RESEARCH ARTICLE

Population genetic analysis of cat populations from Mexico, Colombia, Bolivia, and the Dominican Republic: identification of different gene pools in Latin America

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Abstract

In this paper we identify new genetic profiles of eight Latin American cat populations. In addition, we combine data from the present study and previously published data on 70 other American and European populations to discuss (1) the points of introduction of mutant alleles for cat coat phenotypes from Europe into Latin America, (2) the heterozygosity levels at these loci in the current Latin American cat populations, (3) the level of genetic heterogeneity among Latin American cat populations, and how this compares with levels found in North American and European cat populations, and (4) how many different cat gene pools are currently present in Latin America. We also include in our purview historical records of human migrations from Europe to and within the Americas. Our analyses clearly support the view that the current genetic profiles and structuring of cat populations in Latin America can be largely explained by the historical migration patterns of humans.

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Introduction

The genetic profiles of the loci coding for coat characteristics such as color, pattern and length, as well as for skeletal anomalies have been examined for many domestic cat (*Felis silvestris f. catus* Linn.) populations in North America (Anderson and Jenkins 1979; Blumenberg 1977, 1983; Blumenberg and McDonald 1978; Fagen 1978; Glass 1981; Kerr 1984; Kerr and Halpine 1986; Klein *et al.* 1988; Lloyd 1985; Todd 1964, 1966, 1969; Todd and Todd 1976). The comparison of allele frequencies among populations has led to the identification of genetic relationships among populations and possible routes of migration from ancestral locations in Europe (Blumenberg and Lloyd 1980; Clark 1976; Lloyd 1982; Lloyd *et al.* 1983; Robinson 1987; Todd 1975; Todd *et al.* 1979). However, cat populations in other parts of the New World such as Latin America have gone largely unexamined prior to the 1990s, with the exception of sixteen Brazilian (Watanabe 1981, 1983), three Mexican populations, and those from Caracas and Curacao (Todd *et al.* 1974, 1976). Unfortunately, sampling error that occurred within the Mexican population surveys cause these data to be suspect and not necessarily reflective of the true populations that were originally sampled.

Efforts have been made in the 1990's and in the new century to study the genetics of domestic cat populations in Latin America including Buenos Aires (Argentina) (Kajon *et al.* 1992; Ruiz-García and Alvarez 1999, 2003; Ruiz-García *et al.* 2002), Havana (Cuba), Santiago (Chile) (Ruiz-García *et al.* 2002) and Colombia (Bogotá, Ibagué,

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Bucaramanga and Cali) (Barrera 1997; Ruiz-García 2000; Ruiz-García and Alvarez 1996, 1999, 2003; Ruiz-García *et al.* 2002). These recent population genetics analyses in Latin America support five main findings. (i) Northwest (Amazonas) and Northern Brazilian populations are very different from other Latin American cat populations. (ii) The populations of Buenos Aires, Colombia and the Southwestern USA (California, Colorado and Texas) are genetically similar and have a common genetic pool of Spanish origin. (iii) Southern Brazil, Caracas (Venezuela), Willemstadt (Curaçao), and Tenerife (Canaries Islands) cat populations, are genetically distinct from cat populations in Buenos Aires, Colombia, and the Southwestern USA and are therefore considered a different clade. (iv) The Havana (Cuba) cat population is dissimilar from all the other Latin American populations. This could be the result of founder effect, recent genetic drift, or selection (natural or artificial) not present in other Latin American populations. (v) Santiago (Chile) cat populations have a strong British influence compared to other Latin American cat populations. It is unclear whether this finding is due to direct or indirect influxes from British populations.

Recent increases in the number of genetic studies of Latin American cat populations has led to a more accurate account of migration routes and genetic similarities among populations. These new data have been used to test and negate views that were widely accepted by the scientific community. For example, prior to Ruiz-Garcia's (2000) work, it was thought that natural selection negatively affected the frequencies of *l* (long hair) in the tropics (Watanabe 1983; Lloyd 1985, 1987; Todd and Lloyd 1984; Lloyd and Todd 1989; Klein 1993), but Ruiz-García (2000) demonstrated that tropical climate does not negatively affect this trait. Recent advances of the population genetics of Latin American cats have, nevertheless, left a number of questions that need to be answered.

The routes of migration for the penetration of the domestic cat into Latin America have yet to be adequately described and it is unclear how many gene pools currently exist in this part of the world. Furthermore, the degree of bias within the genetic profiles of the Mexican populations analysed (Todd *et al.* 1976), remains unknown and needs to be clarified. The inclusion of biased data in analyses can result in misunderstandings of the phylogenetic relationships between Latin American cat populations. A more complete explanation of why cat populations of Havana are dissimilar from other Latin American areas must be offered. Our surveys and analyses of cat populations in Mexico (Acapulco, México DF, Veracruz, and Alvarado), Colombia (Duitama), Bolivia (Santa Cruz and La Paz), and Dominican Republic (Santo Domingo), together with previously published data on 70 other populations from North and South America and Europe, attempt to answer these questions.

Materials and methods

In the present study, a total of 1705 cats were sampled from eight populations of Acapulco ($n = 310$), México DF ($n = 443$), Veracruz ($n = 241$), and Alvarado ($n = 123$) in Mexico; Duitama ($n = 58$) in Colombia; Santa Cruz de la Sierra ($n = 146$) and La Paz ($n = 133$) in Bolivia; and Santo Domingo ($n = 251$) in the Dominican Republic between September 1997 and January 1998. The sampling strategy involved tracing several circuits in different areas of the cities in order to cover as much territory as possible. Each circuit was followed only once in order to avoid repeated registers of animals and phenotypic data were recorded of cats observed in streets and houses. In México DF, data were also recorded from animals at the Center of Animal Protection.

The genetic nomenclature used is in accordance with the Committee on Standardized Genetic Nomenclature for Cats (1968). The genetic characteristics studied here included: a sex-linked gene (O, o; orange [epistatic to the observation of the A locus] vs non-orange) and the autosomal loci, A (A, a; agouti vs non-agouti [epistatic to the observation of the T locus]), T (t^+, t^b, T^a; striped or mackerel tabby vs blotched tabby vs Abyssinian tabby), D (D, d; non-dilution vs dilution), L (L, l; short hair vs long hair), S (S, s; piebald white spotting vs non- white spotting), W (W, w; dominant white [epistatic to all the other colors] vs normal color). Other loci analysed were I (I, i; inhibitor or "silver" vs non-silver color), C (C, c^s; normal colour vs Siamese pattern) and M (M, m; Manx, tailless vs normal tail). The characteristic phenotypes related with these genes can be seen in Robinson (1977). To estimate the frequencies of the allele orange, the maximum likelihood approximation of Robinson and Silson (1969) was used, assuming a sex ratio 1:1: $p(O) = (2a + b)/2N$, where a = number of orange cats, (O/O and $O/–$); b = number of tortoiseshell females (O/o), and N = the total size of the sample for this locus. The standard error for the estimate of $p(O)$ was the square root of $p(2–3p)/(3–4p)$ (Robinson and Manchenko 1981). For autosomal loci, recessive mutant frequencies (q) were calculated as the square roots of the observed phenotypic frequencies, and dominant mutant frequencies (p) were calculated with the equation $1–q$. Standard errors were calculated by using the square root of the equations $1–q^2/4N$ and $(2–p)/4N$ for the recessive and dominant alleles, respectively.

The allele frequencies for seven loci (O, A, T, D, L, S and W) were used in the relationship analyses. The loci I, C and M were not included in the phylogenetic analyses because they were not reported in other population genetics studies. Various population genetics and phylogenetic analyses that were carried out include:

(i) The expected heterozygosity and the corresponding standard deviation were calculated for the eight popula-

tions sampled, and were analysed along with 42 other North and South American populations of possible Iberian origin based on previously published data (Lloyd and Todd 1989). This statistic yields the genetic diversity of each population independently of breeding system, is insensitive to the action of selection for a given genotype, and is very useful in order to detect populations which might have undergone a stronger genetic drift, or are derived from a founding population with multiple origins. This statistic was also calculated for a larger group of 78 populations, including the 8 populations of the present study, the 39 of the 42 North and South American populations referred to above and a further 31 populations from North America and Western Europe (Spain, Portugal, Italy, France and Great Britain) (Lloyd and Todd 1989), in order to see whether there were differences in the genetic diversity between the European and the American populations, the latter presumed to be derived from the former. The locus *W* was excluded from the expected heterozygosity calculation for the set of 78 populations because its value of genetic diversity was very small and similar in all the populations analysed. However, the locus W was included in the set of 42 populations to determine the influence in the estimation of the heterozygosity of a locus with scarce gene diversity.

(ii) For the two groups of populations mentioned, the values of the statistics H_T (genetic diversity in the total population), H_S (average genetic diversity in the subpopulations involved), and G_{ST} (genetic differentiation between the subpopulations in relation to the total population), were calculated. It is very important to establish which loci introduced more or less genetic heterogeneity in order to determine the evolutionary processes affecting the genes under study during the process of migration from the Old World to the New World.

(iii) Different ensembles of populations were constructed in order to apply the various phylogenetic analyses: (a) For example, one ensemble comprised of 43 Latin American populations, of which two were from Tenerife (Canary Islands) (A. T. Lloyd *unpublished data*; Ruiz-García 2000). The names of the populations are displayed in the respective figures. (b) Another ensemble was comprised of 68 American cat populations, 50 from North America (USA and Canada), and 18 from Latin America. This ensemble was made in order to detect the existence of two possible gene pools in the USA populations, one of Hispanic and the other of Anglo origin, as had been suggested earlier (Blumenberg and Lloyd 1980; Blumenberg 1986; Ruiz-García 1990a,b, 1991; Ruiz-García *et al.* 2002). (c) Another ensemble was comprised of 62 populations, 44 from Europe (Spain, Portugal, Italy, France and UK), and 18 from Latin America. This ensemble was made in order to examine the extent of similarity between Latin America and European populations, and to determine

the degree of genetic differentiation between the populations of the Old and the New Worlds.

Using these ensembles of populations, the corresponding matrices of genetic distances were obtained for pairs of populations, with Nei's unbiased (1978), and Cavalli-Sforza and Edwards' chord (1967). These two genetic distances were used because of their differing mathematical properties, which might influence the derived classifications. The algorithms of hierarchical classification UPGMA and WPGMA were applied to the matrices of genetic distance (Sneath and Sokal 1973). The first one was chosen due to the properties shown by Nei *et al.* (1983) and Nei (1987), while the second was chosen because of its interesting phylogenetic properties (Pamilo 1990). The phylogenetic trees presented here are those with the best cophenetic correlation coefficients (Sneath and Sokal 1973), and the smaller standard deviation of Fitch and Margoliash (1967). Four trees were obtained for each ensemble, and consensus trees were derived applying the Strict method of Rohlf (1982). The indices of Colles (I_c), Mickevich (I_m), and Schuh and Farris (I_{SF}) were used to determine the degree of resemblance between the trees which originated the consensus trees. Simplified trees, without root of origin, and minimum spanning trees (Gower and Ross 1969; Rohlf 1970) were also obtained for each ensemble of populations. In addition, a non-metric multidimensional scale analysis (MSD) was generated for each population ensemble, and for each genetic distance used. In order to calculate the statistic called "Stress", 50 iterations were used, as a measure of the goodness of fit of the distances in the configuration space to the monotone function of the original genetic distances. The process of iteration was stopped before 50, if a minimum stress was obtained equal to 0.001, or a maximum stress ratio equal to 0.999. The non-metric multidimensional scale shown here were those with the best "final stress" statistics.

(iv) Finally, a canonical population analysis was performed, separating groups of populations along axes with high discrimination power using the Mahalanobis square distance, which is based on two hypothesis: (a) There is homogeneity between all covariance matrices corresponding to the population groups (measured by a maximum-ratio likelihood test), and, (b) The means of the *k* groups are significantly different (measured by a Wilks' Lambda test, and the associated value of the Fisher-Snedecor *F* test) (Rao 1951). Subsequently, a canonical transformation, the eigenvalues, and the significance of the first canonical axis with the Bartlett's test, were found. Also, the factorial structure of the canonical variables, the canonical representation, and the radius of the confidence regions (for a 90% level), were calculated. These analyses were applied to different groups of American populations of presumed Iberic origin. Fifteen groups of populations were considered: Havana-Santo

Domingo (Caribbean islands of Spanish settlement), Buenos Aires (the two samples), Mexico, Venezuela-Curacao, Southern Brazil, Northern Brazil-Brazilian Amazonia, Colombia, Tenerife (Canary Islands, the two samples), the populations of presumed Hispanic origin in the USA, Bolivia, and the individual populations of Santiago (Chile), Jamaica, the most recent sample of Rio de Janeiro (Brazil), Duitama (Colombia), and Leticia (Colombian Amazonas).

Results

The observed phenotypes, estimated mutant allele frequencies, and standard deviations for 10 morphological loci in Acalpulco, México DF, Veracruz, Alvarado, Duitama, Santa Cruz, La Paz, and Santo Domingo cat populations for which new data were collected in the present study are listed in table 1.

