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EUROPEAN WILD BOAR PUREBRED AND *SUS SCROFA* INTERCROSSES. DISCRIMINATION PROPOSALS. A REVIEW

EL JABALI EUROPEO PURO Y MESTIZOS DE *SUS SCROFA*. PROPUESTAS DE DISCRIMINACION. UNA REVISION

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ABSTRACT

This paper reviews the literature about differentiation between European wild boars, pigs (feral and domestic) and their crosses. In the past, cranial and external body measurements, coat coloration patterns and hair measurements were used with limited success, as a differentiating method. Later, the differential chromosomal number offered better possibilities of discrimination, where 2n36 is the diploid number of wild boars from central Europe, while domestic pigs and wild boars from East Asia exhibit 2n38. The odd number corresponds to crosses or crossbreeds. In recent years, Polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) techniques have been developed to assess specific genes on DNA (nuclear & mtDNA), such as MC1R*1, TYR*2, GPIP*4 and mitochondrial cytB variants, in order to understand the relationship between wild boars and domestic pigs and for genetic traceability in byproducts. Some of these methods allow clear differentiation between wild boar and pig but they are not conclusive when analyzing crosses, especially on F2 wild boar x domestic pig. Some of the tests are feasible in live animals (e.g. karyotype), on death animals (skull) or in both (e.g. genomic analysis) or in foods. We conclude that discrimination between wild boar and pig offers no difficulties; nevertheless the differentiation of crosses or hybrids is currently complex and requires a sequence of tests for discrimination.

Keywords: Karyotype, phenotype, genomic analysis, hybrids.

RESUMEN

Este trabajo analiza las publicaciones disponibles a la fecha relativas a la diferenciación entre jabalí europeo, cerdo (doméstico y asilvestrado) y sus cruzas. En el pasado, las medidas craneales y corporales, patrones de coloración de la capa y características del pelo fueron utilizados con limitado éxito como métodos diferenciadores. Posteriormente, el número de cromosomas ofreció posibilidades de discriminación, siendo 2n36 el número cromosomal del jabalí de Europa central, mientras que los cerdos domésticos y jabalíes de Asia oriental poseen 2n38. El número impar (2n 37) corresponde a las cruzas entre ambos. En los últimos años, el desarrollo de las técnicas de amplificación en cadena de la polimerasa (PCR) acopladas a restricción enzimática (PCR/RFLP) han permitido analizar genes específicos del ADN (nuclear y mitocondrial), como MC1R*1, TYR*2, GPIP*4 y variantes mitocondriales (cytB), con la finalidad de entender la relación genética entre jabalí y cerdo doméstico y para la trazabilidad de sus subproductos. Algunas de las

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pruebas permiten diferenciar claramente entre jabalí y cerdo, pero no son concluyentes al analizar sus cruzas, en particular la segunda generación (F2) de híbridos entre cerdo doméstico y jabalí. Algunas de estas pruebas son factibles de aplicar en animales vivos (cariotipo), otras sólo en cadáveres (morfometría de cráneo) o en ambos (análisis genómico) e incluso en alimentos. Finalmente, concluimos que la diferenciación entre jabalí y cerdo no ofrece grandes dificultades, sin embargo, lograr una correcta discriminación entre cruzas o híbridos de ambos es actualmente complejo, siendo necesario seguir una secuencia de pruebas discriminatorias.

Palabras claves: Cariotipo, fenotipo, análisis genómico, híbridos.

1. INTRODUCTION

Sus scrofa (Linnaeus, 1758) order Artiodactyla, can exist as populations of wild boar, feral pigs or domestic pigs, or as hybrid combinations. These animals are referred to as wild boar, wild hogs, wild swine, feral pigs, wild pigs or razorbacks.

The term European wild boar or simply "wild boar", describes animals living in central Europe (*Sus scrofa scrofa*); the rest correspond to an uncertain number subspecies, which sum 24 for Briedermann (1986), 23 for Mayer and Brisbin (1991), and only four for Genov (1999).

Wild boars naturally occur from Western Europe to the northern coast of Africa, eastwards to Japan, and south to Sri Lanka, Sumatra, Malasya and Indonesia (Long, 2003). Formerly found in southern Scandinavia and Great Britain, at present they have reintroduced in both (Lemel *et al.*, 2003; Wilson, 2005). They also occur in Sardinia and Corsica (Briedermann, 1986). They have been widely translocated in Europe (Genov, 1999) and have significantly increased in numbers across Europe in recent decades (Sáez-Royuela & Tellería, 1986).

Wild boar or feral pigs have been introduced by humans in Norway, Sweden, South Africa, Sudan, the USA, the West Indies, Central and South América, Egypt, Australia, New Zealand, New Guinea and numerous oceanic (Randi, 2005) islands including Fiji, Mauritius, and many Indonesian, Hawaiian and Galápagos islands. As a general rule: wild boar populations live in Europe, Russia, North Africa and Asia; feral pigs (escaped domestics) live in Australia and New Zealand; feral pigs and wild boar/feral pig intercrosses live in the Americas (Lever, 1985; Long, 2003; Randi, 2005; Wilson, 2005).

