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ANALYSIS OF GENETIC RELATIONSHIPS IN HORSE BREEDS

J. Jordana, P.M. Pares, A. Sanchez

INTRODUCTION

SUMMARY

The relationships between twenty horse breeds and two species of wild horses were studied using qualitative and quantitative analyses of data from 30 morphological characters. The average morphological distance between breeds, measured as MCD (mean character difference), had a value of 0.57 (± 0.17 of STD), with extreme values of 0.13 between Clydesdale-Shire pair, and of 0.87 for the Tarpan-Andalusian, Tarpan-Ardenne, Tarpan-Brabant, and Exmoor-Brabant pairs. The results show the formation of two large groups. One is formed by members of the Tarpanic Trunk, which would include the breeds descending from *Equus ferus gmelini* and *Equus ferus przewalski*; this supports the hypothesis postulated by other authors that *Equus przewalski* could be the south-oriental variant of Tarpan (*Equus gmelini*). Another large group would be formed by breeds belonging to the Solutrensis Trunk, descendants of *Equus ferus stenonis*, *robustus* or *solutrensis*. The different influences received by some breeds, which would contribute to a large extent to the present-day morphological relationships, is discussed. The inter-racial relationships obtained agree with those presented by ethnologists.

Keywords: Horse breeds / genetic distance / morphological character / dendrogram / morphological analysis

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The systematic classification of different breeds of domestic livestock into the most related groups and research on the phylogenetic relationships between them has always been a goal. In the horse, these ethnological arrangements have mainly been carried out on morphological similarities, complemented by historical references and archaeological findings,¹⁻⁴ or biochemical polymorphisms.⁵⁻⁸

Discussion of the evolution of the horse is still continuing.⁹ However, the *Pliohippus* or *Pleshippus* is considered as the ancestor of the genus *Equus* in all its forms (e.g. *E. caballus*, *E. asinus*, *E. zebra*, etc...). The *Equus* was probably developed in North America, from where it passed to Europe, Asia and Africa. Nevertheless, at the end of Pleistocene or the beginning of Holocene (9,000 to 10,000 years ago), *Equus* disappeared completely from the American continent, and the subgenus *Equus caballus* developed in the Old World.^{10,11}

It seems that the origin of domestic horses dates back to the third millennium BC: the domestication would have been produced in the Ukraine and western Asia,⁹ and only a millennium later in Europe.¹²

The current domestic horses would be descendants of three fundamental types: the *Equus ferus gmelini*, the *Equus ferus przewalski*, and the *Equus ferus stenonis*, *robustus* or *solutrensis*.^{10,13,14,15}

1) *Equus ferus gmelini*: rectilinear profile variant, whose most genuine representative would be the Tarpan or Plateau horse. The Tarpan was originally from the West of Mongolia, and the last wild animal was officially declared extinct in 1879.^{13,16} The Tarpan might present the most

stylized forms and the lighter weight of these three ancestral lines of current horses. According to Sotillo and Serrano,¹⁵ *Equus gmelini* may have been introduced to Europe in two ways: the Central European and the Northern European. All the rectilinear horses, the present-day light ponies, descend from Tarpan.

2) *Equus ferus przewalski*: convex profile variant, whose most genuine representative would be Przewalski's horse, Steppe horse or Mongolia horse, also extinct. The present-day subconvex profile and long-headed breeds would derive from Przewalski. According to Sotillo and Serrano¹⁵ the original convex horse could have been crossed massively in prehistorical times with the Tarpan (*Equus gmelini*), and the current Przewalski (*Equus przewalski*) with corrected profiles; that is, subconvexes could have originated. Groves' opinion¹⁷ is similar; he postulates that Przewalski's horse could be the oriental variant of the Tarpan, and that it could have been introduced to Africa and Europe through Egypt and the Strait of Gibraltar (Spain).

3) *Equus ferus stenonis*, *robustus* or *solutreensis*: concave profile variant, whose most genuine representative was Solutre's horse or Forest's horse. It originated in Central Europe,¹³ and it was the first to disappear. *Equus stenonis* could be the ancestor of the present-day draft concave massive horses.

In short, we could say that the present-day dolicomorf and mesomorf breeds could have descended from the Tarpan and Przewalski's horse, and the draft braquimorf breeds in Central and Septentrional Europe¹⁸ could derive from the Solutre's horse.

All the different types and breeds of horses were developed as a result of artificial selection in combination with natural selection for adaptation to local climatic and environmental conditions. So, some of the differences—coloration, size, body proportions, etc.—can be regarded as resulting from domestication.¹²

Despite this artificial selection, it can be seen that the breeds of horses conform in their territory of origin to the two rules that relate environmental temperature to the size of the body—Bergmann's rule—and the length of their extremities—Allen's rule.¹² So, we have small stocky ponies in northern Europe, heavy horses in north and central Europe and slender-limbed horses in the south.