Analysis of expected heterozygosity

In the analysis of the ensemble of populations of Latin America and those of presumed Iberian origin in the USA (50 populations), in which 7 loci were studied, Acapulco showed the highest expected heterozygosity, followed by Santiago (table 2a). The populations of Colombia, Curacao and Caracas, and most of the populations from North Brazil and Brazilian Amazonas, had lower heterozygosity values. The Colombian population of Leticia, in the Amazonas, had the lowest heterozygosity. When the locus W was excluded from the analysis of the larger ensemble of 78 North and South American and European populations, the values of expected heterozygosity increased (table 2b). The Acapulco and Portland (USA) populations had the highest heterozygosity values. The position of the populations in the scale derived from this value is similar to that presented above. Among the Colombian populations the higher heterozygosity value was Cali, in both cases. The heterozygosity values for the Spanish populations included in this analysis were very similar to those of the populations of Colombia, Curacao, Caracas, and some Brazilian populations, and were substantially lower than the values observed in the populations of Havana, México DF, Buenos Aires, Santiago, Texas, Colorado, California, South Brazil, Bolivia and Santo Domingo. The same pattern was observed in the comparison between the populations from the UK and those of Anglo origin in North America. Colonisation seems to have increased the genetic diversity in these cat populations. The Leticia Colombian population (Amazonas) seemed to have low genetic diversity compared to other populations.

Analysis of genetic heterogeneity

The statistic G_{ST} was 0.061 for the ensemble of 50 Latin American and corresponding USA cat populations of Hispanic origin (table 3a). Although this value is significant, it is relatively small, showing that any of these 50 populations have on average 93.9% of the total genetic diversity. When the heterogeneity resulting from each locus was analysed separately, the situation was different. The three loci responsible for the bulk of the heterogeneity, in decreasing order, were L, D and T. The loci S, A and O contributed much less heterogeneity, and the W locus caused the least heterogeneity, a pattern concordant with previous analyses of European cat populations (Ruiz-García 1991, 1994, 1997). The results of the analysis of heterogeneity for the ensemble of 78 North and South American and European populations, with the exclusion of the locus W, are summarised in table 3b. G_{ST} increased slightly to 0.073, and although highly significant ($P < 0.0001$), this value was still relatively small. The genes with larger contributions to genetic heterogeneity were T, followed by L and D. The loci S, A and O were responsible for little heterogeneity, just as for the previous ensemble.

Phylogenetic analysis

(A) Two trees identify which of the 43 Latin American populations had the best coefficients of cophenetic correlation, and smaller values of standard deviations of Fitch and Margoliash (1967) (figure 1a,b). The tree derived by applying the UPGMA algorithm with the distance of Cavalli-Sforza and Edwards (1967) showed Duitama (Colombia) as the most divergent population, followed by Leticia (Colombian Amazonas). Five well defined clusters were observed. The first cluster to diverge was comprised of North Brazilian and Amazonas populations. The second diverged cluster was a clade including two populations of presumed British influence, Jamaica and Santiago de Chile (Lloyd *et al.* 1981; Ruiz-García *et al.* 2002). The third diverged cluster contained two groups of populations: one including populations from the Spanish-speaking North Caribbean; and a second with the old sample of México DF and La Paz (Bolivia). Of the remaining two clusters, one contained the Colombian populations (except Leticia), together with the two samples of Buenos Aires, and a sub-cluster conformed by the new sample of México DF, Santa Cruz and Acapulco. The last cluster contained the populations of South Brazil, and the samples of Tenerife (Canary Islands), Los Mochis (Mexico), Willemstadt (Curaçao), and Caracas (Venezuela).

The tree derived by applying the WPGMA algorithm with the distance of Nei (1978), also showed Duitama as the most divergent population. The next diverged was the group of populations of North Brazil, and the Brazilian Amazonas, with Leticia clustering with them. The remaining populations fell into two big clusters, of which one was formed by the populations of South Brazil, Tenerife, Los Mochis, Curaçao, Caracas, and Jamaica.

Table 1. Mutant phenotypes observed (MPO), number of cats studied (NCS), mutant allele frequencies and standard errors of the eight cat populations sampled from Acapulco, México DF., Veracruz, and Alvarado (México), Duitama (Colombia), Santa Cruz and La Paz (Bolivia), and Santo Domingo (Dominican Republic) that were documented in the present study. O = orange; A = agouti; T = tabby pattern (t^b = blotched tabby; T^a = Abyssinian tabby); D = dilution; L = hair length; S = white spotting pattern; W = dominant white; C^s = Siamese; I = inhibitor (silver colour); M = Manx. n = Sample size; O/O & $O/-$ = orange cats; $O/+$ = heterozygote females (calico); $+/+$ & $+/-$ = non-orange cats.

Population	n	O					A		T			D		L	
		O/O & $O/-$	$O/+$	$+/+$ & $+/-$	MPO	NCS	MPO	NCS	MPO t^b	T^a	NCS	MPO	NCS	MPO	NCS
Acapulco	310	73	72	144	108	276	108	276	12	0	200	64	281	59	303
		$p(O) = 0.377\pm0.027$					$q(a) = 0.707\pm0.024$		$q(t^b) = 0.245\pm0.034$			$q(d) = 0.477\pm0.026$		$q(l) = 0.441\pm0.026$	
Mexico DF	443	54	63	243	167	306	167	306	6	0	209	46	357	90	365
		$p(O) = 0.237\pm0.020$					$q(a) = 0.739\pm0.019$		$q(t^b) = 0.169\pm0.034$			$q(d) = 0.359\pm0.025$		$q(l) = 0.497\pm0.023$	
Veracruz	241	47	40	129	93	169	93	169	2	1	142	9	216	46	206
		$p(O) = 0.310\pm0.019$					$q(a) = 0.742\pm0.026$		$q(t^b) = 0.119\pm0.041$ $p(T^A) = 0.004\pm0.004$			$q(d) = 0.204\pm0.033$		$q(l) = 0.472\pm0.031$	
Alvarado	123	20	15	82	49	97	49	97	3	1	77	2	116	26	116
		$p(O) = 0.235\pm0.035$					$q(a) = 0.711\pm0.036$		$q(t^b) = 0.197\pm0.056$ $p(T^A) = 0.006\pm0.006$			$q(d) = 0.131\pm0.046$		$q(l) = 0.473\pm0.041$	
Duitama	58	16	9	32	30	41	30	41	0	0	29	7	56	23	54
		$p(O) = 0.359\pm0.061$					$q(a) = 0.855\pm0.040$		$q(t^b) = 0$			$q(d) = 0.354\pm0.063$		$q(l) = 0.653\pm0.052$	
Santa Cruz	146	23	25	81	58	106	58	106	2	0	85	28	126	22	130
		$p(O) = 0.275\pm0.036$					$q(a) = 0.739\pm0.032$		$q(t^b) = 0.153\pm0.053$			$q(d) = 0.471\pm0.039$		$q(l) = 0.411\pm0.039$	
La Paz	133	18	12	97	44	109	44	109	2	0	88	21	122	59	130
		$p(O) = 0.189\pm0.189$					$q(a) = 0.635\pm0.037$		$q(t^b) = 0.151\pm0.053$			$q(d) = 0.415\pm0.041$		$q(l) = 0.668\pm0.033$	
Santo Domingo	251	52	47	148	105	195	105	195	8	0	148	16	238	71	249
		$p(O) = 0.306\pm0.027$					$q(a) = 0.734\pm0.024$		$q(t^b) = 0.232\pm0.040$			$q(d) = 0.259\pm0.031$		$q(l) = 0.534\pm0.027$	

	S		W		C^s		I		M	
	MPO	NCS	MPO	NCS	MPO	NCS	MPO	NCS	MPO	NCS
Acapulco	167	290	13	303	7	297	16	288	0	303
	$p(S) = 0.349\pm0.022$		$p(W) = 0.022\pm0.005$		$q(C^s) = 0.153\pm0.028$		$p(I) = 0.029\pm0.007$		$p(M) = 0$	
Mexico DF	166	362	18	380	63	425	5	359	2	379
	$p(S) = 0.264\pm0.018$		$p(W) = 0.024\pm0.006$		$q(C^s) = 0.385\pm0.022$		$p(I) = 0.007\pm0.003$		$p(M) = 0.002\pm0.002$	
Veracruz	124	216	5	221	20	236	6	216	0	221
	$p(S) = 0.347\pm0.025$		$p(W) = 0.011\pm0.005$		$q(C^s) = 0.291\pm0.031$		$p(I) = 0.014\pm0.006$		$p(M) = 0$	
Alvarado	64	117	2	119	4	121	16	116	0	119
	$p(S) = 0.327\pm0.034$		$p(W) = 0.008\pm0.006$		$q(C^s) = 0.182\pm0.045$		$p(I) = 0.071\pm0.017$		$p(M) = 0$	
Duitama	26	57	0	57	1	58	0	57	0	57
	$p(S) = 0.325\pm0.049$		$p(W) = 0$		$q(C^s) = 0.131\pm0.065$		$p(I) = 0$		$p(M) = 0$	
Santa Cruz	53	128	6	136	10	140	19	125	0	135
	$p(S) = 0.234\pm0.028$		$p(W) = 0.011\pm0.006$		$q(C^s) = 0.267\pm0.041$		$p(I) = 0.079\pm0.017$		$p(M) = 0$	
La Paz	49	127	4	131	2	129	50	120	1	131
	$p(S) = 0.216\pm0.027$		$p(W) = 0.015\pm0.007$		$q(C^s) = 0.124\pm0.044$		$p(I) = 0.236\pm0.029$		$p(M) = 0.004\pm0.004$	
Santo Domingo	195	248	3	251	0	248	8	238	0	248
	$p(S) = 0.538\pm0.028$		$p(W) = 0.006\pm0.003$		$q(C^s) = 0$		$p(I) = 0.017\pm0.006$		$p(M) = 0$	

Table 2. (**A**) Expected heterozygosity (genic diversity) and standard error of 50 North and South American cat populations with Iberian influences, calculated from seven coat loci (*O*, *A*, *T*, *D*, *L*, *S* and *W*). (**B**) Expected heterozygosity (genic diversity) and standard errors of 78 North and South American and European cat populations calculated from six coat loci (*O*, *A*, *T*, *D*, *L* and *S*).

