

Genetic relationships in Spanish dog breeds. I. The analysis of morphological characters

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Summary – The relationships between 10 Spanish dog breeds have been studied using qualitative and quantitative analyses of data from 32 morphological characters. The average distance between breeds, measured as a morphological index, has a value of 4.228 (± 0.681), with extreme values of 1.732 between Mastín del Pirineo and Mastín Español, and of 5.099 for the Gos d'Atura – Sabueso Español pair. The morphological phylogeny obtained in this study confirms the classifications made previously by means of dental, cranial, historical and behavioral comparative criteria. The results suggest the formation of 2 large clusters; one formed by the breeds belonging to the ancestral trunks *Canis familiaris intermedius* and *Canis familiaris inostranzewi*, and the other which includes the members of the *Canis familiaris leineri* and *Canis familiaris metris-optimae* trunks.

Spanish dog breeds / genetic distance / morphological character / dendrogram / morphological analysis

Résumé – Relations génétiques entre des races canines espagnoles. I. Analyse des caractères morphologiques. À partir de l'analyse qualitative et quantitative des données provenant de 32 caractères morphologiques, on a étudié les relations existant entre 10 races canines espagnoles. La distance moyenne entre races, mesurée par un indice de distance morphologique, prend une valeur de 4,228 ($\pm 0,681$), avec des valeurs extrêmes de 1,732 entre Mastín del Pirineo et Mastín Español, et 5,099 pour le couple Gos d'Atura – Sabueso Español. La phylogénie morphologique obtenue dans ce travail, confirme les classifications précédentes, réalisées à partir de critères comparatifs dentaires, crâniens, historiques et comportementaux. Les résultats suggèrent la formation de deux grands groupes. L'un comprend les races qui appartiennent aux troncs ancestraux du *Canis familiaris intermedius* et du *Canis familiaris inostranzewi*, et l'autre serait formé par les composants des troncs du *Canis familiaris leineri* et du *Canis familiaris metris-optimae*.

races canines espagnoles / distance génétique / caractère morphologique / dendrogramme / analyse morphologique

INTRODUCTION

Archaeological studies show the existence of differences within populations of prehistoric dogs in the same area. These studies also show that there were already distinguishable and separated classes of dogs about 5 000 years ago (Villemont *et al*, 1970).

Two main factors have determined the differentiation of canine breeds: natural selection in the environment and conscious selection by man. The length of time from prehistoric times to the present and the number of generations elapsed explain the proliferation of canine breeds. Added to this has been the modern tendency of selective breeding to produce specialist and distinguishable breeds, with strict definitions of desirable and undesirable traits for each breed.

Man first began to influence the classes of canines when he began to adapt them to his needs. Sheep farming, extensive throughout Eurasia, created the need for gentle, intelligent animals which would respond to orders from the shepherd and help manage the flock. Dogs were adapted for defence: here the desired traits were fierceness, toughness and suspicion of strangers. Dogs were also used for hunting: some would have to be very fast to catch their prey, others would track and flush the prey and others would retrieve the dead prey. Each had a specialist task. Finally, a general category of dogs served for defence, for company or merely for decoration.

The first known classification of dogs dates from 1486 and is found in the *St Albans' Book*, attributed to Juliana Barnes, prioress of the convent of Sopwell, England (Peters, 1969). But the systematic classification of different dog breeds began to have greater importance at the end of the 19th century with the creation of the Kennel Clubs in England and North America.

Despite the huge difficulties involved in the reconstruction of the phylogenies of the more than 400 dog breeds currently recognized, the systematic classification into groups, as closely related as possible, as well as the search for their phylogenetic relationships has been an uninterrupted task. There have been studies based on archaeological findings (Olsen and Olsen, 1977; Clutton-Brock, 1984), historical studies (Gómez-Toldrà, 1985), cranial, dental and skeletal morphology (Clutton-Brock *et al*, 1976; Wayne, 1986), comparative studies of behaviour (Scott, 1968), and immunological and electrophoretic studies of proteins and blood enzymes (Leone and Anthony, 1966; Tanabe *et al*, 1974).

Although part of the variation observed among morphological traits may have an environmental component, in general, the heritability values for morphological traits are relatively high. The differences observed among breeds therefore should be good indicators of the genetic relationships among them.

So far, however, no studies have been published on the genetic relationships between Spanish dog breeds from the analyses of morphological characters. Since statistical methods and computing packages are available to perform such analyses (Felsenstein, 1986; Swofford, 1991), the present paper is a contribution to the study of the genetic relationships between Spanish canids from qualitative and quantitative analyses of data on morphological characters.