The taxonomy of the different sub-species is difficult due to interbreeding, breeding between wild and domestic pig stock (Genov, 1999) and the proper phenotypic plasticity of the species in response to environmental factors (Berg, 2006). Recently, Wilson (2005) concluded that all European boars belong to one sub-species *Sus scrofa scrofa*. The wild boar can freely inter-breed with domestic pigs (*Sus scrofa domestica*), and thus animals with a general appearance of wild boar could be pure wild boar, feral pigs, or intercrosses (Wilson, 2005). Genomic analysis, using meat and hair as samples, principally through PCR-RFLP (Johansson *et al.*, 1992; Kijas *et al.*, 1998; Koh *et al.*, 1998; Carrión, 2003; Alderson & Plastow, 2004; Butschke, 2004; Fajardo *et al.*, 2007; and others) was predicted to solve the systematic problem, but unfortunately results were not as good as expected.

In many European and American countries, wild boar farms have been established specifically for its production (Salgheti, 1998; Pinet, 2002; CRAAQ, 2003; Gongora *et al.*, 2003; Miranda & Lui, 2003; Vieites *et al.*, 2003; Skewes & Morales, 2006). Some farmers cross pure wild boar males with domestic pig sows to increase sow productivity and daily gain of piglets (Góngora *et al.*, 2003) or to get less aggressive animals (Malmheden *et al.*, 2002). Wild boar meat attracts a premium price and some meat sold as wild boar does not originate from genuine wild boar, and may actually be derived from these crosses between wild boar and domestic pigs since pure wild boar and crossbreed phenotypes are similar (Góngora *et al.*, 2003; Skewes & Morales, 2006). Often, experimental animals are captured in the wild, assuming they are pure but may contain varying amounts of domestic pig genes in their bloodline that may affect the results (Randi, 2005). In fact, Fang *et al.* (2006) and Scandura *et al.* (2008) presumed gene flow of domestic pigs into the wild boar population in Europe.

This paper reviews the knowledge about traits that allows a differentiation between European wild boar, intercrosses and domestic pig. Some of the tests are only feasible in live animals (e.g. karyotype), on death animals (skull) or in both (e.g. genomic analysis). We also presented analyses that discriminate between pig and wild boar but in foods.

2. MORPHOLOGY

2.1. Skull

Skull characteristics, especially size and shape of the cranial bones, have long been recognized by taxonomists as one of the best means to classify verte-

brates. Subspecies of *S. scrofa* differ in the concavity of the cranium profile for males. The combination of the shapes of the lacrimal bone and the rear end of the *palatum durum* can be used as diagnostic criteria (Genov, 1999).

Mayer & Brisbin (1991) separate known groups of pure European wild boar, pure feral hogs, hybrids, and domestic swine with a high degree of resolution, using seven cranial measurements in adult males. Genov (1999) using seven diagnostic characters combined in *Sus scrofa* populations and subspecies to form four groups on both levels: group one (North Africa, Europe and West Asia), group two (Middle Asia), group three (Central and South Asia) and group four (the indo-Malaysia Archipelago), which generate some controversy among authors (Briedermann, 1986; Mayer & Brisbin, 1991; Genov, 1999) and is only applicable to death animals.

2.2. Phenotype

In comparison with domestic pigs, wild boars show striking phenotypic differences for many traits including coat color, canine development and body conformation.

The shape and appearance of the animals are mentioned by Wild Boar breeders of France (Pinet 2002) Canadá (Nixdorf & Barber, 2001) and Britain (Goulding, 2003) as criterion for purity, summarized as follows: Head is narrow with a straight profile; Muzzle is always black; Coat color is usually dark brown to black or grey; Tail is straight with long tassels at the end; Body weight lies forward; Coat color is brindled and an underlying brown pelage is present; Snout is narrow straight and long; Ears are pointed and held erect; Hind quarters are sloped and the shoulders (in males) are large; Piglets have brown and cream stripes.

Henry (1969) reported for a wild swine population in USA, three characteristics as being indicative of at least partial wild boar ancestry: Striped pattern in the juvenile pelage; Split tips on the bristles, and a diploid chromosome number of 36. Later Marchinton *et al.* (1974) and Mayer & Brisbin (1991) stated that these characteristics were either incorrect or inaccurate.

Brisbin *et al.* (1977) compared linear external body measurements from adult specimens of known ancestry i.e., pure Eurasian wild boar, pure feral hogs or hybrids. The body measurements and weights were inconclusive to be useful in these comparisons. In body measurements, however, domestic swine were overall the largest except in snout length. Feral hogs were the most variable and the largest in most parameters of the wild forms. In general, captive wild pigs were larger than their wild-living counterparts.

In summary, the phenotype is a good tool for initial discrimination when divergence is manifest but dependent on the experience of the observer.