(A)			(B) (*Contd.*)		
Population	Heterozygosity	Standard Error	Population	Heterozygosity	Standard Error
Havana	0.3486	0.0591	Richmond	0.3975	0.0226
Mexico D.F.	0.3521	0.0592	Jamaica	0.3948	0.0356
Santiago	0.3719	0.0621	Tenerife 2	0.3563	0.0454
Bogota	0.2993	0.0554	Los Mochis	0.4277	0.0152
Ibague	0.3066	0.0603	Rio do Janeiro 1	0.3933	0.0231
Bucaramanga	0.2658	0.0568	Tenerife 1	0.4157	0.0237
Cali	0.3239	0.0618	Willemstad	0.3322	0.0328
Pasto	0.3106	0.0655	Caracas	0.3455	0.0482
Denver	0.3344	0.0590	Rio do Janeiro 2	0.3824	0.0334
Buenos Aires 1	0.3628	0.0596	Porto Alegre	0.3866	0.0247
Buenos Aires 2	0.3586	0.0594	Casa Grande	0.3774	0.0236
Lubbock	0.3617	0.0638	Brasilia	0.3817	0.0275
Mineralwells	0.3587	0.0632	Cuiaba	0.3079	0.0441
Denton	0.3411	0.0582	Salvador	0.3846	0.0493
Dallas	0.3491	0.0520	Rio Branco	0.3286	0.0701
Houston	0.3427	0.0598	Manaos	0.3152	0.0695
Richmond	0.3491	0.0520	Belem do Para	0.3331	0.0594
Jamaica	0.3495	0.0544	Juzairo do Norte	0.3657	0.0594
Tenerife 2	0.3054	0.0637	Fortaleza	0.3706	0.0509
Los Mochis	0.3694	0.0596	Sao Luis	0.3310	0.0717
Rio do Janeiro 1	0.3481	0.0492	Teresina	0.3349	0.0706
Tenerife 1	0.3572	0.0618	Bello Horizonte	0.3789	0.0232
Willemstad	0.2903	0.0502	Curitiba	0.3763	0.0249
Caracas	0.2990	0.0618	Sao Paulo	0.3966	0.0289
Rio do Janeiro 2	0.3309	0.0587	Mahon	0.3274	0.0414
Porto Alegre	0.3369	0.0538	Villacarlos	0.3411	0.0381
Casa Grande	0.3291	0.0522	Girona	0.3406	0.0368
Brasilia	0.3300	0.0567	Barcelona	0.3526	0.0312
Cuiaba	0.2749	0.0498	Sitges	0.3548	0.0297
Salvador	0.3353	0.0646	Ciudadela	0.3450	0.0433
Rio Branco	0.2816	0.0756	Palma Majorca	0.3981	0.0232
Manaos	0.2785	0.0692	Rimini	0.3928	0.0392
Belem do Para	0.2883	0.0672	Oporto	0.3803	0.0347
Juzairo do Norte	0.3135	0.0724	Lisbon	0.3294	0.0620
Fortaleza	0.3233	0.0639	Venice	0.3481	0.0554
Sao Luis	0.2865	0.0751	Philadelphia	0.4378	0.0294
Teresina	0.2953	0.0716	New York	0.3905	0.0530
Bello Horizonte	0.3304	0.0523	Minneapolis	0.4408	0.0230
Curitiba	0.3282	0.0525	Chicago	0.4357	0.0200
Sao Paulo	0.3482	0.0541	Reno	0.4084	0.0287
Popayan	0.3158	0.0611	Salem	0.4403	0.0289
Duitama	0.2994	0.0824	Quebec	0.4293	0.0299
Leticia	0.2146	0.0814	Montreal	0.4359	0.0284
Mexico D.F. 2	0.3475	0.0566	Phoenix	0.4406	0.0289
Acapulco	0.3934	0.0608	Portland	0.4562	0.0282
Veracruz	0.3329	0.0630	Boston	0.4432	0.0246
Alvarado	0.3272	0.0617	Vancouver	0.3905	0.0352
Santa Cruz	0.3465	0.0620	Cleveland	0.4236	0.0230
La Paz	0.3348	0.0604	Burlington	0.3933	0.0255
Santo Domingo	0.3677	0.0628	Paris	0.3418	0.0480
			Marseille	0.3742	0.0461
(B)			London	0.4161	0.0222
Havana	0.3995	0.0357	Bristol	0.3812	0.0251
Mexico D.F.	0.4042	0.0332	New Castle	0.3794	0.0313
Santiago	0.4222	0.0432	Glasgow	0.3479	0.0179
Bogota	0.3462	0.0349	Popayan	0.3658	0.0416
Ibague	0.3567	0.0397	Duitama	0.3494	0.0776
Bucaramanga	0.3094	0.0431	Leticia	0.2503	0.0865
Cali	0.3762	0.0389	Mexico D.F. 2	0.3975	0.0313
Pasto	0.3624	0.0476	Acapulco	0.4517	0.0202
Denver	0.3868	0.0321	Veracruz	0.3847	0.0424
Buenos Aires 1	0.4163	0.0310	Alvarado	0.3791	0.0395
Buenos Aires 2	0.4131	0.0279	Santa Cruz	0.4006	0.0359
Dallas	0.4073	0.0278	La Paz	0.3856	0.0387
Houston	0.3998	0.0210	Santo Domingo	0.4273	0.0243

The other main cluster was made up of two subclusters, one comprising of the North Caribbean populations, and the second containing the Colombian populations, and the populations of México DF, Santa Cruz, Buenos Aires, and Acapulco. The most divergent populations within this main cluster were Santiago, the old sample of México DF, and La Paz.

The derived strict consensus tree supported Duitama as the first population to diverge (figure 2). The remaining association of four groups of populations was stable and consisted of: (i) the populations from the Spanish-speaking North Caribbean, (ii) the populations of Colombia, Buenos Aires, México DF, Santa Cruz and Acapulco, (iii) some of the populations of South Brazil, and (iv) two populations of the North Brazil (Manaus and Belem). The non-metric multidimensional scale analysis (figure 3) with the Nei (1978) distance matrix supported a similar situation, with an acceptable final stress of 0.1515. Two minimum spanning trees are presented here which were derived using the distances of Nei (1978) and Cavalli-Sforza and Edwards (1967) (figure 4a,b). In the first tree, the Caribbean populations formed a compact cluster, related through Sao Paolo to the group of populations of Southern Brazil. The populations of Rio de Janeiro or Curitiba emerged from this area and were linkage points for the samples of Tenerife, populations of Northern Brazil, and Los Mochis. Curitiba made a nexus with Caracas and Willemstad. Willemstadt served as a union point through Bucaramanga to the rest of the Colombian populations. Bucaramanga was the geographically closest Colombian population to Venezuela amongst those sampled. A link was established from the Colombian population of Cali to Buenos Aires, and from there to Santiago. Also, a point of convergence was found between Pasto and México DF, and a link was made with Santa Cruz and La Paz. The second minimum spanning tree showed a similar situation, but in this case Buenos Aires was derived from Rio de Janeiro. Buenos Aires made another link with the Colombian populations through Cali, then, from Ibague a connection was made with Santa Cruz, and from Popayan, a link was established with one of the samples of Tenerife (Canary Islands).

(B) Figure 5 shows the tree generated in the analysis of the ensemble of 68 cat populations from North America and Spanish-speaking Latin America as well as the best coefficient of cophenetic correlation, and the smaller value of standard deviation of Fitch and Margoliash (1967). The tree was obtained by applying the UPGMA algorithm with the distance of Cavalli-Sforza and Edwards (1967), and showed Leticia as the most divergent of the 68 American populations used in this analysis, followed by the Colombian population of Duitama, and Duluth (USA). Three well defined clusters contained the remaining populations. The first cluster to diverge was comprised of populations from the Spanish-speaking North Caribbean, and La Paz. The other two main clusters were closer to each other. In one of them, we found a divergent clade with the four Colombian populations of Bogotá, Ibagué, Bucaramanga and Pasto, followed by the populations of Texas, Buenos Aires, Denver, Richmond, Bowling Green, Cali, Popayan, México DF, Santa Cruz, and a group of populations of the mid-western USA, being strongly related to Acapulco. The other main cluster contained USA populations of Anglo origin, particularly from the East Coast, Canada, Phoenix (Arizona), Humboldt County (North California) and Santiago (Chile). Santiago was the only Latin American population related to the USA populations of Anglo origin. The strict consensus tree obtained (figure 6), showed four strong associations of populations of Hispanic origin. The two synthetic minimum spanning trees derived from the distances of Nei (1978) and Cavalli-Sforza and Edwards (1967) are shown in figure 7. The first of them revealed that the group of populations from the Spanish-speaking North Caribbean make a compact cluster connected with México DF through Veracruz. Here, this population played a very important role in the relation of many of the American populations. The withdrawal of Brazil, and some Hispanic populations of Latin America, and the

Table 3. Genetic heterogeneity analysis of two cat populations ensembles. (A) Genetic heterogeneity of 50 North and South American cat populations with Iberian influences, for seven coat loci (O = orange; a = non-agouti; t^b = boltched tabby; d = dilution; l = long hair; S = white spotting; W = dominant white). (B) Genetic heterogeneity of 78 North and South American and European cat populations, for six coat loci (O = orange; a = non-agouti; t^b = blotched tabby; d = dilution; l = long hair; S = white spotting). G_{ST} = genetic heterogeneity among the subpopulations in regards to the overall genetic diversity. H_t = total genetic diversity; H_s = average genetic diversity within the subpopulations (individual populations within the geographical ensembles).

(A)

	G_{ST}	H_t	H_s
O	0.0231	0.3456	0.3376
a	0.0367	0.3930	0.3796
t^b	0.0510	0.3824	0.3628
d	0.0710	0.4055	0.3767
l	0.1425	0.4324	0.3707
S	0.0345	0.4363	0.4212
W	0.0098	0.0277	0.0274
Average	0.0609	0.3461	0.3250
(B)			
O	0.0252	0.3273	0.3191
a	0.0282	0.3963	0.3824
t^b	0.1473	0.4523	0.3856
d	0.0715	0.4344	0.4033
l	0.1205	0.4166	0.3663
S	0.3205	0.4311	0.4173
Average	0.0737	0.4092	0.3790

inclusion of the populations of Anglo origin in this analysis revealed a remarkable connectence value of the México populations to other populations by displaying relationships with Duitama, La Paz, Pasto (Colombia), and Denton (Texas). The latter was strongly related to other Texan populations, such as Houston, which served as a transition to the divergent population of Leticia. Pasto was a nexus to the remaining Colombian populations, except for Popayan and Cali. Bogotá was connected to Denver (Colorado) and displayed an outstanding role in the relations to the rest of populations of Hispanic origin in America. Buenos Aires appeared connected to Chicago. Chicago served as the point of connection with the populations of Anglo origin in the USA and Canada. Saint John in New Brunswick, Canada was connected to Santiago (Chile). Stevens County was connected with the Latin American populations of Santa Cruz and Acapulco. The second minimum spanning tree showed a few differences in relation to the previous one. México DF had a smaller range of relations to other populations, and was connected with the two Bolivian populations. Santa Cruz was a nexus to the populations of the Mid-Western USA through Stevens County. This group of populations of the Mid-Western USA displayed connections in two directions. First, they were connected to the USA and Canadian populations of Anglo origin, and second, they were connected to Chicago. Bowling Green displayed an important role in the net of connections with the remaining Hispanic American populations because it was strongly related to Buenos Aires, Richmond, and Denver. It played a particularly important role with Colombia and presented separate connections with Popayan, Cali and Bogotá, which served as the connection point for all Colombian populations.

(C) An analysis of the 62 cat populations from Europe and some of Hispanic origin in Latin America presented two trees with the best coefficients of cophenetic correlation, and the smaller values of standard deviation of Fitch and Margoliash (1967) (figure 8a,b). The UPGMA tree with the Nei (1978) distance supported that Leticia was the most divergent population. Two big clusters were observed next, one was comprised of Latin American, Spanish, Portuguese and Italian populations while the second cluster was comprised of English and French populations. The first main cluster showed two subclusters: one contained all the Latin American populations, except Rio de Janeiro, and two small populations of Menorca (Mahón and Villacarlos, Balearic Islands).
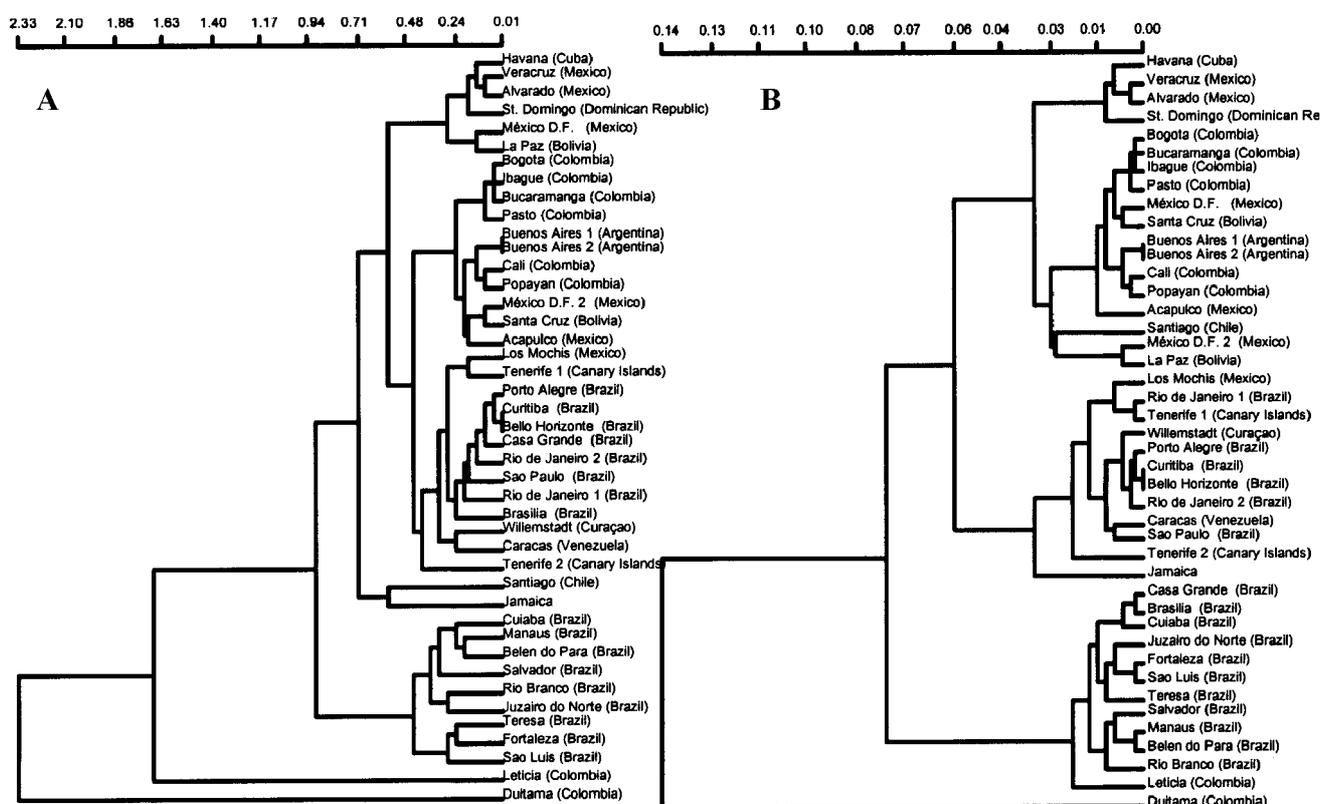