MATERIALS AND METHODS

Breeds studied

We have studied 9 Spanish dog breeds recognized by the Fédération Cynologique Internationale (FCI): Gos d'Atura, Mastín del Pirineo, Mastín Español, Perdiguero de Burgos, Galgo Español, Sabueso Español, Ca de Bestiar, Podenco Ibicenco and Podenco Canario, and a tenth breed not yet recognized, Podenco Ibérico. The geographical distribution of the original breeds is shown in figure 1. There are several existing hypotheses about their origin (Jordana *et al*, 1990), which we summarize in the following way:

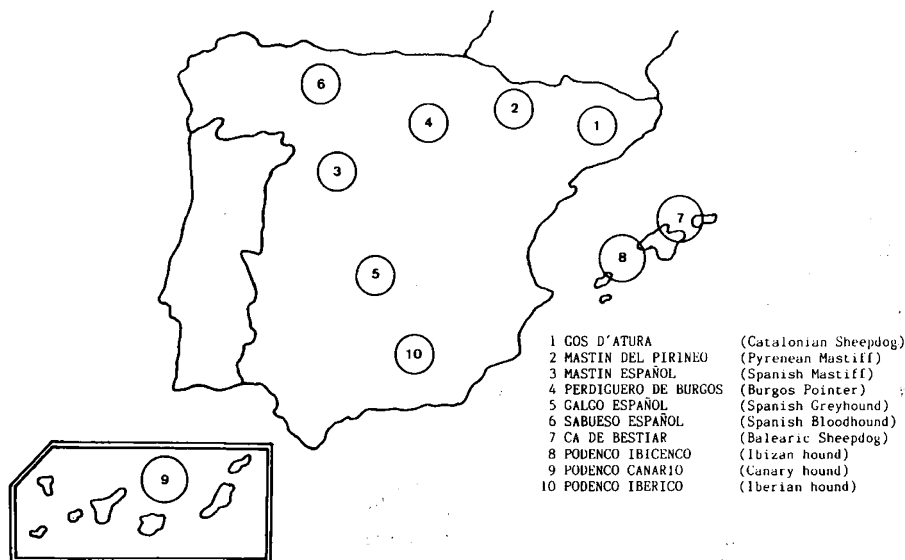


Fig 1. Geographical location of the Spanish dog breeds.

Gos d'Atura (Catalonian Sheepdog) or Perro de Pastor Catalán

Andreu (1984) points out that the Romans took an ancient Shepherd dog on their campaigns, which could have been the Bergamasco. This dog was adapted to the different climatic environments and types of shepherding, and was the basis of a large number of breeds existing today in Central Europe. Gómez-Toldrà (1985) and Delalix (1986) agree with the opinion of the Roman origin of the Gos d'Atura breed, and placed the origin of the Bergamasco in the Polish Shepherd dogs, which might have descended from the old Eastern Shepherds.

Mastín Español and Mastín del Pirineo (Spanish Mastiff and Pyrenean Mastiff)

These are breeds included in the "ortognated moloses" which seem to descend from the legendary Mastiff of Tibet (in central Asia). These dogs are supposed to have reached Spain by 2 routes: the Central European route and *via* the Mediterranean (Esquiró, 1982).

Perdiguero de Burgos (Burgos Pointer)

This breed probably originated from matings between the Sabueso Español and the short-coated Pachones from Navarra (Sanz Timón, 1982; Rousselet-Blanc, 1983; Gómez-Toldrà, 1985; Delalix, 1986). These Pachones from Navarra, also called Perros de Punta Ibéricos, are the ancestors of the current English Pointer (Rousselet-Blanc, 1983; Sotillo and Serrano, 1985).

Sabueso Español (Spanish Bloodhound)

Several authors (Villemont *et al*, 1970; Gondrexon and Browne, 1982; Rousselet-Blanc, 1983; Gómez-Toldrà, 1985) have attributed a Celtic origin to the Bloodhounds. Most of the European Bloodhound breeds seem to descend from the Saint Hubert, a modern-day Belgian breed, the direct descendant of the Segusius of the Celts and the Gauls, which the Greek historian Arrian of Nicomedia talks about in his *Cinegetics* (Villemont *et al*, 1970; Rousselet-Blanc, 1983).

Ca de Bestiar (Balearic Sheepdog): also called Perro de Pastor Mallorquín and Ca Garriguer

The FCI includes this breed in the second group, within the molosoid breeds, together with the Boxer and the Dogo among others. Several authors (Guasp, 1982; Sotillo and Serrano, 1985; Delalix, 1986) agree that the origin of this breed seems to be the result of crossing between Podencos Ibicencos, Perdigueros (Ca Mé) and Mastiffs.

Galgo Español (Spanish Greyhound)

For some authors (Villemont *et al*, 1970; Sotillo and Serrano, 1985) the English Greyhound and the Galgo Español are descendants of the Arabian Sloughi, brought to Europe *via* Spain during the Moslem invasion. Another hypothesis (Rousselet-Blanc, 1983) supports the idea that the Galgo was brought to Western Europe by the ancient Celts when they settled down in Gaul. Nevertheless, the same author points out a second contribution of blood from the Sloughi.

Podenco Ibicenco (Ibizan Hound): also known as Ca Eivissenc, Xarnelo, Lebrél de Mallorca, Mallorquí or Charneque

It is generally accepted that the Podenco Ibicenco breed descends from the Dog of the Pharaohs (Villemont *et al*, 1970; Mora, 1982; Gondrexon and Browne, 1982;

Rousselet-Blanc, 1983; Gómez-Toldrà, 1985) and that it was brought to Ibiza by the Phoenicians (Pugnetti, 1981; Maza, 1982; Delalix, 1986), even though other hypotheses state that it arrived much later, with the Moslems, at the same time as the Galgo (Villemont *et al*, 1970; Rousselet-Blanc, 1983).