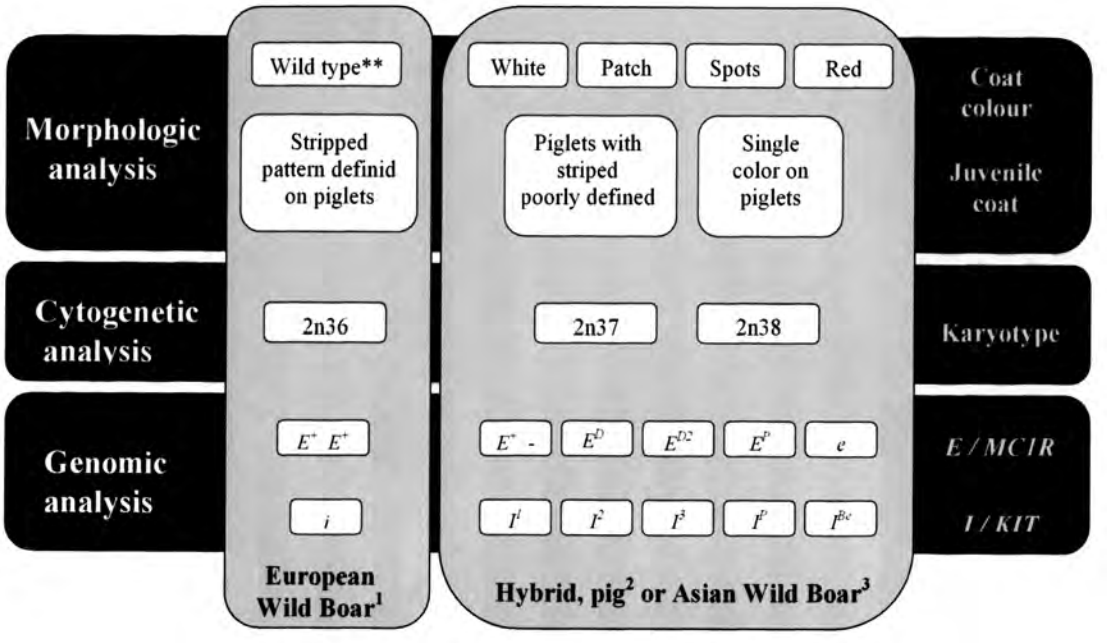

Figure 1. Recommended step by step methodology for testing purity in European wild boar.

** : Smoke gray to dark brown, in almost all a cases, it is lighter than the base color of the overlying brisles
[1]: *Sus scrofa scrofa*
[2]: *Sus scrofa domestica*
[3]: *Sus scrofa ussuricus, Sus scrofa cristatus, Sus scrofa vittatus, Sus scrofa taivanus*

2.3. Coat & Underfur

Brisbin *et al.* (1977) described differences in coat coloration and hair morphology as useful for separating wild boar and hybrids from feral hogs and domestic feral hogs in USA. Curly, wool-like underfur can be found in any of the three types of wild swine (Mayer & Brisbin, 1991). In wild boar, the underfur is variable in color, ranging from smoke gray to dark brown; in almost all cases, it is lighter than the base color of the overlying bristles. Feral hogs have underfur that is the color of the bristles found in the same area of the pelage. The underfur in hybrids varies from white/smoke gray to black, and can be the same or different in color from the overlying bristles (Mayer & Brisbin, 1991).

Wild boars are usually dark in color but can vary from pale grey-buff through red-brown to black (MacDonal & Frädrich, 1991). The piglets at birth have a red-brown coat, with longitudinal stripes, which they molt to uniform red-brown at four to five months of age then to the adult coat at about ten to 12 months (Rossel *et al.*, 2001; Wilson, 2005). In comparison with domestic piglets, neonatal wild piglets have greater average pelage weight density and pelage population density, both traits directly related to pelage insulation. Furthermore, wild piglet's hair shafts have a larger medulla and contained more medullar vacuolation: relative medulla size and vacuolation are directly related to pelage insulation by decreasing hair-shaft conductivity (Hansen *et al.*, 1972).

In general, indicators of hybridization with domestic pig are: white areas on body, spots saddles or other splotches of colors in the coat, light colored hooves, straight upper body line, young with only faint stripes and dished nose (Goulding, 2007).

In summary, crosses (wild boar x domestic sow) show intermediate traits (Hansen *et al.*, 1972). Lachrymal and palatum bones can be used as diagnostic criteria in the skull; some colors or patches in the coat reveals hybridism; and since crosses and wild boars can display similar phenotypes, we did not recommend using this feature as a unique tool for differentiation, but rather as an initial discriminatory method.

3. CYTOLOGICAL DIFFERENCE

3.1. Karyotype

In general, two different karyotypes (2n36 and 2n38) take place in native wild boar populations. Wild boars in Western Europe (European wild boar) have a 2n36, whereas most wild boars from East Europe and Asia, as well as all domestic pigs, have 2n38 (Table 1).

Nevertheless, there is controversy respect the real number of chromosomes in European wild boar since some authors indicate as normal a diploid number of 37 and 38 chromosomes. The confusion –in our opinion– arises with results of Bosma (1976) who first found intrapopulation polymorphism in wild boars, detecting animals with 2n36, 37 and 38 chromosomes. Later Bosma *et al.* (1983) concluded that the basic chromosome number in *Sus* is

Table 1. Diploid chromosome number of *Sus Scrofa* worldwide.

Region	Locality	Species	n	2n Chromosome number	Condition of sampled animals	Reference
IN NATIVE RANGE						
Europe		*S.scrofa domestica*	44	38	Farm	Tikhonov & Troshina 1975
Central Europe	Germany	*S. scrofa scrofa*	4 (2 ♂♂, 2 ♀♀)	36	Wild	Gropp *et al.*,1969
	Poland	*S. scrofa scrofa*	1 (♂) 3 (1 ♂, 2 ♀♀) 1 (♂)	36 37 38	Wild	Rejduch *et al.*, 2003
	Yugoslavia	*Sus Scrofa*	9	38	Wild	Zivkovic *et al.*, 1971
West Europe	Netherlands	*S. scrofa scrofa*	11 (6 ♂♂, 5 ♀♀) 3 (1 ♂, 2 ♀♀) 1 (♂)	36 37 38	Wild	Bosma, 1976
	Italy (Piedmont's): Areas montainous	*S. scrofa*	6 (4 ♂♂, 2 ♀♀)	36	Wild	Macchi *et al.*, 1995
	Flat areas	*S. scrofa* *S. scrofa* *S. scrofa*	2 (♂♂) 2 (♀♀) 2 (1 ♂, 1 ♀)	36 37 38		