Figure 1. (A) UPGMA tree with the Cavalli-Sforza and Edwards genetic distance with 43 Latin America cat populations. (B) WPGMA tree with the Nei genetic distance with 43 Latin America cat populations.
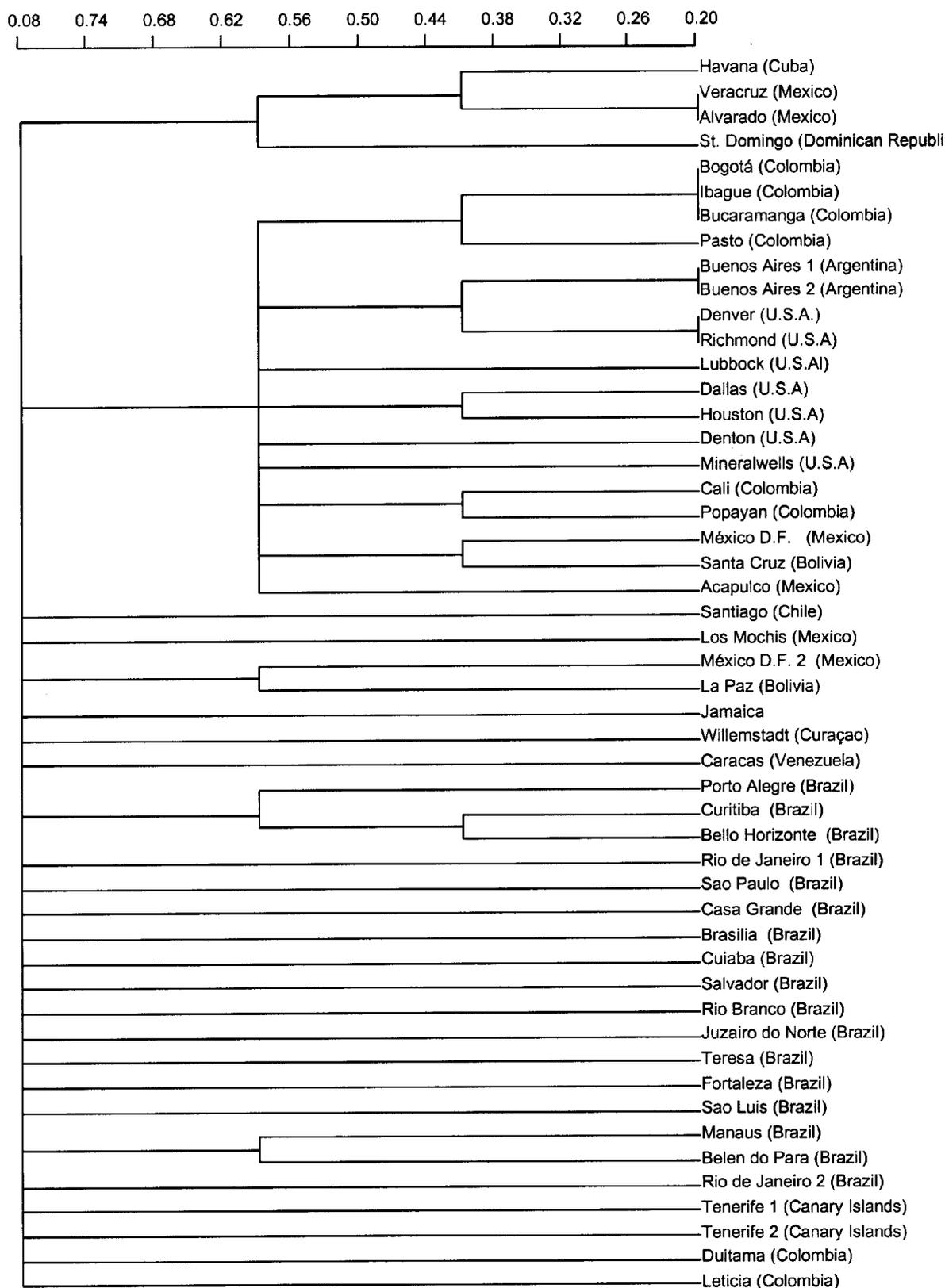
Figure 2. Strict consensus phenogram with 43 Latin American cat populations.

This revealed two associations. The first involved Buenos Aires, the populations of Colombia, México DF, Santa Cruz, and, the internally more divergent populations of Acapulco and Menorca (Mahón and VillaCarlos). The second association involved the populations from the Spanish-speaking North Caribbean, as well as Duitama and La Paz. The second subcluster of the first main cluster contained three well defined groupings: one comprised by the populations of Catalunya and Balearics (except for Tarragona and Palma), Rio de Janeiro, the samples of Tenerife (Canary Islands), and two populations from the Atlantic Portuguese Islands. A second grouping was

comprised by populations from Italy, Portugal and Palma (Majorca). A third grouping was comprised of Tarragona, Mediterranean Spanish populations of the south of the Peninsula, and some insular Atlantic Portuguese populations. The UPGMA tree with the distance of Cavalli-Sforza and Edwards (1967) showed Duitama to be the most divergent population after Leticia. Three main clusters were found, with the most divergent one comprised by Mediterranean populations located south of the Iberic Peninsula, Tarragona, and some populations of the Atlantic Portuguese Islands. The second cluster contained British and French populations. The third cluster contained
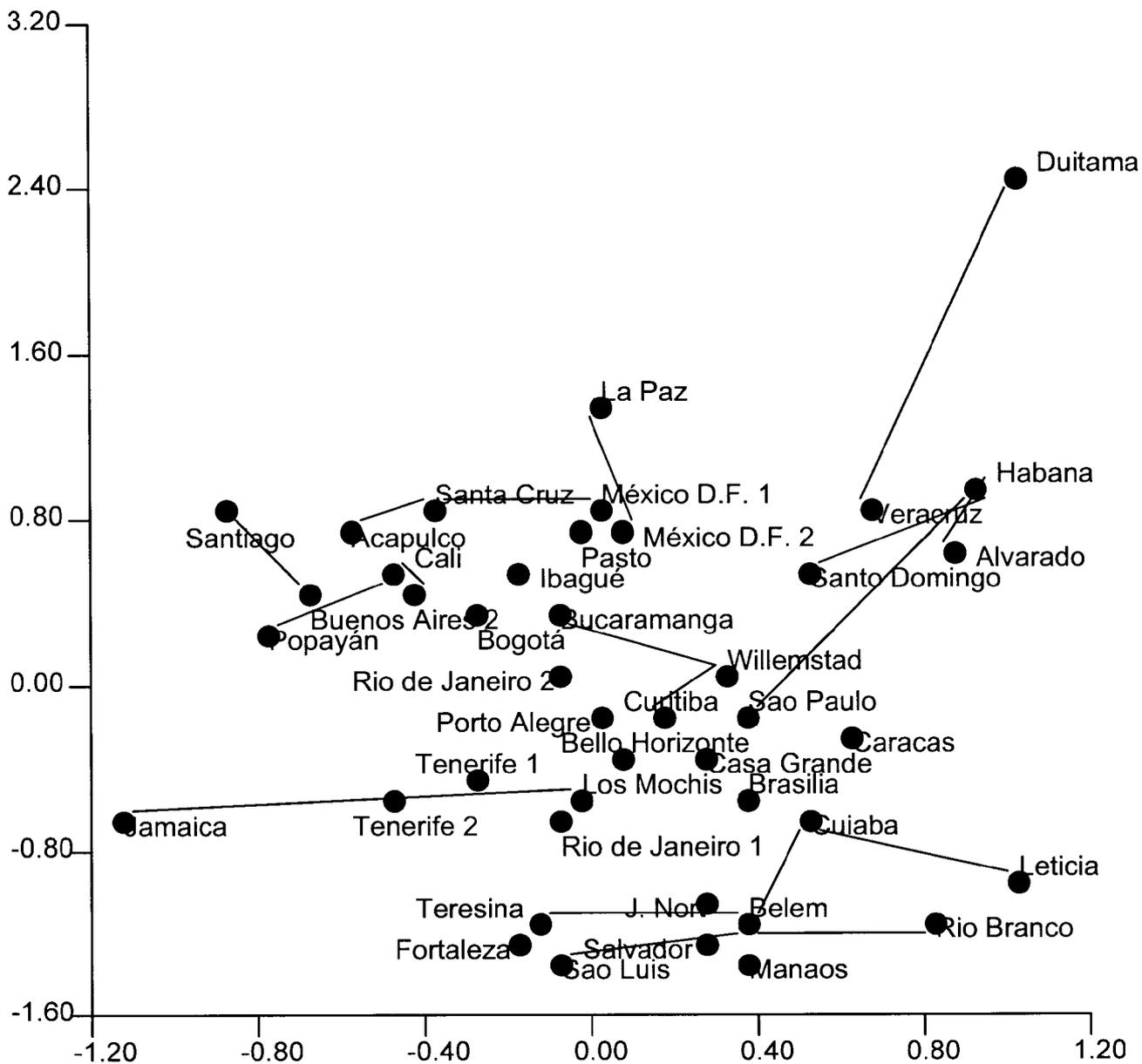
Figure 3. Multidimensional Scaling Analysis with the Nei's genetic distance with 43 Latin American cat populations.
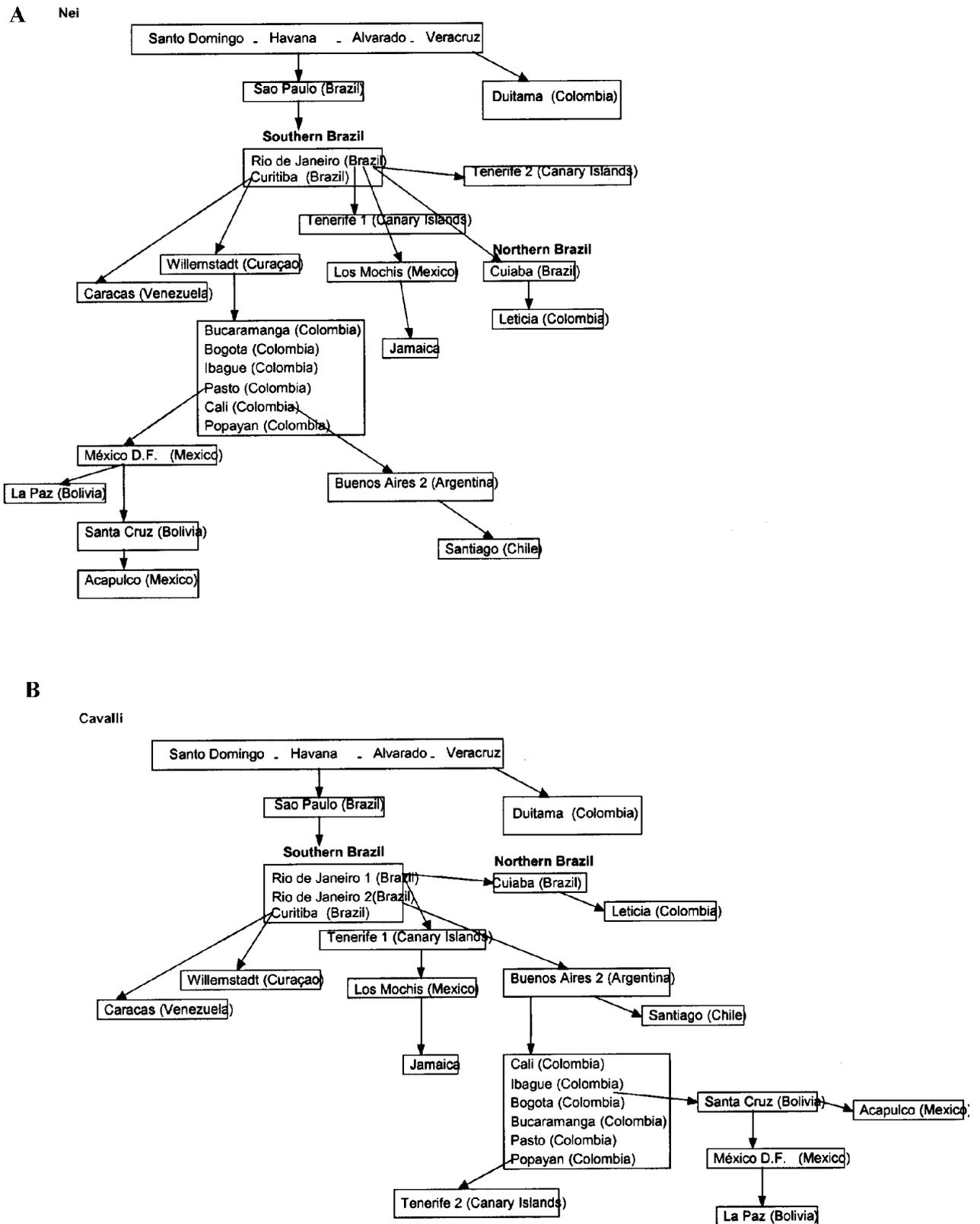
Figure 4. (A) Minimum spanning tree with the Nei's genetic distance with 43 Latin American cat populations. (B) Minimun spanning tree with the Cavalli-Sforza and Edwards genetic distance with 43 Latin American cat populations.

