,000 years) from the Middle East to all parts of the world, and persistent gene flow driven by human migrations and trade (Todd, 1977). Genetic heterogeneity was low among domestic cat samples from Japan ($F_{ST} = 0.01$—Nozawa et al., 1985) and Italy ($F_{ST} = 0.03$—this study).

The average F_{ST} value between populations of domestic and wild cats indicates that only 5% of the total allelic variation is distributed between populations and 95% is found within populations. Such genetic heterogeneity is lower than the average F_{ST} value of 0.230 ± 0.037 computed by Barrowclough (1983) from 25 studies of mammalian populations. Although gene flow between

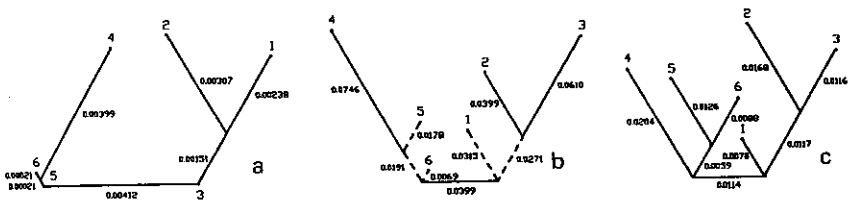

FIG. 3.—Unrooted dendrograms for six populations of *F. silvestris* (numbered as in Fig. 1): a, FITCH; b, CONTML; and c, PHYLAL trees. Branch lengths are indicated on the trees. Dashed branches are not significantly different from zero.

wild and feral populations of domestic cats cannot be discounted, it seems improbable (Ragni, 1988). Domestication was a relatively recent event, and the genetic structure of domestic cat populations probably has changed little.

Most biases in estimates of heterozygosity and genetic distance are caused by the limited number of loci rather than individuals examined (Gorman and Renzi, 1979; Nei and Roychoudhury, 1974). This is not the case when genetic distances are low ($D < 0.020$) and average heterozygosity is high ($\bar{H} > 0.10$), and in this study, both genetic distances and average heterozygosities were low ($D < 0.01$; $\bar{H} < 0.07$). Although reliable estimates of heterozygosity were obtained, standard errors of the genetic distances were high. Accordingly, unbiased genetic distances were computed and clustered by use of different algorithms to reduce the effects of sample size. Dendrograms obtained with the various programs were concordant. The African and European wild cat lineages are well separated. The *F. s. catus* sample is linked to the *F. s. libyca* lineage, which supports the hypothesis that the domestic cat originated from an African wild cat population (Robinson, 1982). The basic topology changed minimally when different algorithms were used.

The average Nei's (1978) genetic identity value (Table 2) within European wild cat samples ($\bar{I} = 0.995$), within domestic cat samples (0.999), between European wild and domestic cats (0.992) and between African wild domestic cats (0.996) are higher than the mean value (0.978) computed by Thorpe (1982) for conspecific population of several animal species. Although the regularity of the molecular clock is a controversial issue (Gillespie, 1986), the recently separated African and European wild cat lineages (indicated by the short genetic distances) appear to have evolved at similar evolutionary rates because branch lengths in the FITCH, CONTML, and PHYLAL dendrograms (Fig. 3) are remarkably similar in the two lineages (although standard errors can result in branches of zero length). Time since divergence of *F. s. silvestris* and *F. s. libyca* can be estimated by calibrating the molecular clock by use of the known age of domestication of the African wild cat. Domestication and subsequent genetic isolation did not occur >10,000 years ago and was probably completed in Egypt not >4,000 years ago; diffusion of the domestic cat around the Mediterranean basin began about 3,000 years ago (Davis, 1984; Robinson, 1982). The Sardinian wild cat is phenotypically and genotypically similar to the North African and Near Eastern *F. s. libyca* populations (Haltenorth, 1953; Pocock, 1951; Ragni, 1981). Prehistoric remains indicate that when the cat was introduced by man into Sardinia, it was not yet a fully domesticated form, but rather a wild cat reared in captivity (Agosti, 1980; Cassoli, 1974). Consequently, we can assume that the average genetic distance ($\bar{D} = 0.0043$) between the Sardinian and the domestic cat has accumulated since about 5,000 years ago. Because the average genetic distance between *F. s. libyca* and *F. s. silvestris* ($\bar{D} = 0.0167$) is about four times greater, it may represent approximately 20,000 years of divergence. Collier and O'Brien (1985) suggested a much earlier time of divergence based on albumin-immunologic evidence.

Paleontologic evidence, although scarce, indicates that the *F. s. silvestris* phenotype was present in Europe from the Emuronian of the Villafranchian, about 1.6 million years ago, to the present (Ficcarelli and Torre, 1975; Kurtén, 1965*b*), in Palestine during the Würm, the last Palearctic

glaciation, about 35,000–15,000 years ago, and in South Africa 40,000–30,000 years ago (Klein, 1986). At the end of the Würm, about 5,000 years ago, the *F. s. silvestris* phenotype was replaced rather quickly by the *F. s. libyca* phenotype in Palestine (Kurtén, 1965*a*) and in South Africa (Klein, 1986).