We have used morphological information to complement our knowledge of genetic relationships between different present-day equine breeds. Morphological characters can provide very useful information which complement other research on the genetic relationships of domestic breeds in general. Statistical techniques such as multivariate analyses and the application of numerical taxonomy¹⁹ to the data derived from morphological characters allow a different treatment of the information generated.^{20,21,22,23,24,25}

This paper presents studies from qualitative and quantitative data analyses, using statistical methods and avail-

able computing packages specifically designed for such analyses.^{26,27}

MATERIALS AND METHODS

Breeds studied

We have studied 22 equine populations: 3 breeds are currently used for riding (dressage): Andalusian (AND), Arab Thoroughbred (ARB) and Criollo (CRI); 2 breeds are of mixed use (dressage and racing): Barb or Berber (BAB) and Selle Francais (SEF); 3 were pony breeds: Exmoor (EXM), Merens (MER) and Potttock (POT); and 12 were carriage breeds: Ardennes (ARD), Auxois (AUX), Boulonnais (BOL), Brabant (BRB), Breton Cerda (BRC), Breton Gros (BRG), Breton Postier (BRP), Clydesdale (CLY), Comtois (COM), Percheron (PER), Shire (SHI) and Suffolk (SUF); and two now extinct wild horse breeds: Tarpan (TAR) or *Equus gmelini* and Przewalski's horse (PZW) or *Equus przewalski*.

The studied breeds are found mainly in Western Europe (France, Belgium, Great Britain and Spain), with the exceptions of Arab and Barb (North Africa), Criollo (South America) and the two wild horses (Tarpan and Przewalski).

Qualitative and quantitative analyses

A total of 30 morphological characters were studied using an ideal specimen for each of the 22 horse breeds. The state of each of the characters for each breed was established according to the descriptions offered by several authors.^{9,14,15,18,28,29,30,31} Numbers were assigned to each state of the different characters in an arbitrary manner. These numbers did not represent any specific weight. The number of states for each character was established depending upon the number of distinguishable phenotypic classes. The characters used and their state numbers are shown in Table 1. Continuous quantitative characters (Z, B and C characters in Table 1) may be split into a small number of classes, each representing one of the states of the character in the data matrix. The original matrix of morphological resemblances is shown in Table 2.

When possible, we have looked up precise morphological studies of the breed in question; e.g., Andalusian,³² Boulonnais,³³ Breton Cerda³⁴ Criollo,^{35,36,37} Potttock.³⁸

All analyses were made using different programs from the computing packages PHYLIP (Phylogeny Inference Package)²⁶ and PAUP (Phylogenetic Analysis Using Parsimony).²⁷

For the qualitative analysis of morphological characters the PAUP package²⁷ was used from the discrete characters shown in Table 2. This analysis is based upon the parsimony principle, and the criterion is to find the tree requiring the minimum number of changes. The method used was Fitch parsimony.³⁹ To give an evolutionary direction, resulting trees were rooted using the midpoint and outgroup methods;⁴⁰ the two species of wild horses,

Table 1. Characters and their states, used for the construction of the morphological resemblance matrix.