(continuaciòn Table 1)

Europe	France; Continental French	*S.scrofa scrofa*	28 6 1	36 36 38	Wild Farm Farm	Popescu *et al.*,1980
	Corsica	*S. scrofa*	24	38	Wild	
	France	*S. scrofa scrofa*	22	36	Wild	Fang *et al.*,2006
	Spain	*S. scrofa scrofa*	8 (1 ♂, 7 ♀♀) 3 (2 ♂♂, 1 ♀) 1 (♂)	36 37 38	Wild	Arroyo *et al.*, 1990
East Europe	Turkey	*Sus scrofa*	4 (3 ♂♂, 1 ♀♀)	38	Wild	Albayrak & Inci 2006
	Lituania, Byelorussia, Rusia	*S. scrofa ferus* *S. scrofa ferus*	15	37 38	Wild	Tikhonov & Troshina 1975
	Far East and Amur region of U.S.S.R.	*S. scrofa ussuricus*	20	37 38	Wild	Tikhonov & Troshina 1975
West Asia	Thailand	*S. Scrofa jubatus*	4 (2 ♂♂, 2 ♀♀)	38	Zoo	Tanomtong *et al.*, 2007
Central Asia	Azerbaijan	*S. scrofa attila* *S. scrofa attila*	8	36	Wild	Tikhonov & Troshina 1975
	Kirghizia	*S. scrofa nigripes* *S. scrofa nigripes*	37	36	Wild	Tikhonov & Troshina 1975
East Asia	China	*Sus scrofa*	6	38	Wild	Fang *et al.*,2006
North América	USA (Tennessee)	*S. scrofa scrofa*	26 - 10	36 - 37	Wild	McFee *et al.*,1966
		Sus scrofa *Sus scrofa (hibrid)* *S.scrofa domestica*	34 (13 ♂♂, 21 ♀♀) 58 (31 ♂♂, 27 ♀♀) 16 (9 ♂♂, 7 ♀♀)	36 37 38	Wild	Rary *et al.*, 1968
AS INTRODUCED OR EXOTIC SPECIES						
South America	Chile	*Sus Scrofa*	20 (11 ♂♂, 9 ♀♀)	36-37-38	Farm	Sandoval, 2002
	Chile	*Sus Scrofa*	200	36-37-38	Farm	Skewes unpublished
	Chile	*Sus Scrofa*	11	36	Wild	Skewes unpublished
	Brazil	*S. scrofa scrofa* *S. scrofa* (hibrid) *S. scrofa* (hibrid)	593 400 144	36 37 38	Farm	Lui, 2000
	Brazil	*S. scrofa scrofa* *S. scrofa* (hibrid) *S. scrofa* (hibrid) *S. scrofa domestica*	615 517 176	36 37 38 38	Farm	Miranda & Lui, 2003

2n38 rather than 36. Soon after, polymorphism e.g. animals with 2n36, 37 and 38 chromosomes were reported by Arroyo *et al.* (1990) from animals of Spain, Machi *et al.* (1995) from Italy, Rejduch *et al.* (2003) from Poland. However, the presence of individuals with 2n37 and 38 present a greater probability of being the result of some domestic breeding in the wild herd, a fact which is described by the same authors. Bosma (1976) sampled in the Netherlands 15 animals from a herd that has been kept well isolated in a forest reserve during about 30 years, which no longer represents the status of a free ranging population. Arroyo *et al.* (1990) are not sure if the numerical polymorphism observed in Spanish wild boars is due to a recent translocation or to interbreeding of domestic pig and wild boar. Finally, the results of Redjuch *et al.* (2003) in Poland give account of the analysis of a single litter and not a population.

A distinct argument for supporting that 2n36 as characteristic of wild boars is that karyotype 2n36 or 37 are absent among breeds or populations of domestic pigs. Diploid chromosome number 2n37 is only possible due to crosses with wild boars. Large numbers of analyzed F2 crosses (wild boar x pig) show hat they exhibit intermediate traits (Johansson et al., 1992; Weiler *et al.*, 1995; Mariani *et al.*, 1996; Andersson-Eklund *et al.*, 1996; Knorr *et al.*, 1997; Andersson-Eklund *et al.*, 1998; Knott *et al.*, 1998; Weiler *et al.*, 1998; Müller *et al.*, 2002). The crosses 2n37 and 38 have comparable performance to pigs in live weight gain while 2n36 has performance more similar to wild boar (Skewes *et al.*, 2008). The fact that it is also possible to obtain animals with 2n36 from crossbred 2n37 x 2n37 and 2n37 x 2n36 (Rary, *et al.*, 1968) implies that the 2n36 criterion has to be used associated to population level, e.g. parents also have to be 2n36 or the entire population has to be 2n36 (Santos, 2002).

Recently, Scandura *et al.* (2008) found free-ran-

Table 2. Expected ratios of F1 animals with different diploid chromosome numbers from the six mating combinations of *Sus scrofa* that posses a diploid chromosome number of either 36, 37 or 38 (from Rary *et al.*, 1968).