Paleobiogeographic evidence relating to the time of appearance and diffusion of the *F. s. libyca* phenotype is in general agreement with time estimates based on genetic distances. At the end of the last glacial period, about 20,000 years ago, climatic and ecological changes may have caused rapid phenotypic and, possibly, genotypic divergence of the *F. s. libyca* lineage from the ancestral *F. s. silvestris* lineage. Similar phenotypic shifts in Carnivora and in other mammals with wide latitudinal distribution were found by Davis (1977, 1984) in the same Near East areas, and by Klein (1986) in South Africa. They found a significant correlation between phenotypic shifts and temperature changes that occurred after the Ice Age.

The *F. s. libyca* phenotype, adapted to xeric postglacial Asian and African ecosystems, may have radiated easterly and southerly (Kurtén, 1965*b*) replacing the *F. s. silvestris* phenotype. The apparent absence of *F. s. libyca* phenotypes before the Holocene in the African fossil record (Klein, 1986; Savage, 1978) supports this hypothesis.

High genetic similarity among these cat populations is consistent with the phenotypic continuities shown by multivariate analysis of morphology (Ragni and Randi, 1986). Ethological evidence (Ragni and Possenti, in press) and karyological evidence (Jotterand, 1971; Wurster-Hill and Gray, 1973) also support these findings.

The European wild cat, the African wild cat, and the domestic cat belong to the same polytypic species: *Felis silvestris* Schreber, 1777. The genetic affinity between *F. s. libyca* and *F. s. catus* is consistent with historical and morphologic evidence indicating that the African wild cat is ancestral to the domestic cat. Low genetic variability in wild *F. s. silvestris* populations may result from small effective population size, although natural selection in the wild cannot be discounted.

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CYTOGENETICS AND SYSTEMATICS OF THE RODENT GENUS *GERBILLURUS*

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ABSTRACT.—Chromosomal G- and C-band data for all four species of the genus *Gerbillurus* (*paeba, vallinus, setzeri, tytonis*) document extensive variation both within and among species when using *Tatera* as an outgroup. *G. setzeri* and *G. vallinus* have 2n = 60 karyotypes and share several derived chromosomal conditions. They probably shared a common ancestor after divergence from *G. paeba* and *G. tytonis*. Although *G. paeba* and *G. tytonis* have similar karyotypes, the G-band data suggest that these two species shared only plesiomorphic states for their chromosomal characters. The presence of interstitial insertions of homogeneously staining chromosomal material in this genus is reported. It is concluded that these regions result from gene amplification, a phenomenon rarely encountered in natural populations.

Rodents living in arid regions evolve rapidly to meet the conditions of such existence. Specializations and rapid evolutionary changes perhaps are illustrated best by the muroid family Gerbillidae (Lay, 1972; Petter, 1956; Petter et al., 1984). The family Gerbillidae (gerbils and jirds) contains about 83 species in 13 genera (Carleton and Musser, 1984). The subfamily Taterillinae (*Gerbillurus*, *Tatera*, and *Taterillus*) is a specialized group of gerbils found in deserts, subdeserts, woodlands, and savannas from South Africa to Senegal (Chaline et al., 1977; Pavlinov, 1982). The genus *Gerbillurus* contains only four named species and is endemic to arid and semiarid regions of southern Africa with some members restricted to sand dunes (Schlitter et al., 1984).

Karyotypic data derived from nondifferentially stained material for the four species of the genus *Gerbillurus* indicate the presence of species with 2n = 36 (*G. paeba* and *G. tytonis*) and 2n = 60 karyotypes (*G. setzeri* and *G. vallinus*; Schlitter et al., 1984). These data, however, usually provide underestimation for the number of chromosomal rearrangements and are not conducive to phylogenetic analyses (Baker and Bickham, 1980; Baker et al., 1987; Haiduk et al., 1981). Banding data for Gerbillidae also indicate extensive rearrangements and variation that would not be recognized with nondifferentially stained karyotypes (Benazzou et al., 1982*a*, 1982*b*, 1984; Qumsiyeh, 1986; Qumsiyeh and Chesser, 1988; Qumsiyeh et al., 1987). G-band data are available for representatives of *G. paeba* and *G. vallinus* (Qumsiyeh, 1986; Qumsiyeh et al., 1987), and R-band data are available for *G. tytonis* (Benazzou et al., 1982*b*). In none of these papers were relationships within *Gerbillurus* addressed because of limited taxonomic sampling. Here, we present new data for all four species of *Gerbillurus*, and generate a phylogenetic hypothesis of their relationships.

MATERIALS AND METHODS

Specimens were collected in the field and either processed shortly thereafter or retained for several months before sacrificing. Preparation of bone-marrow cells for karyotypic analyses followed Lee and Elder (1980). G-bands were obtained by the trypsin-Giemsa method of Seabright (1971) as modified by Baker and Qumsiyeh (1988). C-bands were as described by Stefos and Arrighi (1971) and modified by Baker and Qumsiyeh (1988).

Our data were compared to those for specimens of *G. paeba*, *G. vallinus*, and species of *Tatera* reported by Qumsiyeh (1986) and Qumsiyeh et al. (1987). Identification of homologous G-band sequences for gerbils was facilitated by using the standard-numbering system developed for gerbillid chromosomal segments based on the karyotype of *Tatera leucogaster* (Qumsiyeh, 1986).