<p>(A) Size</p> <ol style="list-style-type: none"> 0. Elipometrical 1. Eumetrical 2. Subhypermetrical 3. Hypermetrical 	<p>(M) Loin length</p> <ol style="list-style-type: none"> 0. Short 1. Long 	<p>(W) White markings</p> <ol style="list-style-type: none"> 0. Absence 1. Presence on head and lower extremities
<p>(B) Cranial profile</p> <ol style="list-style-type: none"> 0. Subconcave 1. Rectilinear 2. Subconvex 3. Convex 	<p>(N) Rump</p> <ol style="list-style-type: none"> 0. Horizontal 1. Horizontal and double-muscled 2. Drooping 3. Drooping and double-muscled 	<p>(X) Zebra stripings on the legs</p> <ol style="list-style-type: none"> 0. Absence 1. Presence
<p>(C) Length/width proportions</p> <ol style="list-style-type: none"> 0. Brevilinear 1. Mesolinear 2. Longilinear 	<p>(O) Root of tail</p> <ol style="list-style-type: none"> 0. Down 1. Middle 2. Up 	<p>(Y) Aptitude</p> <ol style="list-style-type: none"> 0. Wild form 1. Riding 2. Riding and career 3. Draft horse 4. Pony
<p>(D) Neck length</p> <ol style="list-style-type: none"> 0. Short 1. Middle length 2. Long 	<p>(P) Hooves</p> <ol style="list-style-type: none"> 0. Small and high 1. Medium-sized 2. Big and flat 	<p>(Z) Live weight in sires</p> <ol style="list-style-type: none"> 0. < 450 Kg 1. 450–500 Kg 2. 500–650 Kg 3. 650–1000 Kg 4. >1000 Kg
<p>(E) Neckform</p> <ol style="list-style-type: none"> 0. Pyramidal 1. Prominent 2. Cervune 	<p>(Q) Horsehair</p> <ol style="list-style-type: none"> 0. Short mane and tail 1. Long mane and tail and few feathers on the pastern 2. Long mane and tail and prominent feathers on the pastern 	<p>(A) Head size in relation to body</p> <ol style="list-style-type: none"> 0. Small 1. Middle (proportionate) 2. Large
<p>(F) Neck profile</p> <ol style="list-style-type: none"> 0. Arched 1. Straight 2. Deep-set 	<p>(R) Face profile</p> <ol style="list-style-type: none"> 0. Concave 1. Straight 2. Convex 	<p>(B) Withers height</p> <ol style="list-style-type: none"> 0. < 149 cm 1. 149–154 cm 2. 155–160 cm 3. 161–170 cm 4. > 170 cm
<p>(G) Withers</p> <ol style="list-style-type: none"> 0. Simply pronounced 1. Well-defined 	<p>(S) Face length</p> <ol style="list-style-type: none"> 0. Short 1. Long 	<p>(C) Thoracic perimeter</p> <ol style="list-style-type: none"> 0. <170 cm 1. 171–185 cm 2. 186–200 cm 3. >200 cm
<p>(H) Shoulder length</p> <ol style="list-style-type: none"> 0. Short 1. Middle 2. Long 	<p>(T) Eyebrow</p> <ol style="list-style-type: none"> 0. Protruding 1. Slightly prominent 	<p>(D) Biotipology</p> <ol style="list-style-type: none"> 0. Muscular 1. Hypermetabolic 2. Anabolic 3. Temperamental 4. Very good stamina
<p>(I) Chest</p> <ol style="list-style-type: none"> 0. Slightly arched 1. Well-sprung 	<p>(U) Ear size in relation to head</p> <ol style="list-style-type: none"> 0. Large 1. Middle (proportionate) 2. Small 	
<p>(J) Breast conformation</p> <ol style="list-style-type: none"> 0. Medium-sized 1. Broad 2. Very broad 	<p>(V) Coat</p> <ol style="list-style-type: none"> 0. Chestnut (CH) 1. Black 2. Gray 3. Isabella 4. CH. and Bay 5. Bay and Black 6. Bay 7. Bay and Roan 8. CH. and Strawberry 9. Grey, CH. and Bay 10. Various 	
<p>(K) Back length</p> <ol style="list-style-type: none"> 0. Short 1. Medium-sized 2. Long 		
<p>(L) Dorsal line</p> <ol style="list-style-type: none"> 0. Slightly saddled 1. Straight 		