three subclusters: one containing populations from the Spanish-speaking North Caribbean and La Paz, as the most divergent; the second comprised all the Latin American populations, except for Leticia, Duitama and Rio de Janeiro, and the populations of Mahón and Villacarlos (Menorca); the remaining subcluster contained two groupings: one, with the populations of Catalunya, Baleares, Canarias, Rio de Janeiro, and Porto (Portugal), and the other, with Italian and Portuguese populations. The strict consensus tree derived from UPGMA, WPGMA and the application of three genetic distances (figure 9), revealed some of the Latin American clusters as the most consistent. A few small population associations were also observed from Catalunya, Balearic Islands, England and France. The non-metric multidimensional scale with the Nei distance (figure 10) showed a connection between Buenos Aires and the Palma Majorca Balearic population. The samples of Tenerife showed a strong relation to the Ibiza and Ciudadela (Menorca) populations. One of the Tenerife samples was related to the Portuguese Atlantic Island of Madeira. Rio de Janeiro was connected to the Catalan population from Sitges. México DF presented
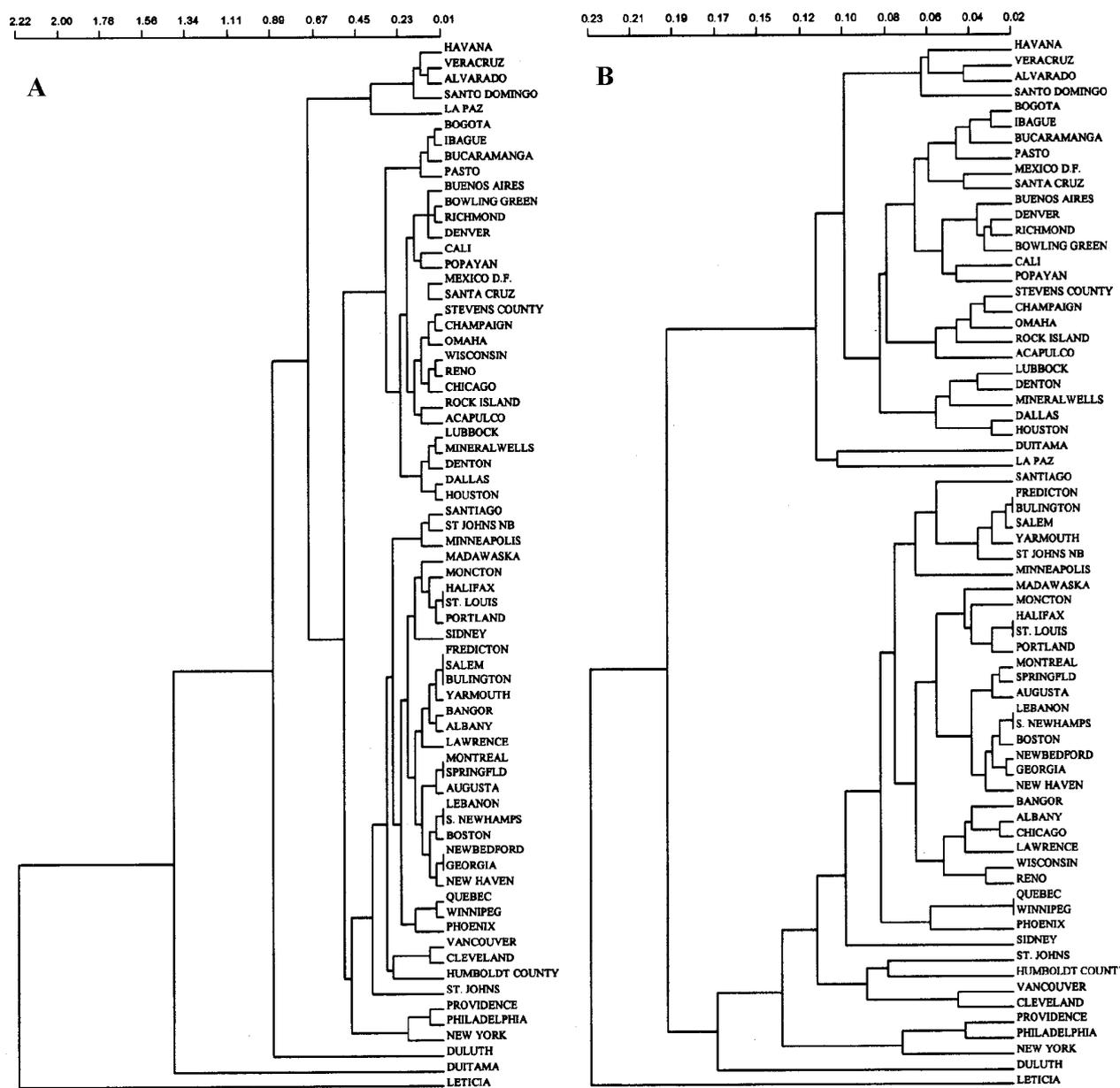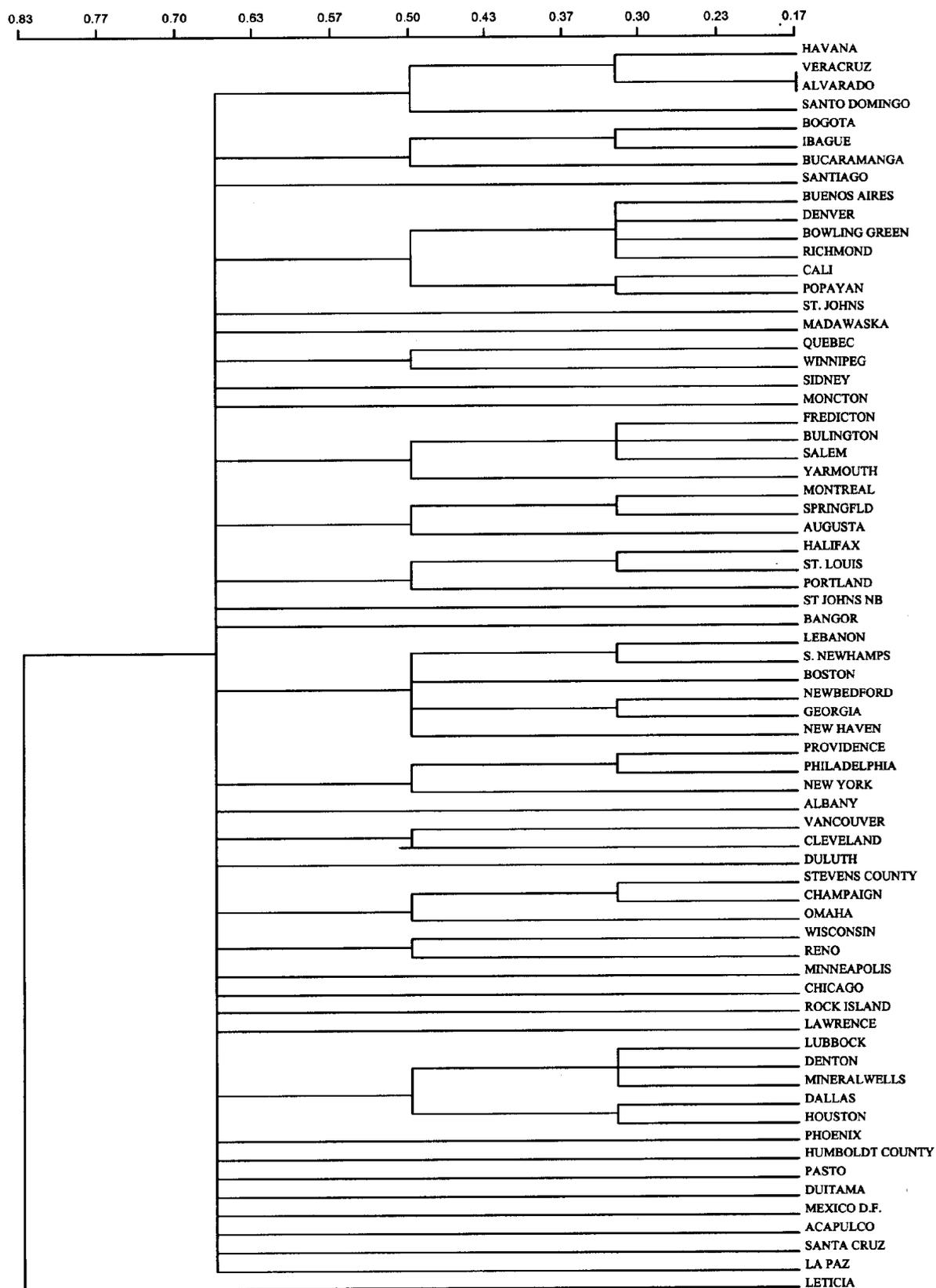

Figure 5. UPGMA tree with the Cavalli-Sforza and Edwards genetic distance with 68 North and South American cat populations.
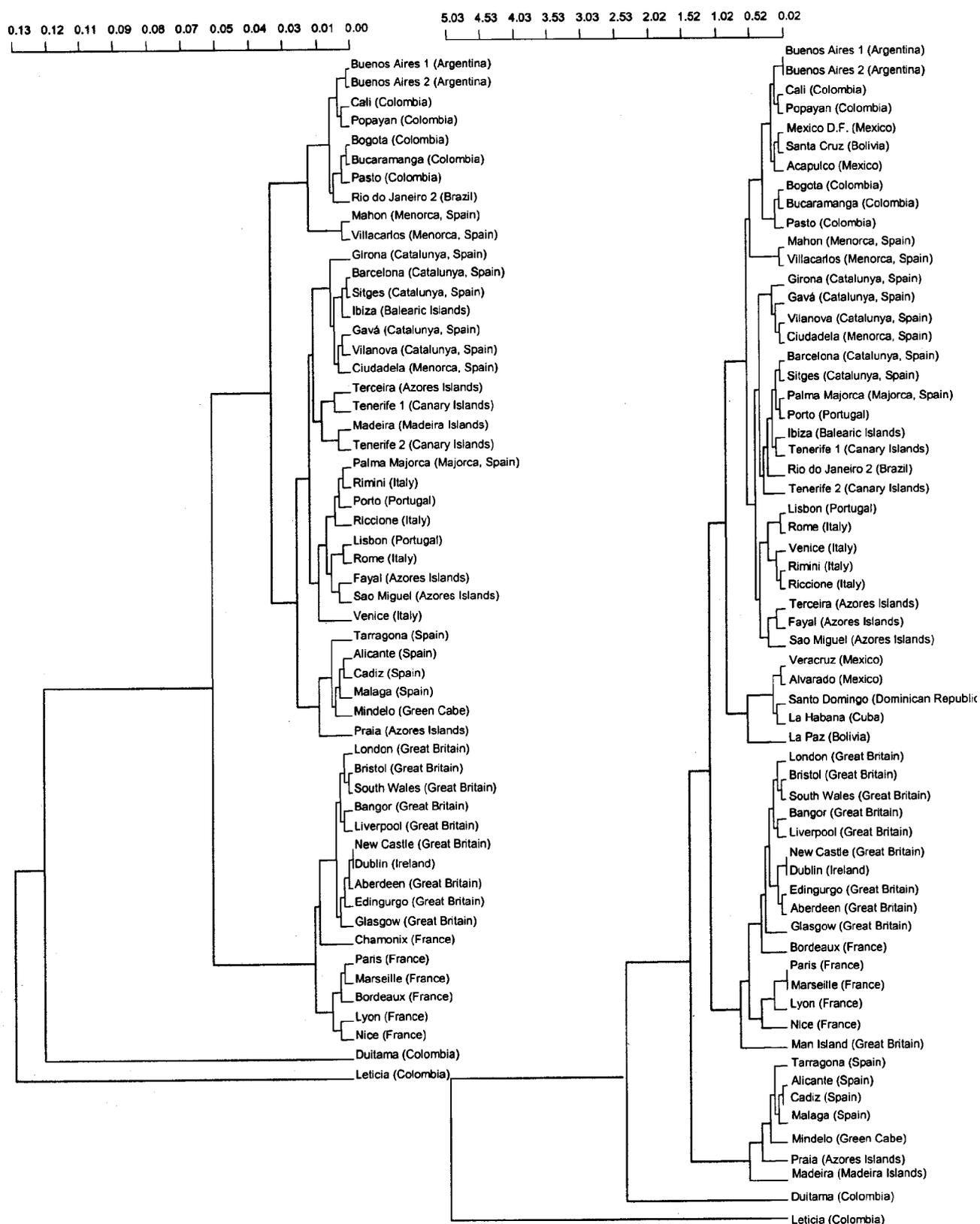
Figure 6. Strict consensus phenogram with 68 North and South American cat populations.