Podenco Canario (Canary Hound)

Certain hypotheses (Delalix, 1986) suppose that this hunter came from Egypt and that it was taken to the Canary Islands, probably by the Phoenicians, Greeks, Carthaginians or even by the Egyptians, but it is possible that Majorcan monks, forced to emigrate to these islands by the Vatican, introduced these dogs (Anonymous, 1982).

Podenco Ibérico (Iberian Hound): also known as Podenco Español, Podenco Andaluz, Podenco Ibérico Andaluz Malagueño and Campanero

The Podenco Ibérico is a recent product obtained by crossing the Podenco Rondeño from Andalusia with the Podenco Ibicenco (García *et al*, 1982).

Qualitative and quantitative analyses

In an ideal specimen of each of 10 Spanish dog breeds, a total of 32 characters have been studied. Some of the characters were established by the official standards of the breed while the other characters came from data of a review (Avila, 1982; I Symposium Nacional de las Razas Caninas Españolas, 1982; Gómez-Toldrà, 1985; Sotillo and Serrano, 1985; Delalix, 1986). The numbers were assigned to each state of the different characters in an arbitrary manner. These numbers did not represent any specific weighting of the state. The number of states for each character was established depending upon the number of distinguishable phenotypic classes. The characters used and their states are shown in table I.

Qualitative analysis

For the qualitative analysis, discrete characters were recoded into a series of (0, 1) 2-state characters, denoting absence or presence of the character, respectively. Continuous quantitative characters (D and E characters in table I) may be divided into a small number of classes, each representing one of the states of the character in the data matrix. For recoding a character with several states we have used the following transformations (Sneath and Soka, 1973) :

Character with 3 states (0, 1 and 2)

<i>State of the character</i>	<i>State in the program</i>
0	00
1	10
2	01

Character with 4 states (0, 1, 2 and 3)

<i>State of the character</i>	<i>State in the program</i>
0	000
1	100
2	010
3	001

and so on. The original and recoded matrices of morphological resemblances are shown in tables II and III respectively.

The MIX program of the phylogeny inference package (PHYLIP) (Felsenstein, 1986) was used to construct the dendrogram of Spanish breeds of dogs from qualitative data of morphological characters. This analysis is based upon the "parsimony" principle, and the criterion is to find the tree requiring the minimum number of changes. Two dendrograms can be obtained: the first, using Wagner parsimony (Farris, 1970), is used when the ancestral state of the character is unknown; the second, using Camin and Sokal's method (1965), presupposes the knowledge of the ancestry. Several possible criteria have been proposed to infer the ancestral state of the character: the fossil record, the frequency criterion and outgroup analysis (Avice, 1983). Each of these criteria has been seriously and justifiably criticized (Stevens, 1980), although it has been recognized that the outgroup analysis provides a particularly compelling rationale for estimating the character state polarity (in our case, for example, the wolf, *Canis lupus*). We have chosen, however, the frequency criterion (the state of the character appearing most frequently in the group being examined) in order to make comparisons between these dendrograms and those obtained in a second study (Jordana *et al*, 1992) on the phylogenetic relationships among Spanish dog breeds derived from the analysis of biochemical polymorphisms. The reason for choosing the frequency criterion was the lack of adequate literature on electrophoretic results of any species of wolf candidate to be used as an outgroup. The tree generated by Wagner parsimony is unrooted, so we chose arbitrarily the Galgo Español breed as an outgroup in order to make comparisons with other dendrograms.

An evolutionary tree generated by a parsimony criterion was also computed using the phylogenetic analysis using parsimony computer package (PAUP) (Swofford, 1991). The resulting tree was rooted and the midpoint rooting method (Farris, 1972) was chosen to give the tree an evolutionary direction. The PAUP package allows us also to compute the confidence limits of the topology by means of a bootstrap analysis (Efron, 1979), adapted to the inference of phylogenies (Felsenstein, 1985). One hundred bootstrap replicates were made, and a consensus tree was obtained based upon the majority-rule method (Margush and McMorris, 1981). The minimum frequency of the bootstrap replicates in which a group is supported in order to be included in the bootstrap consensus tree was set to 50 (Conlevel = 50).

Table I. Characters and their states, used for the construction of the morphological resemblance matrix.

(A) <i>Size</i>	(B) <i>Length/width proportions</i>
0. Medium	0. Longilinear
1. Large	1. Mesolinear
2. Small	2. Brevilinear
(C) <i>Cranial profile</i>	(D) <i>Withers height</i>
0. Subconvex	0. ≤ 55 cm
1. Convex	1. 58 – 62 cm
2. Rectilinear	* 2. 63 – 67 cm
3. Concave	3. 68 – 75 cm
	4. > 75 cm
(E) <i>Cranium ratio</i>	(F) <i>Cranio-facial lines</i>
* 0. 1,00 – 1.10	0. Parallel
1. 1,11 – 1.20	* 1. Divergent
2. 1,21 – 1,30	2. Convergent
3. 1,31 – 1,40	
4. 1,41 – 1,50	
(G) <i>Occipital crest</i>	(H) <i>Stop</i>
* 0. Pronounced	0. Pronounced
1. Slightly pronounced	1. Moderate
2. Null	* 2. Slightly pronounced
	3. Null
(I) <i>Face profile</i>	(J) <i>Tooth position</i>
* 0. Straight	* 0. Scissors
1. Subconvex	1. Pincers
2. Convex	
(K) <i>Ear insertion</i>	(L) <i>Ear position</i>
* 0. Up (above eye line)	* 0. Fallen
1. Middle (same height)	1. Erect
2. Down (below eye line)	2. Folded
(M) <i>Ear size in relation to head</i>	(N) <i>Eye form</i>
0. Small	0. Rounded
* 1. Middle (proportionate)	* 1. Almond
2. Big	2. Oblique
(O) <i>Eye colour</i>	(O) <i>Truffle colour</i>
* 0. Hazelnut (dark)	* 0. Black
1. Amber	1. Meat
	2. Brown
	3. Various
(P) <i>Lips</i>	(Q) <i>Corner of mouth</i>
0. Straight	* 0. Not evident
1. Sup just covers inf	1. Moderate
* 2. Sup covers inf	2. Pronounced