Table 2. Morphological resemblance matrix

BREEDS\CHARACTERS	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	A	B	C	D
ANDALUSIAN	1	2	0	1	1	0	1	2	0	1	0	0	2	0	1	1	2	1	0	1	2	1	0	1	1	1	2	1	3	
ARAB	1	1	1	2	0	0	1	2	0	1	0	1	0	0	2	1	1	1	0	1	2	9	1	0	1	0	0	1	1	
ARDENNES	2	0	0	0	1	0	1	0	1	2	0	1	0	3	1	2	2	0	0	0	2	8	1	0	3	2	2	2	2	
AUXOIS	2	0	0	0	1	0	1	0	1	2	0	1	0	2	0	2	1	0	0	0	2	7	1	0	3	3	0	3	2	
BARB	1	2	1	1	1	0	1	2	0	1	0	1	0	2	0	0	1	2	1	0	2	9	1	0	2	1	2	1	3	
BOULONNAIS	3	1	0	1	1	0	0	0	1	2	0	1	0	1	2	2	0	1	0	1	2	2	0	0	3	3	0	3	0	
BRABANT	3	0	0	0	1	0	1	0	1	2	0	1	0	3	0	2	2	0	0	0	2	4	1	0	3	4	0	4	2	
BRETON CERDA	2	2	1	0	1	0	0	1	1	2	0	1	0	2	1	2	2	1	0	0	2	4	1	0	3	2	1	1	2	
BRETON GROS	3	0	0	0	1	0	0	1	1	2	0	1	0	3	1	2	2	1	0	0	2	4	1	0	3	3	1	3	2	
BRETON POSTIER	2	0	1	0	1	0	0	1	1	2	0	1	0	3	1	2	2	1	0	0	2	4	1	0	3	1	1	2	1	
CLYDESDALE	3	1	2	2	1	0	1	0	1	2	0	1	1	2	1	2	2	1	0	0	0	6	1	0	3	3	0	3	0	
COMTOIS	3	0	0	0	1	1	1	0	1	2	0	1	0	2	1	1	2	1	0	0	2	0	1	0	3	3	1	2	2	
CRIOLLO	1	1	1	2	0	0	1	2	0	1	0	1	0	2	1	0	1	2	1	0	2	10	1	1	1	1	0	1	3	
EXMOOR	0	1	1	1	0	1	1	2	0	1	2	0	1	2	1	0	1	1	0	1	2	6	0	0	0	0	1	0	4	
MERENS	1	1	1	1	0	1	1	1	0	2	2	1	1	0	2	1	2	1	0	1	2	1	0	0	4	0	0	0	1	
PERCHERON	3	1	0	1	1	0	0	0	1	2	0	1	0	0	2	1	1	1	0	1	0	2	0	0	3	3	2	3	0	
POTTOCK	0	1	0	0	2	2	1	2	0	1	0	1	0	2	0	0	1	0	0	1	2	5	0	0	4	0	1	0	4	
SHIRE	3	3	2	2	1	0	1	0	1	2	0	1	1	2	1	2	2	1	0	0	0	4	1	0	3	4	0	4	3	
SELLE FRANÇAIS	1	1	1	2	0	1	1	2	0	1	0	1	0	2	1	1	1	1	0	1	0	4	1	0	2	1	0	2	1	
SUFFOLK	3	3	0	2	1	0	0	2	1	2	0	1	1	2	1	2	1	1	0	0	2	0	0	0	3	3	2	3	0	
TARPAN	0	1	1	0	0	1	0	2	0	0	2	1	1	2	1	0	1	1	0	1	0	10	0	1	0	0	0	0	4	
PRZEWALSKI'S HORSE	0	2	1	0	0	1	0	2	0	0	2	1	1	2	0	0	0	1	0	1	2	3	0	1	0	0	2	0	4	

Equus gmelini (Tarpan) and *Equus przewalski* (Przewalski's horse), were chosen as outgroups. The PAUP package also allows us to compute the confidence limits of the topology by means of a bootstrap analysis,⁴¹ adapted to the inference of phylogenies.⁴² One hundred bootstrap replicates were made, and a consensus tree was obtained based upon the majority-rule method.⁴³ 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 at 50 (CONLEVEL=50).

For the quantitative analysis, qualitative data were transformed and processed in the form of a matrix of distances. An Euclidean distance¹⁹ was used to estimate distances between populations, under the assumption of independence between characters.

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

where, $d_{(j,k)}$ = value of the distance between the breed j and the breed k. The distance ranges from 0 to \sqrt{n} , where n is the number of traits; $(X_{ij} - X_{ik})$ = alternative values (0,1) for the differences between j and k breeds within the character i.

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

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

The mean character difference (MCD) proposed by Cain and Harrison⁴⁴ was calculated also as a measure of taxonomic resemblance. The MCD varies between 0 and 1.

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

Fitch and Margoliash's method⁴⁵ was used to find the tree that would adapt best to the data matrix (KITSCH 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, and 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).

In this method, a rooted tree similar to that generated by the cluster analysis was computed and the topology of the tree was subsequently altered in order to improve its goodness-of-fit. By assuming that a) the expected rates of change are constant through all lines; b) 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.^{46,26}