	Diploid chromosome number		
Cross	36	37	38
36 x 36	1	-	-
36 x 37	1	1	-
36 x 38	-	1	-
37 x 37	1	2	1
37 x 38	-	1	1
38 x 38	-	-	1

ging wild boar specimens in Southern Italy with Asian pig mtDNA, usually described in some ameliorated European breeds crossbred with Asian pigs. This and the results from Fang *et al.* (2006) also support the view that some levels of hybridization between wild boars and domestic pigs occurred in the past and possibly still occur today (Scandura *et al.*, 2008). Clearly a wider sampling of European populations is necessary to elucidate the exact border between wild boar populations with different karyotypes and to determine the extent of the hybridization.

Outside their native range, wild *Sus scrofa* populations exhibit variation in chromosome number as in USA (McFee *et al.*, 1966; Rary *et al.*, 1968) or in farmed animals in Brazil (Lui, 2000; Miranda & Lui 2003; Giménez *et al.*, 2003) and in Chile (Skewes & Morales, 2006). In Brazil, from a total number of 1137 animal analyzed, 52% exhibit 2n36, 35% 2n37 and 13% 2n38 (Lui, 2000). Skewes & Morales (2006) reported that 13% of the breeders in Chile have boars certified as 2n36 animals. To explain this polymorphism, the authors assume that some domestic breeding has gained access to the wild stock or that some farmers cross wild boar with domestic pig to increase sow productivity and daily gain of piglets. In France, Darré *et al.* (1992) analyzed 2550 animals from wild boar farms and found only a mean ratio of 28% of animals with 2n36 (range from 0-85%).

Thus, the standard karyotype for the Western European wild boar is 2n36 (Hsu & Benirschke, 1967; Gustavsson *et al.*, 1973; Tikhonov & Troshina, 1974; Sysa, 1980; Darré *et al.*, 1992; Chowdhary 1998; Berg, 2006; Fang *et al.*, 2006), which is due to a centric fusion of chromosomes 15 and 17 (Tikhonov & Troshina, 1975; Sysa, 1980; Miranda & Lui, 2000; Fang *et al.*, 2006), 16 and 17 (Gustavsson, 1973) or homozygotic for the Robertsonian translocation 15 - 18 (Popescu *et al.*, 1980; Macchi *et al.*, 1995).

Table 3. Types and frequencies of Melanocortin Receptor 1 (MC1R) extension gene, described for *Sus scrofa.*

Locality	n	Type of animals	Coat colour	Extension genotipe	Frequencies MC1R genotype 1/1	1/3	1/6	1/7	2/2	2/4	3/3	3/4	3/6	3/7	4/3	4/4	4/6	6/6	6/7	7/7	References
Sweden	3	Wild boar	Wild type	E^{+}	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Kijas *et al.*,1998
	2	Large Black	Black	E^{D1}	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	
	9	Meishan	Black	E^{D1}	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	
	23	Large White	White	E^{p}	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	
	10	Pietrain	White and black spots	E^{p}	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	
	16	Hampshire	Black and white belt	E^{D2}	-	-	-	-	-	-	13	3	-	-	-	-	-	-	-	-	
	24	Duroc	Red	e	-	-	-	-	-	-	-	-	-	-	24	-	-	-	-	-	
Finland	20	Not typical Wild Boar.	—	—	19	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Góngora *et al.*, 2003
	21	Typical Wild Boar			20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Spain	31	Wild boar	Wild type	E^{+}	25	2	1	3	-	-	-	-	-	-	-	-	-	-	-	-	Fernández, 2003
	31		Black	E^{D1}	-	-	-	-	-	-	31	-	-	-	-	-	-	-	-	-	
	109	Iberican breed	Red	E^{D1}	-	-	-	-	-	-	-	-	-	2	6	-	-	48	45	8	
	15		Torbiscal	E^{p}	-	-	-	-	-	-	-	-	-	-	-	-	-	9	3	-	
	79		Entrepelado	E^{p}	-	-	-	-	-	-	-	-	1	-	-	-	-	9	3	-	
	14	Spotted of Jabugo	Spotted	E^{D2}	-	-	-	-	-	-	--	-	-	11	-	-	-	30	25	13	
	104	Duroc	Red	e	-	-	-	-	-	-	-	-	-	1	-	-	2	11	-	-	
					-	-	-	-	-	-	-	-	-	-	-	104	-	-	-	-	
UK	300	Wild boar	Brown	E^{+3}	—																Carrión *et al.*, 2003
		Meishan/large Black	Black	E^{D1}																	
		Hampshire	Black	E^{D2}																	
		Pietrain/LW/LR/																			
		Berkshire/Tamworth	Red and/or Black spots	E^{p}																	
		Duroc	Red	E																	
		Iberian	Red	e^{b}																	
Germany	9	Wild boar	Wild type	E^{+}	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Skewes & Rodríguez unpublished
Chile	11	Wild boar		E^{+}	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Skewes & Rodríguez unpublished
		Domestic pig			-	-	-	-	-	7	-	4	-	-	-	-	-	-	-	-	

The karyotype of wild boars from Eastern, Central Europe and from Asia has 2n38 chromosomes (Grop *et al.*, 1969; Zivkovic *et al.*1971; Gustavsson *et al.*, 1973; Tikhonov & Troshina, 1975; Popescu *et al.*, 1980; Fang *et al.*, 2006; Albayrak & Inci, 2007), identical to that of domestic pig (Bosma, 1976; Chowdhary, 1998; Rosell *et al.*, 2001; Berg, 2006). Its consists of 12 metacentric, submetacentric, subacrocentric and/or submetacentric chromosomal pairs, 6 acrocentric pairs (Muramoto *et al.*, 1965; Hsu & Benirschke, 1967; Zivkovic *et al.*, 1971; Popescu *et al.*, 1980; Macchi *et al.*, 1995; Redjuch *et al.*, 2003; Albayrac & Inci, 2007), and 2 gonosomes (submetacentric X-chromosome and a small metacentric Y).