Table I. (*Continued*).

(R) <i>Inferior eyelid relaxation</i>	(S) <i>Dorsal line</i>
* 0. Not	* 0. Straight
1. Moderate	1. Slightly saddled
2. Pronounced	2. Slightly carped
(T) <i>Neck dewlap</i>	(U) <i>Sternum tip</i>
0. Present	0. Slightly pronounced
1. Absent	* 1. Pronounced
(V) <i>Back</i>	(W) <i>Withers</i>
0. Slightly oblique	0. Simply pronounced
* 1. Oblique	* 1. Well-defined
2. Straight	
(X) <i>Skin</i>	(Y) <i>Hair</i>
* 0. Tensed	0. Long
1. With pleat	1. Short
	* 2. Straight
	3. Various
(Z) <i>Belly</i>	(A') <i>Spurs</i>
* 0. Slightly contracted	0. With
1. Contracted	* 1. Without
2. Very contracted	2. With or without
(B') <i>Interdigital membrane</i>	(C') <i>Tail insertion</i>
0. Without	0. Up
* 1. Moderate	* 1. Middle
2. Pronounced	2. Down
(D') <i>Tail form</i>	(E') <i>Foot form</i>
* 0. Fallen (sword)	* 0. Cat
1. Sabre	1. Hare
2. Sickle	
3. Others	

* The asterisk signals the ancestral state of the character, based upon the criterion of the maximum frequency. This criterion was not discriminant for the characters *B*, *C* and *T*.

Quantitative analysis

For the quantitative analysis of morphological characters, qualitative data were transformed and introduced in the form of a matrix of distances. An Euclidean distance (Sneath and Sokal, 1973) was used to estimate distances between populations, under the assumption of independence between characters.

$$d_{(j,k)} = [\sum_i (X_{ij} - X_{ik})^2]^{1/2}$$

where:

$d_{(j,k)}$ = value of the distance between the j and the breed k . The distance ranges from 0 to \sqrt{n} , where n is the number of traits;

Table II. Morphological resemblance matrix.

Breed	A	B	C	D	E	F	G	H	I	J	K	L	M	N	Ñ	O	P	Q	R	S	T	U	V	W	X	Y	Z	A'	B'	C'	D'	E'	
Gos d'Atura	0	1	0	0	3	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	2	2	0	0	0
Mastín del Pirineo	1	1	0	4	2	1	0	1	0	0	0	0	1	1	0	0	2	2	1	1	0	1	1	1	1	0	0	2	1	1	1	0	0
Mastín Español	1	1	1	4	1	0	1	0	0	0	0	1	1	0	0	2	2	1	1	0	1	1	1	1	1	1	0	2	1	1	1	0	0
Perdiguero Burgos	0	1	1	2	1	1	1	2	1	0	1	0	2	1	0	2	2	2	0	0	1	0	1	1	1	2	0	1	1	1	3	0	0
Galgo Español	0	0	0	2	1	1	1	2	0	0	2	1	1	0	0	1	0	0	2	1	1	1	0	0	2	2	1	1	2	2	1	0	0
Sabueso Español	0	0	1	2	0	1	1	2	1	0	2	0	2	1	0	3	2	2	1	1	0	1	1	0	1	2	0	2	1	1	1	0	0
Ca de Bestiar	1	1	0	3	0	1	0	0	0	0	0	2	0	1	0	0	2	1	0	0	0	0	1	1	0	1	0	1	0	0	2	1	0
Podenco Ibicenco	0	0	1	3	0	1	0	2	0	0	0	1	1	2	1	1	0	0	0	1	1	1	1	0	3	1	1	0	2	0	1	0	0
Podenco Canario	0	0	1	1	0	1	0	2	0	0	0	1	1	2	1	3	0	0	0	1	0	1	1	0	2	1	1	0	2	0	0	0	0
Podenco Ibérico	0	0	0	1	0	1	1	2	0	0	1	1	1	0	0	3	0	0	0	1	1	0	0	0	3	1	1	0	1	0	1	0	0

Table III. Recoded matrix of morphological resemblances.