Table 3. Mean character differences (MCD). Genetic distance

BREEDS	AND	ARB	ARD	AUX	BAB	BOL	BRB	BRC	BRG	BRP	CLY	COM	CRI	EXM	MER	PER	POT	SHI	SEF	SUF	TAR	
ARAB (ARB)	0.53																					
ARDENNES (ARD)	0.67	0.70																				
AUXOIS (AUX)	0.60	0.63	0.23																			
BARB (BAB)	0.27	0.43	0.63	0.57																		
BOULONNAIS (BOL)	0.73	0.60	0.53	0.43	0.73																	
BRABANT (BRB)	0.67	0.67	0.23	0.23	0.63	0.43																
BRETON CERDA (BRC)	0.67	0.63	0.30	0.37	0.57	0.53	0.40															
BRETON GROS (BRG)	0.70	0.70	0.27	0.30	0.70	0.40	0.27	0.20														
BRETON POSTIER (BRP)	0.63	0.63	0.27	0.40	0.63	0.53	0.33	0.17	0.17													
CLYDESDALE (CLY)	0.73	0.60	0.47	0.40	0.70	0.37	0.40	0.47	0.40	0.50												
COMTOIS (COM)	0.60	0.67	0.27	0.30	0.67	0.50	0.33	0.33	0.23	0.33	0.40											
CRIOLLO (CRI)	0.40	0.33	0.70	0.63	0.27	0.77	0.73	0.63	0.73	0.63	0.63	0.70										
EXMOOR (EXM)	0.67	0.53	0.83	0.83	0.63	0.73	0.87	0.77	0.80	0.77	0.70	0.70	0.60									
MERENS (MER)	0.77	0.40	0.80	0.77	0.70	0.60	0.73	0.70	0.73	0.67	0.67	0.67	0.67	0.40								
PERCHERON (PER)	0.67	0.53	0.57	0.50	0.70	0.17	0.53	0.60	0.47	0.60	0.40	0.50	0.80	0.73	0.60							
POTTOCK (POT)	0.60	0.53	0.70	0.57	0.57	0.67	0.63	0.67	0.70	0.73	0.77	0.63	0.60	0.37	0.57	0.67						
SHIRE (SHI)	0.73	0.67	0.47	0.47	0.70	0.47	0.30	0.43	0.43	0.47	0.13	0.43	0.67	0.77	0.70	0.50	0.80					
SELLE FRANÇAIS (SEF)	0.50	0.27	0.50	0.67	0.47	0.70	0.70	0.63	0.70	0.60	0.57	0.57	0.37	0.50	0.50	0.63	0.57	0.57				
SUFFOLK (SUF)	0.70	0.67	0.50	0.43	0.63	0.33	0.50	0.47	0.37	0.50	0.30	0.43	0.67	0.67	0.73	0.33	0.67	0.33	0.67			
TARPAN (TAR)	0.87	0.60	0.87	0.80	0.77	0.73	0.87	0.73	0.80	0.77	0.70	0.77	0.60	0.27	0.47	0.70	0.47	0.73	0.50	0.67		
PRZEWALSKI (PZW)	0.83	0.67	0.83	0.80	0.67	0.73	0.83	0.70	0.80	0.77	0.83	0.77	0.70	0.33	0.50	0.77	0.47	0.83	0.67	0.67	0.20	

RESULTS

Qualitative analysis

Using Fitch parsimony method (PAUP package), a dendrogram of the studied equine breeds was obtained. To give an evolutionary direction to the generated tree, two different criteria were employed:⁴⁰ the midpoint rooting criteria (Figure 1), and the outgroup method (Figure 2), using in this case the populations of Tarpan (*Equus gmelini*) and Przewalski's horse (*Equus przewalski*) as outgroup populations. Branch and internodal distances are proportional to the number of character-stage changes required. In both cases, the Fitch parsimony method needed 143 steps (total length of the tree) to rearrange the characters and to obtain the maximum parsimonious tree. The consistency index (a measure of the homoplasy) was 0.497.

Midpoint rooting (Figure 1) gives two large groups. One of them is formed of ten breeds: Andalusian, Barb, Criollo, Arab, Selle Francais, Merens, Exmoor, Pottock, Tarpan and Przewalski (Cluster A); it is possible in its turn to differentiate two subgroups: Cluster A1, which would correspond to the first four breeds, and Cluster A2, which would correspond to the six remaining breeds. The other large group includes twelve breeds: Ardennes, Breton Cerda, Breton Postier, Breton Gros, Comtois, Auxois,

Brabant, Clydesdale, Shire, Boulonnais, Percheron and Suffolk (Cluster B).

The same relationships are maintained when outgroup rooting was used (Figure 2). The breeds which are genetically closer to the outgroups are those from Clusters A2 and A1, in that order. Members of Cluster B, as indicated by the length branch (12 steps), seem to maintain a weak genetic relation with the two outgroup populations (Tarpan and Przewalski's horse). Figure 3 represents the consensus tree formed after one hundred bootstrap replicates; the values in the tree indicate the number of replicates from the bootstrap analysis (loosely, the width of the confidence interval).

Quantitative analysis

The values for the mean character differences (MCD) between horse breeds are shown in Table 3. The average MCD between breeds has a value of 0.57 (± 0.17 of STD), with extreme values of 0.13 between the Clydesdale-Shire pair, and of 0.87 for the Tarpan-Andalusian, Tarpan-Ardennes, Tarpan-Brabant, and Exmoor-Brabant pairs. The average distance between breeds (1) has a value of 4.10 (± 0.67 of STD), with extreme values of 2.00 between the Clydesdale-Shire pair, and 5.10 for the four pairs indicated above (TAR-AND; TAR-ARD; TAR-BRB; and EXM-BRB). The table corresponding to this genetic dis-