Animals with karyotype 2n37 present a Robertsonian translocation between chromosome 15 and 18, which gives a submetacentric chromosome, according to Popescu *et al.* (1980), 15 and 17 (Bosma, 1976), or 16 and 17 (Gustavsson *et al.*, 1973; Tikhonov & Troshina, 1974).

Sus scrofa with a chromosome number of either 36, 37 or 38 are reproducibly viable and can originate six 2n chromosome combination possibilities (see Table 2) depending on the progenitors' karyotype (Rary *et al.*, 1968; Mauget, 1980; Sysa *et al.*, 1984; Tanchev & Katsarov, 1993; Miranda & Lui, 2003).

The phylogenetic tree analysis by Fang *et al.*. (2006) showed that all five haplotypes found in European wild boars with a confirmed 2n36 karyotype and that four out of five haplotypes from wild boars with a presumed 2n36 karyotype belonged to one cluster and were identical or closely related to those found in European domestic pigs with 2n38. Neither the exact border between wild boar populations with different karyotypes nor the extent to which hybridization occurs between populations has been studied in any detail (Fang *et al.*, 2006).

In brief, the karyotype is appropriate for segregating crosses with phenotypes of wild boar which exhibit diploid chromosome numbers of 37 and 38. Animals with 2n36 karyotype are not necessarily pure as long as this diploid number covers the entire population or many generations.

4. GENOMIC ANALYSIS

4.1. Melanocortin receptor 1 (MC1R) and KIT genotipe

MC1R and KIT are the most important genes in pig coat colors genetics, they play an important role in regulation of melanin, eumelanin (black/brown) and phaeomelanin (yellow/red) (Kijas *et al.*, 1998; Pielberg *et al.*, 2002). The molecular genetics research has focused on the I locus (known as the KIT gene) and E locus (known as the MC1R locus, melanocortin receptor 1) with the intent of determining the nucleotide sequence and function of alleles at the I and E loci.

The mutations in KIT encoding the mast/stem cell growth factor receptor (MGF) are responsible for coat color variation in domestic pigs (Johansson Moller *et al.*, 1996; Marklund *et al.*, 1998; Giuffra *et al.*, 1999; Pielberg *et al.*, 2002), and MC1R is a G-protein-coupled receptor involved in physiological variations in hair and skin color and is encoded by the Extension (E) coat color locus, and Agouti (A) loci (Kijas *et al.*, 1998; Fernández, 2003; Fajardo *et al.*, 2007).

Table 4. Type of animal and corresponding allele, duplication, splice and intron haplotype of KIT gene described for *Sus scrofa.*

Locality	n	Type of animals	Allele	Polimorphism Duplication	Splice variant	Intron haplotype	References
Sweden	2	Wild boar	I	-	-	-	Giuffra *et al.*, 2002
	3	Meishan	I	-			
	7	Berkshire	I	-			
	4	Duroc	I	-			
	4	Hampshire	I^{Be}	-			
	1	Linderöd	I	-			
	5	Pietrain	I	+			
	11	Large White	I^{r}	+			
	4	Landrace	I^{r}	+			
UK	300	Meishan, Large Black	i	-	-	1	Carrión *et al.*, 2003
		Berkshire (Japan)	i	-	-	1, 2, 3	
		Duroc, Tamworth	i	-	-	4	
		Hampshire	IBe (Belt)	-	-	4	
			Iro (Roan)	-	-	Not known	
			Ip (Patch)	+	-	4	
		Pietrain	I (Dominant white)	+	+	4	
		Landrace, Large White					
UK Europe Japan US	-	Meishan, Large Black	i	-	-	1	Alderson & Plastow, 2004
		Berkshire (Japan)	i	-	-	1, 2, 3	
		Duroc, Tamworth	i	-	-	4	
		Hampshire	IBe (Belt)	-	-	4	
		Pietrain	Ip (Patch)	+	-	4	
		Landrace, Large White	I (Dominant white)	+	+	4	

Currently, the KIT and MC1R DNA diagnostic tests have been used to identify six main alleles at the KIT locus (I1, I2, I3, IP, IBe and i) (Pielberg *et al.*, 2002), a possible IRo (Carrion *et al.*, 2003) also called Id (Fernández, 2003). In Large White founders there is a locus for dominant white color which is transmitted the dominant white allele (I) or the semidominant patch allele (IP), whereas the wild boar founders transmitted the recessive allele (i) for color (Mariani *et al.*, 1996). However, this locus determined the three types of colored phenotypes (i / i) observed by Mariani *et al.* (1996) and Maklund *et al.* (1998): wild colored, white with black spots, and red with black spots. These phenotypes should reflect segregation at the extension (E) at locus MC1R (Ollivier & Sellier, 1982).