Figure 7. (A) Minimum spanning tree with the Nei's genetic distance with 68 North and South American cat popualtions. (B) Minimun spanning tree with the Cavalli-Sforza and Edwards genetic distance with 68 North and South American cat populations.

Figure 8. (A) UPGMA tree with the Nei genetic distance with some Latin American cat populations and 62 European cat populations. (B) UPGMA tree with the Cavalli-Sforza and Edwards genetic distance with some Latin American cat populations and 62 European cat populations.
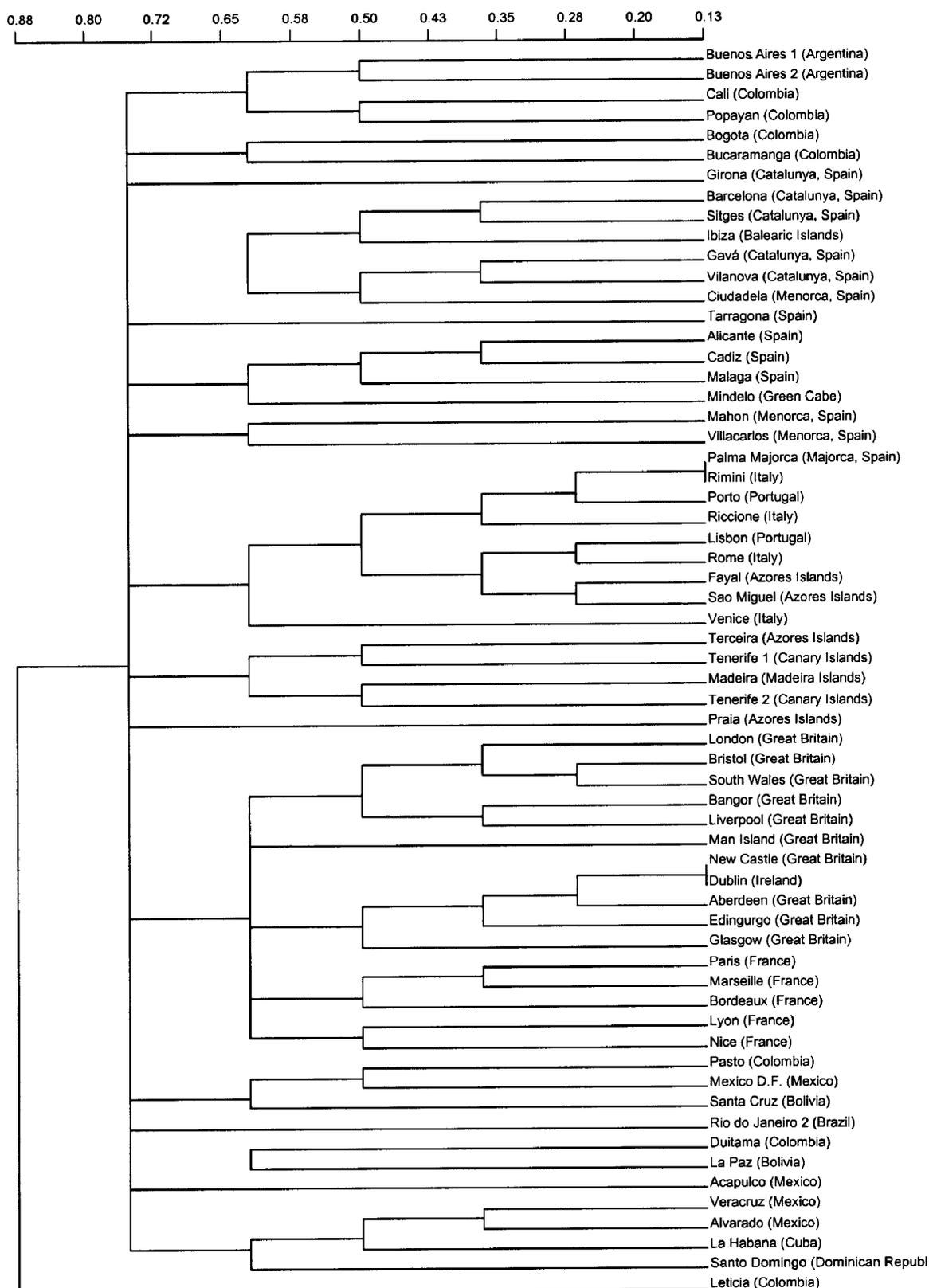
Figure 9. Strict consensus phenogram with some Latin American cat populations and 62 European cat populations

connections with the Latin American populations of Veracruz, La Paz and Duitama. The divergent Leticia population was related to the Mexican population of Alvarado. Most of these relationships were observed when the genetic distance of Cavalli-Sforza and Edwards (1967) was applied. A strong relationship was observed between the Barcelona population and one of the Tenerife samples. Additionally, a link was observed between the divergent populations of Leticia and Girona (Catalunya).

The mean canonical analysis values for the group of populations analysed were significantly different (Wilks $L = 0.0003$; $F = 5.0741$; $df = 98$, 186). The first three eigenvalues explained 91.56% of the total variance of the system (table 4). The factorial structure showed that the alleles more closely correlated with the first axis were l ($r = 0.3437$), and a ($r = 0.3134$), with the second axis, again l ($r = 0.7579$), and a ($r = -0.4847$), and with the third axis, d ($r = -0.4618$). The coordinates of the groups of populations, and the radius of the regions of confidence corresponded to the following picture: the most differentiated cluster contained the Northern and Amazonían populations of Brazil. The populations of Leticia and Duitama were not within the 90% confidence area of any of the population groups analysed. Leticia was closer to the group of populations of Northern Brazil, and Duitama was closer to the Bolivian populations group. The area of confidence of the Southern Brazil populations overlapped with those of the Spanish-speaking North
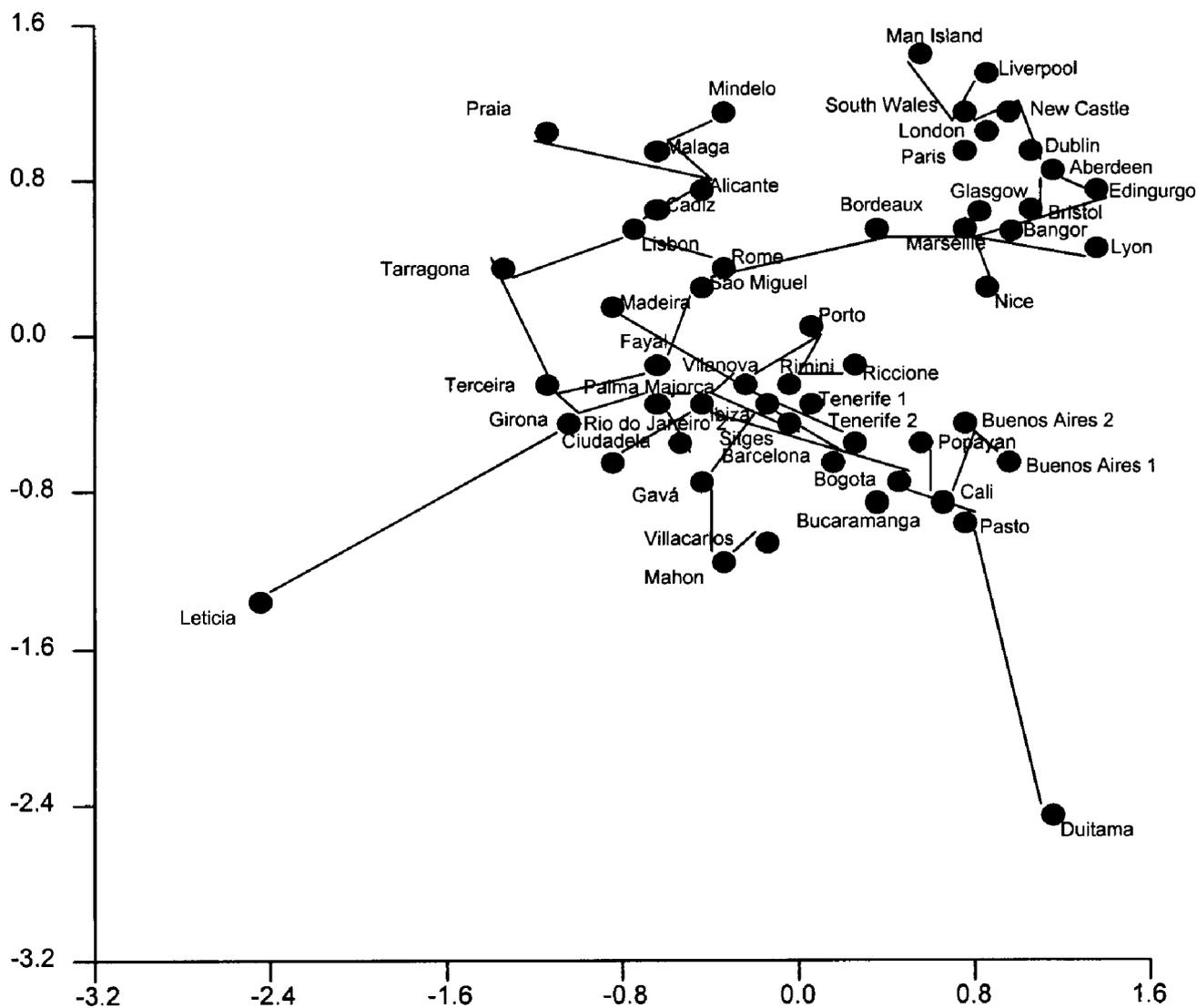

Figure 10. Multidimensional Scaling Analysis with the Nei's genetic distance with some Latin American cat populations and 62 European cat populations.

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Caribbean Islands (Cuba-Dominican Republic), and Venezuela-Curacao. The first of these groups also showed important relationships with Mexico, Bolivia, and Buenos Aires groups, and less intensely, with the USA populations' group of possible Hispanic origin. The Venezuela-Curacao group was partially related to the Mexican populations, the individual sample of Rio de Janeiro, Jamaica, the populations of Tenerife, Buenos Aires, the USA populations of Hispanic origin, and with the Colombian populations. The group of Tenerife showed these same relationships, except with the Mexican populations. The group of Colombian populations was only related to Buenos Aires, Hispanic USA, Tenerife and Venezuela-Curacao populations. The Bolivian group was related to the Caribbean, Mexico, Buenos Aires and Hispanic USA (figure 11).

Discussion

Relevance of some of the allelic frequencies found for the loci analysed

The high frequency found for the locus O in Acapulco (0.377) was one of the highest values registered worldwide. The highest frequencies so far reported for the orange allele correspond to the Asian populations (Pakistan, India, Arabia, Taiwan, Hong Kong, Macau and Singapore), Israel, and those in North America (Alaska, Omaha and Goodland) (Ahmad *et al*. 1980; Davis and Ahmad 1983; Fagen and Meeswat 1981). The high frequency found in Acapulco could be related to Asian influence. Among the 50 populations of Hispanic origin in North and South America we analysed in this study, the population of Acapulco had the highest genetic diversity, thus revealing that this population might have had several different genetic origins. Acapulco had been the main Spanish port since 1532, communicating with the

commercial routes to South East Asia, (mainly the Philippines and China), from where spices were shipped to Acapulco, México DF, Veracruz and then to Havana and Spain. The people of Acapulco commonly believe that they and their domestic animals originated in the Philippines. Much of the cat population observed in Acapulco had the slender and elongated body that is characteristic of the Asian phenotype. However, the frequencies for other loci analysed, corresponded to those of other Latin American populations, which have had no direct contact with South East Asia. High frequencies of O were also found in the Caribbean populations of Veracruz, Havana and Santo Domingo (0.30–0.31), but not in other Latin American populations. The existence of other non-Spanish external influences on those populations may account for their high frequencies, since some US populations also have high frequencies of this allele. Spain's defeat in the Seven Years' War in 1763 motivated a massive British army to march into Havana. The British Field Marshal O'Reilly, who was stationed in Cuba during 1764, claimed that some 1000 British ships had visited Havana during the ten months of occupation (Kuethe 1988). However, UK and USA populations also have high frequencies of t^b and d, which are found at low frequencies in the Caribbean populations. An alternative explanation is the presence of pre-migration selection that favors Orange phenotype individuals, although it would be difficult to explain why the same did not occur in other Latin America locations. It should be mentioned that high frequencies of Orange are found in Spanish populations of the Balearic Islands, and in one of the Tenerife samples (Canary Islands), as opposed to their peninsular counterparts. The various Spanish populations which acted as sources of cats could have been highly heterogeneous for this character. A third explanation is that the frequencies of Orange might have decreased in Spain in the last centuries. The first populations that the Spaniards founded in America were the Caribbean populations, Santo Domingo (in 1492), Havana (in 1501), and Veracruz (in 1519). The high values of $p(O)$ could therefore be an ancestral character of those first populations founded in America. A fourth explanation to be considered is the favourable natural selection for this character in hot tropical climates, such as in Brazil, (Sao Luis, 0.25; J. North, 0.33; Rio Branco, 0.26); Africa (Alexandria, 0.36; Upper Egypt, 0.29; Khartoum, 0.36), and Arabian areas (Khobar, 0.29; Medina, 0.43; Mecca, 0.35) where high frequencies of this allele occurred. (Davis and Ahmad 1983; Todd and Blumenberg 1978) Although the Asiatic character T^a (Abyssinian tabby) was not found in Acapulco, it was detected in Veracruz and Alvarado, and had previously been reported in Havana (Ruiz-Garcia and Alvarez 1999). The presence of this character in Mexico could reveal the introgression of an Asian character. However, its frequency is merely residual and its presence in

Table 4. Eigenvalues and factorial structure of the canonical variables of several Latin American cat groups studied by a Canonical population analysis. O = orange; a = non-agouti; t^b = blotched tabby; d = dilution; l = long hair; S = white spotting; W = dominant white.