<i>Breed</i>		01000	00001	00000	00000	00100	01000	00000	00011	01000	00000	01010	000
Gos d'Atura		01000	00001	00000	00000	00100	01000	00000	00011	01000	00000	01010	000
Mastín Pirineo		11000	01010	01010	00000	00101	00000	01011	01001	11100	00001	10101	000
Mastín Español		11100	01000	11010	00000	00101	00000	01011	01001	11110	00001	10101	000
Perdiguero Burgos		01101	00100	01101	10010	00011	00010	01010	10001	01101	00010	10100	010
Galgo Español		00001	00100	01101	01000	01101	00000	10000	00111	10001	00110	10010	101
Sabueso Español		00101	00000	01101	10001	00011	00001	01011	01001	10101	00001	10101	000
Ca de Bestiar		11000	10000	01000	00000	01001	00000	01100	00000	11010	00010	00000	101
Podenco Ibicenco		00100	10000	01001	00000	10100	11100	00000	00011	11000	11010	00010	001
Podenco Canario		00110	00000	01001	00000	10100	11001	00000	00010	11001	01010	00010	000
Podenco Ibérico		00010	00000	01101	00010	10100	00001	00000	00011	00000	11010	00100	001

$(X_{ij} - X_{ik}) =$ alternative values (0, 1) for the differences between j and k breeds within the character i .

$$X_{ij} - X_{ik} = 0 \quad \text{if } X_{ij} = X_{ik}$$

$$X_{ij} - X_{ik} = 1 \quad \text{if } X_{ij} \neq X_{ik}$$

The mean character difference (*MCD*) proposed by Cain and Harrison (1958) was also calculated as a measure of taxonomic resemblance. *MCD* varies between 0 and 1.

$$MCD = 1/n \sum_i |X_{ij} - X_{ik}|$$

Fitch and Margoliash's method (1967) was used to find the unrooted tree that would best adapt to the matrix (FITCH program in PHYLIP package). The tree that minimizes the sum of squares *SS* was searched for by means of the following expression:

$$SS = \sum_j \sum_k (D_{jk} - d_{jk})^2 / D_{jk}^2$$

where:

D_{jk} = observed distance between populations j and k ;

d_{jk} = expected distance between populations j and k , computed as the addition of tree segment lengths, from population j to population k (patristic distance).

Alternatively, a rooted tree was computed by applying the KITSCH program (PHYLIP package). In this method, a tree similar to that generated by the cluster analysis was computed and subsequently the topology of the tree was altered in order to improve its goodness-of-fit. By assuming: a), that the expected rates of change are constant through all lines; b), that all the subpopulations are contemporary; and c), that the phenotypes behave as an evolutionary clock, this method can be regarded as an estimator of the phylogeny (Felsenstein, 1984, 1986).

RESULTS

Qualitative analysis

The dendrograms resulting from the application of Wagner parsimony and Camin and Sokal's methods are shown in figures 2 and 3 respectively. Two large groups can be observed in each tree. One of the groups is formed by 4 breeds: Mastín del Pirineo, Mastín Español, Sabueso Español and Perdiguero de Burgos; the other group includes Podenco Ibicenco, Podenco Canario, Podenco Ibérico and Galgo Español. In the dendrogram resulting from Wagner parsimony, the breeds Ca de Bestiar and Gos d'Atura are halfway between the 2 large groups, even though Gos d'Atura is nearer the greyhound group (Podencos and Galgo) and Ca de Bestiar is nearer the other group.

The closeness of Gos d'Atura and Ca de Bestiar breeds to one group or the other is more evident in the three resulting from the application of Camin and Sokal's method. Gos d'Atura is placed halfway between 2 subgroups formed by Podenco Ibicenco-Podenco Canario and Podenco Ibérico-Galgo Español breeds. The Ca de Bestiar breed is more closely related to the Mastiffs than to the subgroup formed

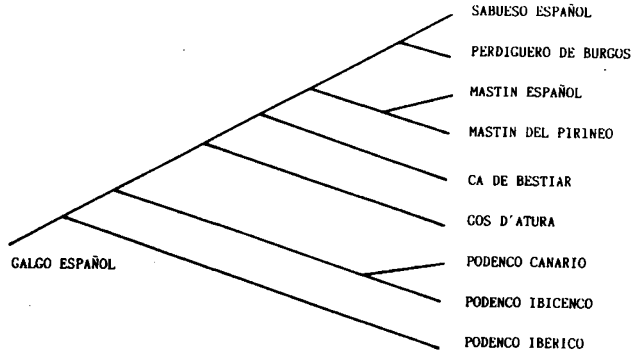


Fig 2. Qualitative analysis of morphological data. Dendrogram resulting from the application of Wagner parsimony.

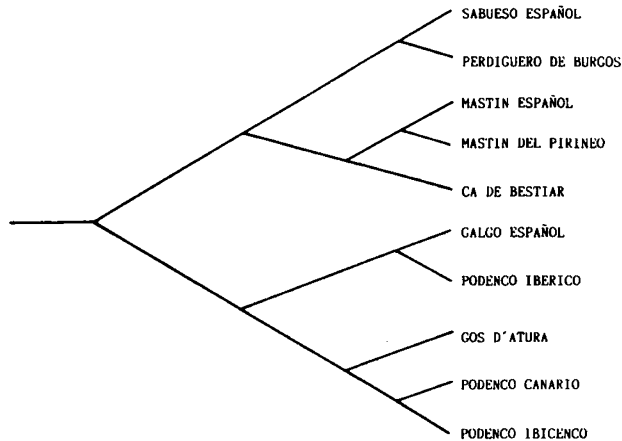


Fig 3. Qualitative analysis of morphological data. Dendrogram resulting from the application of Camin and Sokal's method.

by Sabueso Español and Perdiguero de Burgos. Both topologies are possible, even though the tree obtained by applying Wagner parsimony needed only 96 steps to rearrange the characters and to obtain the most parsimonious tree, while for the tree generated by Camin and Sokal's method, 101 steps were needed. This difference in the number of steps, however, probably reflects the differences in the assumptions of the kinds of changes used in both methods (Felsenstein, 1986), and consequently cannot be considered as a definitive criterion to infer the true relationships.