Six alleles have been identified at the MC1R locus (MC1R*1/E+, MC1R*2/ED1, MC1R*3/ED2 or EP, MC1R*4/e, MC1R*5/E+, MC1R*6/EP) (Kijas *et al.*, 1998; Giuffra, 2000; Kijas *et al.*, 2001; Carrion *et al.*, 2003; Alderson & Plastow, 2004) and the seventh to ninth were mentioned only in Fernández (2003) (Tables 3 and 4). A fragment of 795 bp on the MC1R and subsequent RFLP allowed selection of BspHI and BstUI endonucleases to carry out intraspecific *Sus scrofa* differentiation (Fajardo *et al.*, 2007). These consisted of three RFLPs as well as a small insertion at the 5′ end of the coding sequence (Kijas *et al.*, 1998, Kijas *et al.*, 2001). They correspond to five alleles found in the populations tested: E+, ED1, ED2, EP and e (Alderson & Plastow, 2004). Where ED is for dominant black (Fernández, 2003), E for uniform black, dominant to EP for black spotting, and recessive e for uniform red, establishing the dominance order ED / E / EP / e (Fernández, 2003).

Wild boar specimens possess a unique MC1R receptor variant necessary for the expression of the wild-type coat color. The wild-type coat color (E+/E+) of the European Wild Boar was linked with an MC1R variant (MC1R*1) and Japanese Wild Boar (MC1R*5), which is rare or absent among the major breeds of domestic pig (Kijas *et al.*, 1998; Kijas *et al.*, 2001). However, there are intercrosses, homozygous for the wild-type coat color (E+/E+) but 2n37 chromosome (Skewes, O., unpublished data) as well as body measurements characteristic of hybrids (Marklund *et al.*, 1998) a situation that needs more attention. Fajardo *et al.* (2007) concluded that MC1R is good discriminating between pig, wild boar including crosses in meat, which in our opinion is not entirely correct. In fact, Marklund *et al.* (1998) obtained F2 crossbred (Wild boar x Large White) homocigotes for E+ with white coat and some black patches, which clearly does not correspond to wild boar phenotype (Table 5). We consider more reliable the proposal of Carrión (2003) who suggested that wild boars have to present homocigosis for genes MC1R (E+/E+) and for KIT (i/i) (Mariani *et al.*, 1996; Marklund *et al.*, 1998).

Table 5. Coat Color Phenotypes in the F2 generation of a Wild Boar/Large White Intercross according to the genotypes at the dominant white (I/KIT) and extension (E/MC1R) loci (after Marklund *et al.* 1998).

I/KIT	*E/MC1R*		
	E^+/E^+	E^+/E^p	E^p/E^p
I/ I	White	White	White
I/ IP	White	White	White
I/ i	W/S (7/ 15)[a]	W/S (11/ 20)[a]	W/S (2/ 12)[a]
IP/ i	Patch	Patch	———[b]
i/ i	Wild type	Wild type	Black spots[c]

[a] (W/S) White but the proportion indicated showed pigmented skin spots with white hair or intermingled black and colored hair (roaning).
[b] This phenotype could not be judged, as no good quality slides were available for the few animals with this genotype.
[c] These pigs are white with black spots or red with black spots

4.2. Tyrosinase (TYR) and glucosephosphate isomerase pseudogene (GPIP)

These genes are biparentally inherited and also have been used to analyze European and Asian domestic pigs and wild boar. Like the MC1R analysis, TYR are coding sequences, but the GPIP pseudo-gene was included as a noncoding nuclear sequence (Giuffra *et al.*, 2000).

TYR encodes the tyrosinase enzyme, which has a key role in pigment synthesis. Loss-of-function mutations in this gene cause albinism in many species. GPIP is noticeably a pseudo-gene since it contains several potentially inactivating mutations (Harbitz *et al.*, 1993). Giuffra *et al.* (2000) sequenced the main part of exon 1 (727 bp) from two animals of each of the following: European and Japanese wild boars as well as several domestic breeds. Two alleles differing by four synonymous substitutions were found. There were no predetermined differences between continents but TYR*1 occurred predominantly in Japanese wild boars and Meishan domestic pigs, while TYR*2 was most common in European wild boars and domestic pigs.

GPIP*1 is found only in Asian wild boar. GPIP*3 is highly frequent in Asian domestic pigs and Ohmini miniature pigs, but less frequent in European Wild Boars and at low to intermediate frequencies respectively in both types of European Domestic Pigs (Giuffra *et al.*, 2000). GPIP*4 and GPIP*4a are reported in high and low frequencies in European Wild Boar and European Domestic Pig, respectively (Giuffra *et al.*, 2000; Ishiguro *et al.*, 2002). Ishiguro *et al.* (2002) found that some Japanese Wild Boar had GPIP*3/GPIP*4 and GPIP*4/GPIP*4 genotypes (Table 6).

In summary, both (genes and pseudogenes) have an important role in the synthesis of pigments in the skin and hair of pigs and wild boar, however, neither of these can be used as a discriminator.