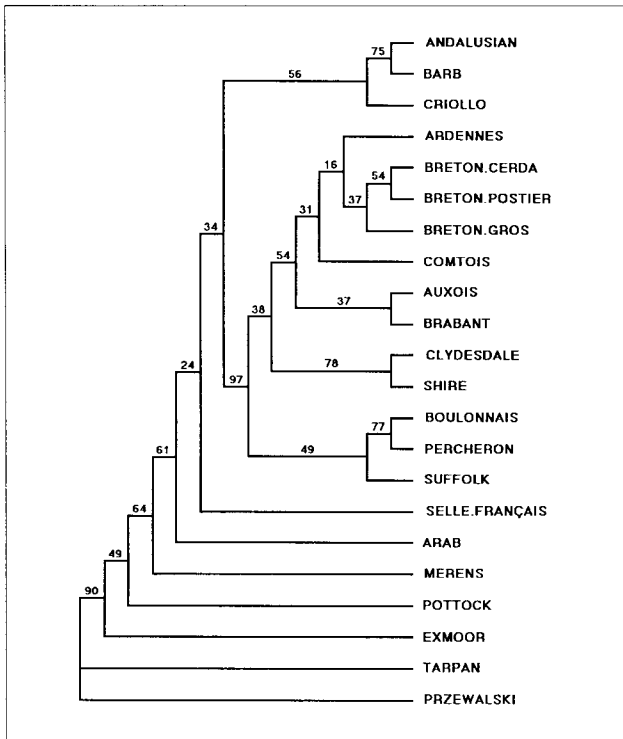


Figure 1. Qualitative analysis of morphological data (Table 2). Dendrogram produced by PAUP analysis, resulting from the application of Fitch parsimony method (Fitch, 1971). Branch and internodal distances are proportional to the number of character stage changes required. The tree was rooted at the midpoint.

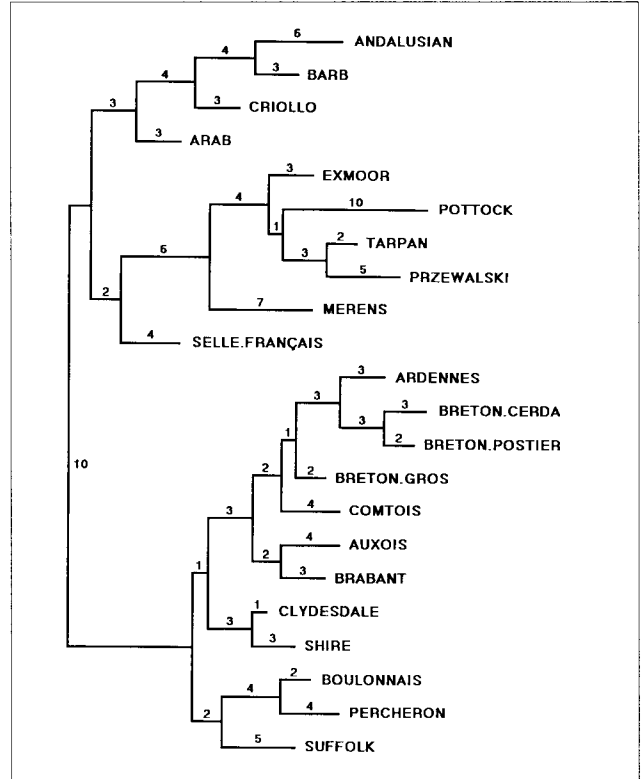


Figure 3. Consensus tree and bootstrap replicates by PAUP analysis.

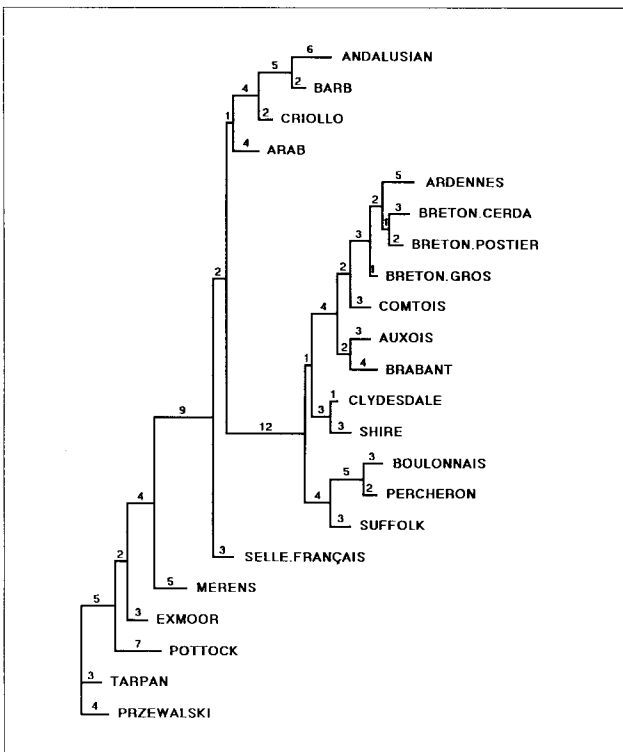


Figure 2. Dendrogram obtained by PAUP analysis, using qualitative data (Table 2). Rooted topology using Tarpan and Przewalski's horse as outgroups.