Figure 4 shows a dendrogram of the Spanish dog breeds estimated according to the parsimony and midpoint rooting criteria (PAUP package). This dendrogram again shows the 2 groups described above. Branch and internodal distances are proportional to the number of character-stage changes required. The total length was 85 (*versus* 96 found in Wagner parsimony), and the consistency index (a

measure of the homoplasy) was 0.671. Included within parentheses are the values of the number of replicates from the bootstrap analysis (loosely, the width of the confidence interval).

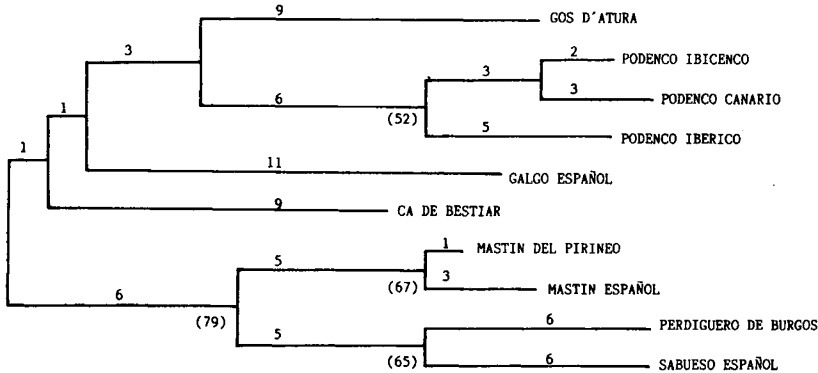


Fig 4. Qualitative analysis of morphological data. Dendrogram produced by PAUP analysis. Within parentheses, bootstrap replicates (%).

Quantitative analysis

The results of the morphological distance indexes between Spanish dog breeds are shown in table IV. The average distance between breeds has a value of 4.228 (± 0.681), with extreme values of 1.732 between Mastín del Pirineo and Mastín Español, and 5.099 for the Gos d'Atura - Sabueso Español pair. The values of the distances within the Podenco group (Ibicenco, Canario and Ibérico) are small, as are the distances between Mastiff breeds (Mastín del Pirineo and Mastín Español), and between Perdiguero de Burgos and Sabueso Español. The values for the mean character differences (MCD) between Spanish dog breeds are shown table V. In the same way, the average MCD between breeds has a value of 0.5645 (± 0.1552), with extreme values of 0.0937 between Mastín del Pirineo and Mastín Español, and of 0.8125 for the Gos d'Atura - Sabueso Español pair.

The trees obtained using FITCH and KITSCH programs are shown in figures 5 and 6. The dendrograms obtained by the FITCH program are unrooted, so we arbitrarily used the Galgo Español breed as an outgroup. Two hundred and twenty-six possible trees were examined. Figure 5 shows the tree that best adjusts to the matrix of data. The sum of squares had a value of 0.183, whereas the average percent standard deviation was 4.56%. In the tree in figure 5, the 2 groups previously described are again observed. The Greyhound cluster (Podenco Ibicenco, Podenco Canario, Podenco Ibérico and Galgo Español) additionally contains the Gos d'Atura breed. The Ca de Bestiar breed remains in an intermediate position, slightly closer to the Greyhound group.

In the resulting tree from the application of the KITSCH program, the 2 large clusters were observed again, Gos d'Atura and Ca de Bestiar being included in

Table IV. Genetic distance matrix between Spanish dog breeds, obtained from morphological data.

<i>Breed</i>	<i>GA</i>	<i>MP</i>	<i>ME</i>	<i>PB</i>	<i>GE</i>	<i>SE</i>	<i>CB</i>	<i>PE</i>	<i>PC</i>
MP	4.243								
ME	4.472	1.732							
PB	4.690	4.000	3.873						
GE	4.472	4.582	4.690	4.359					
SE	5.099	3.605	3.464	3.162	4.243				
CB	4.359	4.000	4.000	4.582	4.243	4.796			
PE	3.873	4.796	4.690	4.796	4.000	4.796	4.123		
PC	4.000	4.796	4.690	4.690	4.123	4.582	4.243	2.236	
PI	4.123	4.899	5.000	4.472	3.873	4.472	4.472	3.162	3.317

Table V. Mean character differences (*MCD*) between Spanish dog breeds.