	The three first eigenvalues obtained		
	96.21	36.86	23.89
	Accumulated variance percentages		
	56.12%	77.62%	91.56%
	Factorial structure of canonical variables		
O	0.0158	0.3266	0.1066
a	0.3146	− 0.4847	0.2470
t^b	− 0.0988	− 0.2120	0.0555
d	0.2444	0.0380	− 0.4618
l	0.3437	0.7579	0.3607
S	− 0.2545	− 0.0131	0.3458
W	− 0.1412	0.1066	− 0.0424

Havana could be due to the high exposure this port had during its history. Thus, the port of Havana would have been a source of the Abyssinian character that later moved into the Mexican Caribbean.

The distribution of the allele *d* in Latin America is particularly important. The Caribbean populations of Spanish origin show low frequencies of this allele, whereas the rest of the Latin American populations, with the exception of those of the Brazilian Amazonas, have significantly higher frequencies, even higher than those found in Spain. The value for México DF was intermediate between the high value of Acapulco and the low values of Veracruz and Alvarado, thus drawing a gradient from the Pacific coast to the Atlantic coast for this character in Mexico. The high frequencies found for *d* from Buenos Aires to California, suggests the presence of pre-migration selection favourable for this allele. On the other hand, the low frequencies found for *d* in the Spanish Caribbean, require an explanation. One possibility is that the tropical climate might impose a negative selection on this allele, in agreement with the low frequencies found in some Brazilian Amazon populations. However, this hypothesis is not supported by the high value of $q(d)$ in the British influenced Caribbean population of Jamaica (0.34). A second hypothesis would be based on the existence of spatial or temporal differences in
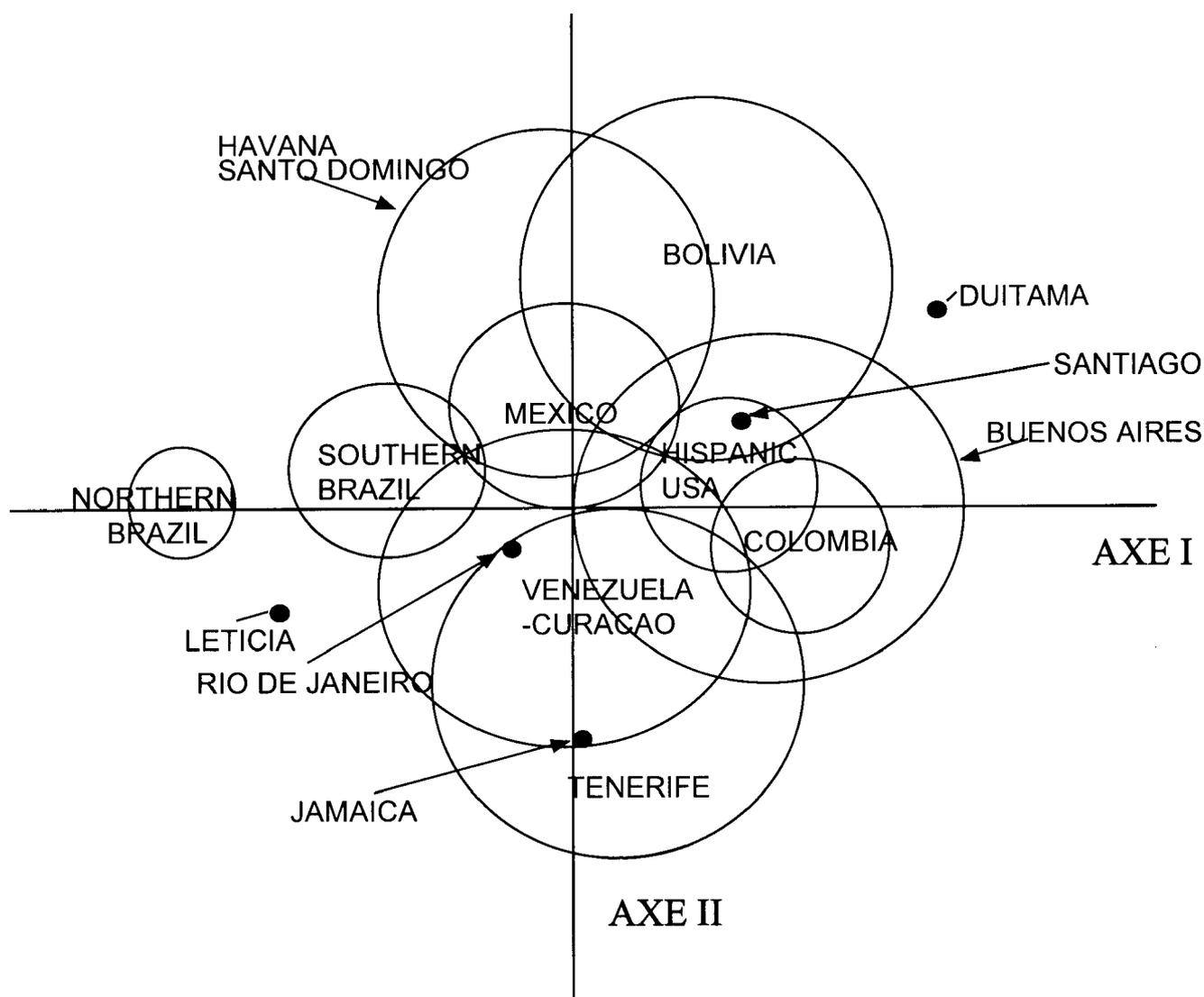
Figure 11. Canonical Population Analysis of 15 sets of cat populations: 1, Havana-Santo Domingo (Caribbean islands of Spanish settlement); 2, Buenos Aires (the two samples); 3, Mexico; 4, Venezuela-Curacao; 5, Southern Brazil; 6, Northern Brazil and Amazon; 7, Colombia; 8, Tenerife (Canary Islands, the two samples); 9, the populations of presumed Hispanic origin in the USA; 10, Bolivia, and the individual populations of 11, Santiago (Chile); 12, Jamaica, the most recent sample of 13, Rio de Janeiro (Brazil); 14, Duitama (Colombia); and 15, Leticia (Colombian Amazon).

Spanish migration origins. That is, the Caribbean cat populations were the first to be founded by the Spaniards in America (centuries XV–XVI) and the propagules of cats that gave place to those populations would come from populations where this character was absent or infrequent. The founder populations of cats arriving in other areas of Latin America came later (centuries XVII–XVIII), and originated from other Spanish populations. This character could have had a higher frequency, giving rise to a favourable phenomenon of pre-migration selection.

The frequencies of *l* are much higher in Latin America than those found in Spain, suggesting a generalised favourable migration selection. This character was probably quite novel in Spanish populations, would have been infrequent, and would have arrived recently from the Eastern Mediterranean (Turkey, Cyprus; Robinson 1972; Todd 1977). This would have produced a phenomenon of selection by novelty (Todd 1977). The phenomenon of natural selection *in situ* would have not taken place in the new American settlements, because populations within highly contrasting environmental conditions such as the tropical areas of Havana and Santo Domingo have very similar frequencies to, for example, La Paz, in the Andean highlands. These three populations have the highest frequencies worldwide for this character, which does not support negative natural selection of long hair in tropical conditions, as had been proposed by Watanabe (1983). These findings support the hypothesis of Ruiz-García (2000). The high frequency of long hair in La Paz (0.668) could be the result of founder effect, or due to positive selection for this character in a cold climate.

Piebald spotting also has an interesting distribution in Latin America. Most of the Spanish populations have frequencies $p(S)$ between 0.20–0.30, and some populations of Menorca (Ruiz-Garcia 1990c,d, 1994) have frequencies lower than 0.20. Some Latin American populations have very similar frequencies, as in the case of some of the Colombian populations (Bogotá, Ibagué and Bucaramanga), as do the two Bolivian populations reported here. These populations could reflect the original Spanish frequencies for this character, with no external influences in their constitution. In contrast, other populations such as Santo Domingo, Havana, Tenerife, and some Brazilian populations have much higher frequencies of *S*. These populations are located in areas of high sun exposure and temperature. We are possibly facing the most evident case of natural selection *in situ* in the newly colonized habitats. The frequency found for México DF (0.264) which exists at 2,300 meters above sea level in a moderate climate, supports the selective hypothesis. This value is lower than that found for other Mexican populations that are located in tropical climates of the Atlantic and Pacific. Even though the frequencies of *d* are different between the populations of Acalpulco and Veracruz, the

selective hypothesis is still supported because their frequencies of $p(S)$, are very similar.

Expected heterozygosity and genetic heterogeneity

As mentioned previously, the Acapulco population had the highest expected heterozygosity of all Latin America. Although the origin of the genetic profile of this population of cats is Hispanic, there might have been mixing with populations of other origins. The well-documented historical routes of the Spanish between Acapulco, the Philippines and China support southeast Asia as a genetic contributor. British commercial routes between North America and the Pacific could also have had some influence on the genetic profile of this population. Nevertheless, the preponderancy of the commercial Spanish routes from Seville throughout the centuries to Acapulco was noteworthy. By 1500, Seville had 14 different ports, a monopoly on travel routes to America and was estimated to be one of the six most important cities in Europe (130,000 inhabitants at the end of the XVI century). The various sized ships had to travel 90 Km up the Guadalquivir river to reach the main port of Seville. Moreover, from 1492 to 1680, 10,000 ships left Seville to the Americas and another 10,000 shops arrived in Seville en route from the main Latin America ports (principally Acapulco, Guayaquil, El Callao, Valparaiso, Cartagena, Santa Marta, Veracruz and Havana). Seville served as the origin of 20,229 Andalusians that eventually settled in the Americas (37% of the Spanish immigration). Many Genovese, German and Dutch families also became established commercially in Seville, as evidenced by the current street names of this city. These foreigners contributed 20% of the population and in 1543 they founded the Chamera Commerce. However, the alleles of Anglo, French, and Dutch origin (such as t^b) typically, do not have significant high frequencies in the Acapulco population. Seville lost its commercial dominance to Cádiz during the XVIII century. Official historical documents, primarily the registers of individual vessels, yielded details of 3,828 departures of ships from Spain to the Americas between 1778 and 1796. Cádiz succeeded in retaining no less than 76.4% of all exports to America during that time period. Other Spanish ports including Barcelona, Alicante, Málaga, Cartagena, Santander, Gijón and La Coruña were open to commercial traffic on October 24, 1765 by royal degree.

In agreement with Ruiz-Garcia *et al.* (2002), the population of Santiago had the second highest genetic diversity after Acapulco and was strongly impacted by Britain. Therefore, its high genetic diversity results from a mix of Hispanic and British influences. The population of La Paz deserves a special comment. Although some of the characters of its genetic profile were clearly differentiated from other populations, it did not have a smaller value of *h*, suggesting that genetic drift has not been an

important factor in the evolution of this population, and it may have instead suffered a distorting founder effect, without losses of genetic variability caused by drift, or compensated by the action of novelty selection on alleles that are infrequent in the populations of origin. The populations of Colombia, Caracas, and Curacao have lower values of expected heterozygosity than the rest of the Latin American populations analysed, with values of *h* similar to those of the Spanish populations of origin. This finding could be interpreted several ways. One explanation would be that these are the most pure Hispanic populations, with little influence from other non-Hispanic sources, or, only minor pre-migratory selection occurred in the election of the animals that originated these Latin American populations, compared to others. The pre-migration selection would increase the expected heterozygosity, since it would occur on characters of low frequency in the original populations (especially for *d*, *l*, *S* and *I*). As the frequencies of these alleles approach 0.5, the expected heterozygosity also increased. The Colombian population with the higher genetic diversity was Cali, which also had the higher frequencies of *d* and *S*. Since the Colombian port of Buenaventura on the Pacific is in close proximity to Cali, this population might have received some external Pacific influences slightly different from those of other Colombian populations. Leticia, in the Amazon, does reveal a considerable loss of genetic diversity, possibly derived by founder effect from other Brazilian Amazon populations of Portuguese origin, with the presence of genetic drift. Two historical reasons could explain the genetic differences of this cat population. The human colonization of the Southern Colombian Amazon was a process which involved a small number of white colonists. For instance, the religious "Capuchina" community in relation with "Concordato" signed by the Vatican and the Colombia Republic in 1887 established the foundation of small villages in the Southern Colombian Amazonas. Similarly, the following populations of San Francisco (founded by Fray Lorenzo de Pupiales, 1902), Caucaya (founded by Bartolomé de Igualada, 1926), and Sucre were founded by a small number of white colonists. In Sibundoy (San Francisco), Montclar had recruited 24 Catalans for the beginning of a village and in Sucre, the initial population consisted of 150 white families, principally of Basque influence, from Catalunya (Spain) and the Antioquia region of Colombia. A few cats were probably transported by these early colonists. On the other hand, these little Amazonian villages were directly connected from a commercial point of view with Manaus (Brazil) by the Amazon river. In 1913, Puerto Asís and Leticia interchanged a considerable amount of bananas, corn, yucca and sugar with the Amazonian Manaus (Misiones Católicas 1913, 1919). A second reason was the presence of stone-age Indian tribes, such as the Ingas and Kamsas that covered large areas of the inner Amazon area. These Indian tribes had a tradition of being involved with commerce between the Colombian, Brazilian, Peruvian and Venezuelan Amazon. Native Indians considered domestic cats to be an unusual and attractive species because they had been unknown prior to the arrival of the Europeans. It is probable that the Indians introduced many cats into Leticia from the developed Amazon cities in Brazil.