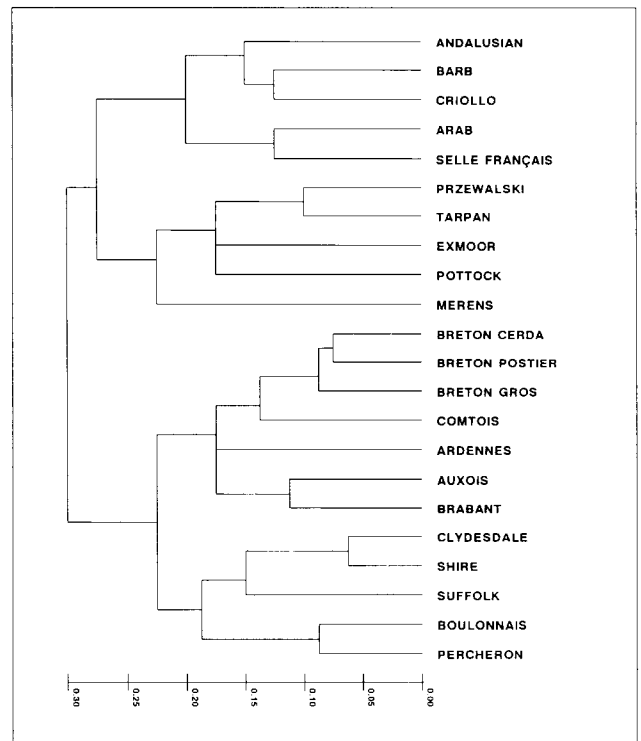


Figure 4. Quantitative analysis of morphological data (Table 3), by applying Fitch and Margoliash's method (1967), assuming contemporaneity of the populations (KITCH program in PHYLIP package). The scale represents patristic distance.

tance (1) has not been included, because the correlation coefficient between both morphological distances is high and very significant.²⁴

The tree obtained using the KITSCH program (PHYLIP package) is shown in Figure 4. The two large groups (Clusters A and B) previously described (PAUP package; Figures 1 and 2) appear again. In Cluster A, the Selle Francais breed changes its position in relation to the remaining breeds, passing from subgroup A2 to subgroup A1; maintaining a strong relation with the Arab breed. An unresolved trichotomy is presented between the Exmoor and Potttock breeds. In Cluster B the differentiation of populations into 2 subgroups is obvious: one is formed by Breton Cerda, Breton Postier, Breton Gros, Comtois, Ardennes, Auxois and Brabant breeds (Cluster B1), and the other is formed by Clydesdale, Shire, Suffolk, Boulonnais and Percheron breeds (Cluster B2). Similarly, an unresolved trichotomy is presented in the Ardennes population. The program examined 7730 possible trees; the figure shows the tree that best adjusts to the data matrix (Table 3). The sum of squares (SS) had a value of 7.582, and the average standard deviation percentage was 12.84%.

DISCUSSION

The average value of MCD between the horse breeds (0.5754 ± 0.1719), has a very similar magnitude to that obtained between other domestic animal species, for instance, in bovine,²² ovine,²¹ canine,²³ and caprine²⁴ the MCD have values of $0.5728 (\pm 0.1184)$, $0.5481 (\pm 0.1261)$, $0.5729 (\pm 0.1562)$ and $0.6615 (\pm 0.1042)$, respectively.

Our results, obtained from both the qualitative and the quantitative analyses, seem to support the existence of two large ancestral trunks. One would include all the breeds belonging to Cluster B, described above, which would correspond to the descendants of the *Equus stenonis*; the other trunk would include the breeds belonging to Cluster A, which could correspond to the descendants from the ancestral trunks *Equus gmelini* and *Equus przewalski*. The strong relationship, in all the dendrograms, between the Tarpan and Przewalski populations (MCD = 0.20; one of the lesser observed distances), allows us to support the hypothesis maintained by Sotillo and Serrano¹⁵ and by Groves,¹⁷ that the current Przewalski's horse (*Equus przewalski*) could descend from prehistorical crossings between original convex horses and the Tarpan (*Equus gmelini*). So, in general terms, we can venture that all the breeds included in Cluster A are descendants of the so-called Tarpanic Trunk.

Tarpanic Trunk

It has been commented that the ten breeds included in Cluster A could be the descendants of this ancestral trunk.