<i>Breed</i>	<i>GA</i>	<i>MP</i>	<i>ME</i>	<i>PB</i>	<i>GE</i>	<i>SE</i>	<i>CB</i>	<i>PE</i>	<i>PC</i>
MP	0.5625								
ME	0.6250	0.0937							
PB	0.6875	0.5000	0.4687						
GE	0.6250	0.6562	0.6875	0.5937					
SE	0.8125	0.4062	0.3750	0.3125	0.5625				
CB	0.5937	0.5000	0.5000	0.6562	0.5625	0.7187			
PE	0.4687	0.7187	0.6875	0.7187	0.5000	0.7187	0.5312		
PC	0.5000	0.7187	0.6875	0.6875	0.5312	0.6562	0.5625	0.1562	
PI	0.5312	0.7500	0.7812	0.6250	0.4687	0.6250	0.6250	0.3125	0.3437

the greyhound group, even though an unresolved trichotomy is presented between Galgo Español, Gos d'Atura and Ca de Bestiar breeds. The sum of squares had a value of 0.248 and the average percent standard deviation was 5.31%.

DISCUSSION

In examining all the topologies of the trees resulting from the analysis of morphological characters, it is possible to verify some stable relationships among different groups of breeds. Sabueso Español and Perdiguero de Burgos form a separate cluster from Mastín Español and Mastín del Pirineo breeds. The last 2 clusters, in their turn, are related and form a new cluster. The bootstrap analysis (figure 4) confirms this grouping (79% of the bootstrap replicates). Podenco Ibicenco, Podenco Canario, Podenco Ibérico and Galgo Español breeds are related in all trees. The bootstrap analysis, however, failed to confirm the relationship between Galgo

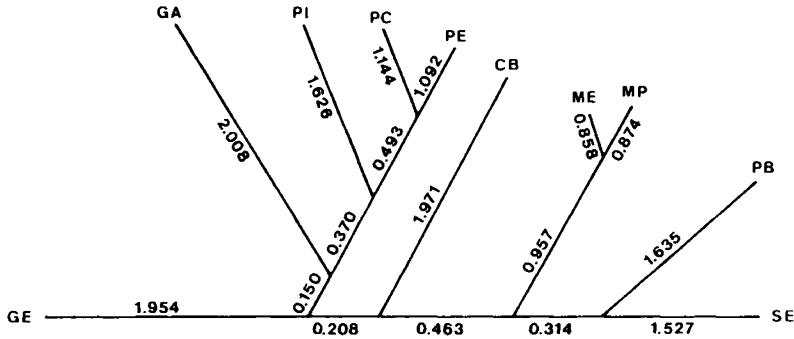


Fig 5. Quantitative analysis of morphological data, by applying Fitch and Margoliash's method (1967) (FITCH program in PHYLIP package).

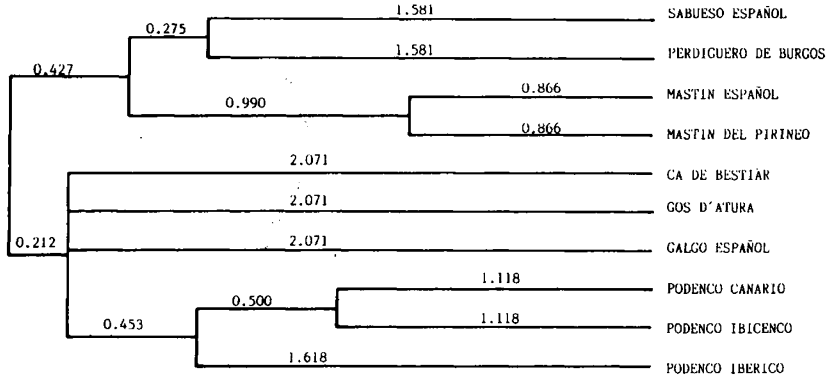


Fig 6. Quantitative analysis of morphological data, by applying Fitch and Margoliash's method (1967), assuming contemporaneity of the breeds (KITSCH program in PHYLIP package).

Español and Podenco breeds (PE, PC and PI), as the value from the bootstrap analysis was below 50%. These breeds correspond to the Greyhound group.

The relationship described above is consistent with assigning the Spanish breeds to the known ancestral trunks. The Spanish dog breeds have been assigned to their hypothetical ancestral trunks by comparing their morphology with some European breeds whose phylogeny was taken as known (table VI). The phylogeny of the European breeds was inferred by comparative studies of dental and cranial morphology, as well as archaeological, historical and behavioral studies (Studer, 1901; Antonius, 1922; Villemont *et al*, 1970; Rousselet-Blanc, 1983). The phylogeny resulting from the qualitative and quantitative analysis of morphological data seems to confirm these classifications. There is a disagreement, however, with Villemont *et al* (1970), who assigned the Bloodhound, Beagle and Grand Bleu de Gascogne (similar to the Sabueso Español breed) breeds to the ancestral trunk *Cf leineri*.

Table VI. Assignment of the Spanish dog breeds to their hypothetical ancestral trunks according to their similarity with other breeds of defined phylogeny.