In general, the colonisation of the Americas by Spain and Great Britain supported an increase in the expected heterozygosity in the new populations. The highest genetic heterogeneity amongst the populations of America and Western Europe is found in Latin American areas. That is, although the value G_{ST} (= 0.061) was not very large when compared with values found in other organisms, it corresponds to a considerable genetic heterogeneity for the populations of cats in Latin America. If we consider all the American and West European populations together, the G_{ST} increased only to 0.073, not including the locus *W* which presents the lesser heterogeneity. The relatively high value of heterogeneity in Latin America was due particularly to the Brazilian populations of the North and Amazonas, as well as Leticia, which were clearly different from the other Latin American populations. The inclusion in the genetic heterogeneity analysis of USA populations of Anglo origin, and of other European populations, such as the British or French, which are different from some of the old Spanish populations, results in only a slight increase in the value of the G_{ST}. In fact, the value of this statistic for Europe (Ruiz-Garcia 1997) was similar (0.069) to that of Latin America. The analysis of heterogeneity for each locus showed that *L*, *D* and *T*, were the three most heterogeneous loci in Latin America, with *L* and *D* being presumably subjected to diverse pre-migratory selective pressures, or were the most heterogeneous in their frequencies in the Iberian populations of origin. When we included Anglo American and all of the Western European populations within the analysis, the allele t^b turned out to be the most heterogeneous marker (G_{ST} = 0.147). This demonstrates that t^b is the character that fundamentally differentiates the populations of British origin from those of other origins, such as the Spanish.

Phylogenetic relations between populations of cats of Latin America and different genetic pools

The analysis of the American populations of Iberian origin analysed so far support the presence, at least, of five clearly differentiated genetic pools. They are:

(i) The group of Brazilian populations of the North and Amazonas, including other Amazonian populations, such as Leticia.

(ii) Some populations throughout Latin America with

clear British influence, such as Jamaica and Santiago, Chile. We must remember that some points in Latin America, such as the Caribbean provinces of New Granada (Riohacha, Santa Marta and Cartagena de Indias, actually Colombia) were places extraordinarily important for smuggling in the Spanish America empire (Grahn 1988). In the seventeenth century, the production of Spanish textiles and agricultural products failed to keep pace with the mounting Latin America demand. The principal rivals of Spain, such as England, The Netherlands and France, established permanent colonies on Curaçao, Jamaica and Saint Dominique, in the Caribbean sea, and in the Pacific area. The English, were a formidable power in the Pacific area, and wanted to expand their trade into Spanish American markets (Mueller 1957). The king´s advisors estimated that the residents of New Granada accounted for fully one-half of all illicit trade through the Caribbean colonies of Spain and collected perhaps six million pesos annually (Fisher 1972). Some individual examples could reflect the magnitude of the smuggling in some points of the Spanish Empire, and the possibility of the introduction of cats without a Spanish origin in specific areas of Latin-America, such as Santiago or Jamaica. In 1734 and 1737, smugglers landed contraband in Riohacha estimated to be worth at least a million pesos. The commercial effects of the Riohacha contraband was so high that the markets in Bogotá and Popayan (Colombia) and Quito (Ecuador) reflected its influence. Legitimate merchants had to lower their prices 25% or more just to compete with the smugglers. Lieutenant General Blas de Lezo in 1737 affirmed that smugglers were so numerous in and around Cartagena that they had virtually blockaded the entire city. In other cities, such as Maracaibo (Venezuela) (Cardozo-Galué 1988), there were extraordinarily important British, Italian, USA and German settlements. From 1831 to 1840, 664 vessels left the Maracaibo port for American and European ports. The eleven principal destinations in decreasing order were: Curaçao, New York, St. Tomas, Boston, Jamaica, Philadelphia, Aruba (Netherland Antillas), Liverpool, Riohacha (Colombia), Veracruz and Nantes (France). So, the commercial relationships of the Maracaibo port were principally with English and Netherland sources (52% and 33.7%, respectively) during these years.

(iii) The populations of the Spanish-speaking North Caribbean: Mexico, Cuba and Santo Domingo.

These genetically similar populations seemed to be linked politically and commercially. The Spanish crown rarely legislated equally across its entire empire (Kuethe 1988). For example, the reforms implemented in the XVIII century by Ricla, O'Reilly and the Marqués de Esquilache showed that the North and Caribbean islands had a different consideration in regards to New Granada and other parts of the Spanish Empire. Also, the Royal Decree of 1765 maintained that Cuba, Santo Domingo, Trinidad and Margarita (Caribbean islands) should be treated as a different political and commercial unit compared to the remainder of the Spanish Empire.

(iv) A fourth group is comprised of populations which span from California and Colorado to Buenos Aires, extending roughly along the Pacific coast. Within this group there are four main subgroupings with minor differences:

One subgrouping consists of the Colombian populations, except Leticia in the Amazon. The high genetic homogeneity found in a great fraction of the Colombian country could be related to the rapid movements of the Spanish conquerors that searched for El Dorado and established many cities and villages. For instance, in 1536 Pedro de Heredia and his troop traveled from Cartagena to Antioquia. Shortly afterwards in 1537, Juan Badillo traveled from Cartagena through much of Colombia and arrived to Cali. The existence of the Magdalena River was a major factor in the rapid Spanish colonization of the Andean part of Colombia.

A second subgrouping consists of Buenos Aires, Cali and Popayan, California and Colorado. This subgrouping reveals the Pacific connection, because a direct relationship between these populations could not have occurred via the Atlantic. We must recall that the Spanish traveled from Southern Spain to Veracruz in Mexico, after having stopped at the Canary Islands, Santo Domingo and Havana. From Veracruz the Spaniards reached México DF, and then crossed the country into Acapulco (Pacific Ocean). The Santo Domingo-Colón, Balboa (Panamá) path was also used. From these points on the Pacific, they traveled along the coasts of Colombia (Buenaventura), Ecuador (Guayaquil), Peru (Lima, El Callao) and Chile (Valparaiso). It should be noted that the maritime commerce of Spain within the Pacific was substantially less than its commerce with Veracruz. In fact, the Peru market was by far the more important area for the merchants of Cádiz in this period than Rio de la Plata (Argentina) and Venezuela put together. Then they traveled inland to silver exploitation sites, in what currently is known as Bolivia. Loaded with silver they crossed, the territory of Paraguay and the Northern deserts of Argentina. The founded settlements of Salta, Jujuy, San Miguel de Tucuman, Santiago del Estero, Córdoba and Santa Fé, in the North of Argentina, provided needed provision until they arrived at the port of Buenos Aires (Río de la Plata), where part of the silver, and other precious minerals, were shipped to Spain. Nevertheless, the current cat populations in Spain do not show a strong genetic resemblance to those in Pacific ports as they do compared to those in Buenos Aires. These findings could be the result of Peru being served by a handful of large ships, carrying extremely valuable cargoes, while Buenos Aires and Montevideo were served by a larger number of small vessels, with less valuable cargoes. For instance, in 1791, five ships left the Cádiz port for Callao, Perú with goods worth 80

million reales and 16 ships left this Spanish port to Buenos Aires with goods for 22 million reales. Moreover, the genetic connection between Buenos Aires and the Pacific area was enforced by Argentina's capital which was used as the door for merchandise that was ultimately destined for Chile or the Southern provinces of Peru. The Pacific ports and the Acapulco port were used to bear the costs of colonization in California which helps to explain the existence of this and the following subgroup. Another subgroup that confirms the presence of the Pacific connection was comprised by populations from Acapulco, México DF and Santa Cruz (Bolivia), and in some analyses La Paz.

(v) The populations of the South of the Brazil, Canary islands, Curaçao and Venezuela in the North of South America. It is a preponderantly Atlantic group.

The addition of new genetic characteristics over time may have eliminated the original characteristics of some Latin America cat populations. On 12 October 1778, Charles III created the famous Imperial Free Trade regulation in Spain, in order to develop the Spanish Empire as a source of raw materials for Spanish manufacturers and distributors, and to develop a market for the industrial and agricultural products of the mother country (Fisher 1981). After 1778 the commercial market expanded by 700%. Within the period 1782–1796 the average annual value of exports was 400% higher than in the base year of 1778. This strong increase in commerce between Spain and its colonies may have added new cats, with different genetic characteristics, to some Latin America cities eliminating the original genetic profiles. The relationships between Popayan (Colombia) and Tenerife and between the association of Los Mochis (Mexico) and the Atlantic populations (Canary islands, Venezuela-Curaçao and South of Brazil) could support this hypothesis.

However, this study supports no consensus about the degree of relatedness between these five groupings. For example, the North Caribbean group was very compact, and there was no doubt about its differentiation. The UPGMA method with the distance of Cavalli-Sforza and Edwards (1967) supported that this was the first group of Spanish origin to diverge, and which supported a strong relationship of groups 4 and 5. On the other hand, other analyses (including some not shown here) did not detect the same relationships among the North Caribbean group and those others.

Depending on the analysis applied, Texas populations were related with group 4 (Pacific connection), although less strongly than were California or Colorado. In other cases, the Texas populations showed a direct connection with México DF and the Spanish Caribbean population groups. While the populations of California and Colorado have the typical genetic profile of the populations of the Pacific connection, Texan populations revealed strong Hispanic influences, to a greater extent than possible An-glo influences, thus contradicts Gerdes' (1973) proposal regarding their origins.

In relation to the European populations, Leticia was found to be entirely divergent. This shows that the genetic pool of the populations of Northern Brazil and Amazonas are different from the genetic profiles of the populations of Western Europe, regardless of how different they are from each other (Great Britain vs Catalunya & Balearic; Ruiz-Garcia 1997; Ruiz-Garcia *et al*. 1995). The comparative analysis of the other Latin American populations showed that, in general, they were more related to each other, than to any European population in particular. The exception was the population of Rio de Janeiro, which seemed to be more similar to certain Catalan populations (such as Sitges), the Balearics or the Canary islands, than to any other Latin American population. For instance, while the Barcelona port did not have any relationship with the Pacific commercial route during the second half of the XVIII century, the Barcelona port did have a relatively important relationship with Atlantic ports (Cartagena-Santa Marta, 9.7%; Cartagena, 10.06%; Cartagena-La Havana, 4.6%; Cartagena-Santiago de Cuba, 76.5%; Santa Marta, 23.7% and Santa Marta-Havana, 100%). This confirms Spanish influence (such as the Catalan one) on Southern Brazil (Ruiz-García 2000), and might suggest that these populations suffered the least distortion from their origin in Spain, or they were the most recently originated, and would therefore, be the most similar to the current Spanish populations. The two populations of Menorca, Mahon and Villacarlos, (Ruiz-García 1990c, 1994), were very similar with the remaining Latin American populations. This demonstrates that these small Balearic populations are old and vestigial remainders of the genetic profiles of the Spanish populations that gave rise to the current Latin American populations of Hispanic origin. This also demonstrates that the processes of pre-migrative selection in the transfer of domestic cats by means of marine ships were very similar in the construction of Balearic and Latin American populations. Among the Spanish peninsular populations, Catalan was considered old and was the most similar to the Latin American populations. On the contrary, populations of Cádiz and Málaga of Southern Spain, from which a great number of ships began their journey to America, did not show a particular likeness with the Latin American populations. Southern Spanish populations may have suffered a similar process of differentiating evolution to what occurred in the British islands, or they may have received direct gene flow from them (Blumenberg 1977; Blumenberg and Lloyd 1980).

It remains necessary to sample additional Latin American populations in order to identify new genetic pools, to determine the relationship between those pools, and to ascertain which is the oldest. The analysis of various nuclear DNA markers (STRPs) will be of immense value to meet these objectives in future studies.

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