However, the comparison of the different dendrograms shows very stable and close relationships between some breeds. Concretely, the populations of Cluster A2 which correspond to light ponies, that is, Exmoor, Potttock and Merens, would be direct descendants of the *Equus gmelini*; they could have been introduced to Europe through Central and Northern Europe. Merens, which is also called Ariegeois, is the furthest population from the ancestral population Tarpan. This could be explained by the fact that this population (located in the Ariège area, in southern France), received the Moslem invasion influence and so it has an oriental genetic contribution.^{14,18,28}

The four breeds Andalusian, Barb, Criollo and Arab form Cluster A1, and are perfectly differentiated from the light pony group (Cluster A2). They could represent the South Oriental variant of the Tarpan; according to Sotillo and Serrano¹⁵ and Groves¹⁷ the Tarpan could have been introduced to Africa and Europe through Egypt and the Strait of Gibraltar (Spain). The Criollo breed descends precisely from Andalusian and Barb horses carried to South America by the Spanish conquistadors in the XVth century.⁴⁷ Furthermore, the Arab breed has made an important contribution to the formation of the present Criollo breed.^{18,36}

The only breed that is not perfectly ascribed to one of the two Clusters (A1 or A2) is the Selle Francais breed; but this is a special case, as it is a new breed, created recently (in 1950 the Stud Book of the Selle Francais breed was established). Draft breeds such as the Normand, and French Trotters, Anglo-Arabs and, especially, Arabs have participated in the formation of the breed. The large Arab influence is shown by the morphological similitude that both breeds manifest (MCD distance = 0.27); it is very clear in all the dendrograms, and especially under quantitative analysis, represented in Figure 4.

Solutrensis Trunk

If in the relations between breeds that configure the Tarpanic Trunk there exist some lacunas in relation to the assignment to *Equus gmelini* or to *Equus przewalski*, this is not the case with the breeds that form Cluster B. All these populations maintain strong relationships, and they form a very stable group (there is a great concordance between qualitative and quantitative analysis). They are the representative of the ancestral trunk *Equus stenonis*, as confirmed by the very high value (97%) of the bootstrap analysis (Figure 3).

All the dendrograms, but especially that of the Figure 4, which corresponds to the quantitative analysis of data, indicate that there is a strong relation between the French breeds Boulonnais and Percheron, and between the UK breeds Shire, Clydesdale and Suffolk. The three British breeds are, according to Weatherley,³¹ direct descendants of the "Black English Horse" (*Equus caballus britannicus*). The very high morphological (MCD distance = 0.13; the

smallest obtained distance) and behavior similitude between Clydesdale and Shire breeds, have caused the Clydesdale breed to be called the "Scottish Shire."⁴⁸

Finally, we must discuss the last seven breeds which form Cluster B1 of the Results chapter. Other breeds have contributed greatly in the formation and improvement of some of these breeds, especially those belonging to the *Equus stenonis* trunk and the Andalusian and Arab breeds.

Nevertheless, these dendrograms indicate that there is a great deal of similarity between the present-day populations of Auxois and Brabant, and between the three variants of the Breton (Breton Postier, Breton Gros and Breton Cerda).

According to Baudoin,²⁸ the Ardennes breed would be one of the most ancient breeds in France. The same author, and Bongianni¹⁸ too, postulate that it could be a very direct descendent of Solutre's horse. Nevertheless, in the 19th century, the Ardennes breed could have received an important influence from Brabant and Boulonnais.^{10,28} But according to Silver,¹⁴ the Ardennes contributed to the formation of the Auxois and Brabant breeds.

The Auxois received equally, in the 19th century, influences from other breeds such as the Boulonnais and the Percheron.²⁸ The Comtois, which originated in the Jura mountains (France), was introduced by the Burgundians in the 4th century, and could have been influenced by the Normand, Boulonnais, Percheron and Ardennes too, at the end of the 19th century.

The Breton horse has a very ancient origin; according to Baudoin,²⁸ it could be the Celtic horse. During the Crusades it was crossed with oriental breeds and until the 19th century it was massively crossed with Boulonnais, Percheron and Ardennes; this crossing originated the Breton Gros and the Breton Postier or Norfolk Breton, of a lighter constitution. The Breton Cerda (located in the Pyrenean area of Cerdanya, between Spain and France), originated through the crossing of local mares with Breton stallions.

According to the results obtained, we can affirm that the generated information from the morphological analysis by Numerical Taxonomy methods is a powerful tool for research on the genetic relations of horses. In some cases, they can support or reject some of the hypotheses maintained by other authors, hypotheses that are postulated from other information sources (historical, archaeological...). Nevertheless, we must point out that the dendrograms obtained in this study attempt to show only the degree of relationship and morphological similarity between current horse breeds, which may or may not be indicators of the true evolutionary history of the populations. We ought to consider that the morphological characters have been subjected, for a long time, to artificial selection, and the fact that there has been genic migration between some of these populations.

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