<i>Group of breeds</i>	<i>Ancestral trunk</i>	<i>Assimilated Spanish dog breeds</i>
{ Bloodhound Grand Bleu de Gascognes	<i>Cf intermedius</i>	Sabueso Español
{ Pointer Braque Francais	<i>Cf intermedius</i>	Perdiguero de Burgos
{ Mastiff Chien de Montagne des Pyrénées	<i>Cf inostranzewi</i>	Mastín del Pirineo Mastín Español
{ Sloughi Greyhound Cirneco dell'Etna	<i>Cf leineri</i>	Podenco Ibicenco Podenco Canario Podenco Ibérico Galgo Español
{ Berger de Brie Cane de Pastore Bergamasco	<i>Cf metris-optimae</i>	Gos d'Atura

The Ca de Bestiar breed, due to its particular formation, has not been assigned to any specific ancestral trunk. Authors: Villemont *et al* (1970); Rousselet-Blanc (1983).

It can be observed from the tree in figure 6 that the cluster formed by the Mastín del Pirineo and Mastín Español breeds would fit in with the ancestral trunk of *Cf inostranzewi*, and the cluster that Sabueso Español and Perdiguero de Burgos form will fit with *Cf intermedius*, both being related groups and forming in their turn a new cluster. On the other hand, a close relationship is observed between the 3 breeds of Podencos that would form the trunk of *Cf leineri*. Galgo Español remains a little farther away, although taking as a basis the trees resulting from the qualitative analysis (MIX program and PAUP program) and quantitative analysis (FITCH program), the breed might be included in the trunk of *Cf leineri*. Gos d'Atura would be the only representative of *Cf metris-optimae*, and Ca de Bestiar would remain isolated. Due to the particular origin of the Ca de Bestiar breed (it is believed that it comes from crossings between Podencos, Perdigueros and Mastines) the breed has not been assigned to any specific ancestral trunk.

According to Felsenstein (1986), the resultant tree could be considered as an estimation of the phylogeny of the breeds, which would suggest that the Sabueso Español, Perdiguero de Burgos, Mastín del Pirineo and Mastín Español breeds would be related and would descend from a hypothetical common ancestor. On the other hand, Gos d'Atura (*Cf metris-optimae*) and Ca de Bestiar would be more related to the members of the *Cf leineri*. A common ancestor might be postulated for the *Cf metris-optimae* and *Cf leineri* trunks. Figure 7 summarizes the hypothetical relationships between ancestral trunks described above.

The methods applied in this study were devised mainly to analyze natural populations. This paper deals with populations of domestic animals whose characteristics were fixed by man in a process of artificial selection, assumed to be very intensive at least at the beginning of breed differentiation. The selection criteria would have

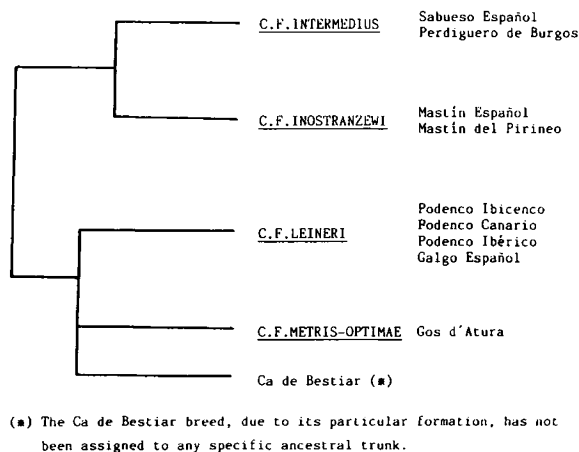


Fig 7. Postulated topology of the relationships between canine ancestral trunks.

been very complex, including both characters related to some specific ability and other traits derived from the caprice of the breeders. Nevertheless, we think that selection is the evolutionary strength that could have had the greatest weight in the process of breed differentiation. In most species of domestic animals, and in a special manner in the canine species, the characteristics that usually define a breed are basically morphological. The breed, consciously or unconsciously, has been created by man, even though the contribution of the environment has operated through natural selection. Orozco's words (1985) about the breed concept in domestic animals are illustrative:

"Nobody can stop a breeder, a technician, or anyone who has access to a group of animals, from establishing a particular population as a breed, if he bases this on fixed, objective, uniform and different characteristics from other breeds. He can speak, if he wants to, about a new breed. The breed has simply to agree with definitive and very strict characteristics: perfection of colour, type, appearance, well determined measures of different parts of the body, etc. If the breed is established in this manner, there is no objection to make".

This assertion acquires great importance in the case of dog breeds. Here, the patterns or prototypes for the inclusion of an animal in a particular breed are very strict, resting on multiple morphological assessments, both qualitative and quantitative, that should be within certain limits. If the qualifiers consider that an animal does not achieve the proper requirements, nobody doubts that this animal does not belong to the breed. This consideration should preclude for most breeds inter-racial crossings that would have resulted in a less tree-like genealogy.

In an ecological context, Crouau-Roy (1990) affirms that morphological data may reflect historical processes but are much more under the influence of differential selective pressures (micro- and macro-environmental influences) than biochemical data. This affirmation might be also applicable to the case of the evolution of canine breeds. In this sense, it has also been argued that the study of the values of the genic frequencies of structural genes that code for proteins and soluble blood

enzymes, without any relation with fitness, *ie* assumed as neutral genes, would be a good indicator of the genetic similarity or divergence between populations (Kimura, 1983). This kind of analysis may allow us to study whether there is an evolutionary parallelism between both types of characters – morphological and blood substances – with would be of great interest in establishing more accurately the relationships between the canine breeds under study.

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