Table 6. Allele frequencies at the Tyrosinase (TYR) and Glucosephosphate isomerase pseudogene (GPIP) loci described for *Sus scrofa.*

Region	n	Type of animals and origin	TYR		GPI P						Types of samples	References
			* 1	* 2	* 1	*2	*3	*3a	*4	*4a		
Europe	20	Wild boar (Italy)	0.05	0.95	-	-	0.04	-	0.96	-	Hair or blood	Giuffra *et al.*, 2000
	13	Wild boar (Poland)	0.45	0.55	-	-	0.12	-	0.88	-		
	20	Large White	0.35	0.65	-	-	0.27	-	0.73	-		
	13	Landrance	0.45	0.55	-	-	0.27	-	0.73	-		
	19	Hampshire	-	1.00	-	-	0.24	-	0.76	-		
	1	Duroc	0.23	0.77	-	-	0.10	-	0.90	-		
	2	Large White Landrance Hampshire Duroc Berkshire	-	-	-	-	0.50	-	0.50	-	Muscle	Ishiguro *et al.*, 2002
	3				-	-	0.33	-	0.50	0.17		
	5				-	-	-	-	1.00	-		
	7				-	-	0.43	-	0.57	-		
	13				-	-	0.19	-	0.73	0.08		
	Farm A: 20 (Finland)	Not typical of Wild Boar	-	-	-	-	0.15	-	0.85		Hair	Góngora *et al.*, 2003
	Farm B: 21	Wild Boar			-	-	-	-	0.52	0.48		
Asia	7	Wild boar (Japan)	0.93	0.07	0.71	-	0.29	-	-	-	Hair or blood	Giuffra *et al.*, 2000
	7	Meishan	0.93	0.07	-	-	0.93	-	0.07	-		
	20	Wild boar (Japan)	-	-	0.82	-	0.03	-	-	-	Muscle	Ishiguro *et al.*, 2002
	1	Wild boar (Ryukyu)			-	-	-	1.00	-	-		
	1	Wild boar (China)			-	-	1.00	-	-	-		
	2	Meishan			-	-	1.00	-	-	-		
Other areas	2	Ohmini miniature pig	-	-	0.25	-	0.50	-	0.25	-	Muscle	Ishiguro *et al.*, 2002
	3	Wild boar (Israel)	0.50	0.50	-	-	-	-	1.00	-	Hair or blood	Giuffra *et al.*, 2000
	1	Domestig pig (Cook Island)			-	-	-	-	-	-		

Table 7. Frequencies of Mitochondrial Cytochrome B (Cyt B) gene variants described for *Sus scrofa.*

Region	n	Type animals and origin	*Cytochrome B variants*							Samples	References
			A1	A2	A3	E1	E2	E3	E4		
Europe	24	Wild boar, Italy	-	-	-	23	-	1	-	Hair or blood	Giuffra *et al.*, 2000
	15	Wild boar, Poland	-	-	-	12	3	-	-		
	27	Large White	11	2	-	13	-	-	1		
	13	Landrance	3	1	-	9	-	-	-		
	20	Hampshire	-	-	-	20	-	-	-		
	12	Duroc	2	-	-	10	-	-	-		
	1	Mangalica	-	-	-	1	-	-	-		
	12	Wild boar, Belgian	-	-	-	12	-	-	-	Hair or skin	Ramírez *et al.*, 2005
	6	Wild boar, Spain	-	-	-	6	-	-	-		
Asia	7	Wild boar, Japan	6	-	1	-	-	-	-	Hair or blood	Giuffra *et al.*, 2000
	7	Meishan	7	-	-	-	-	-	-		
	12	Wild boar, Turkish	-	-	-	12	-	-	-	Hair or skin	Ramírez *et al.*, 2005
América	8	Domestic pig, Perú	6	-	-	-	-	-	-	Hair or skin	Ramírez *et al.*, 2005
	6	Domestic pig, Nicaragua	-	-	-	6	-	-	-		
	6	Domestic pig, Uruguay	-	-	-	8	-	-	-		
Africa	10	Domestic pig, Nigeria	-	-	-	10	-	-	-	Hair or skin	Ramírez *et al.*, 2005
	3	Domestic pig, Benin	-	-	-	3	-	-	-		
	4	Mukota, Zimbabwe	2	-	1	1	-	-	-		
Other areas	3	Wild boar, Israel	-	-	-	3	-	-	-	Hair or blood	Giuffra *et al.*, 2000
	1	Domestig pig, Cook Island	-	-	-	1	-	-	-		

4.3. Cytochrome B (CytB) and Sequence D-loop

The existence of three distinct mitochondrial DNA (mtDNA) clades, two European and one Asian, has been identified when analyzing the entire sequence (1140 bp) of the cytochrome B (cytB) gene and 440 bp of the control region (Giuffra *et al.* 2000). European clade 1 was found in the majority of wild boars from Europe and Israel and in most European domestic pigs. The second European clade was found only in three wild boars from southern Italy. The Asian clade was present in Japanese wild boars, domestic Chinese Meishan pigs, and in some European domestic animals as well as individuals of the Large White, Landrace and Duroc breeds (Giuffra *et al.* 2000; Ramírez, 2005) (Table 7).

A small number of phylogenetic studies have been performed with pigs using mtDNA D-loop sequence variations (Okumura *et al.*, 1996; Giuffra *et al.*, 2000). Detailed analysis of every D-loop sequence obtained indicated a lack of any diagnostic polymorphic nucleotide position that could enable direct differentiation between wild and domestic *Sus scrofa* meats. From the data obtained by Fajardo (2007), it can be concluded that a PCR-RFLP technique based in the selected mt D-loop region cannot be used for direct identification between these two closely related porcine meats. These results are in agreement with other studies (Wolf *et al.*, 1999; Montiel-Sosa *et al.*, 2000; Brodmann *et al.*, 2001; Góngora *et al.*, 2003; Krkoska *et al.*, 2003) reporting that PCR-RFLP differentiation of wild and domestic swine meats based on mtD-loop sequences may be hampered as a result of their phylogenetically close relationship and by intraspecies mutations that can occur in a restriction site.

5. PRODUCTS AND BYPRODUCTS

5.1. Muscle and Meat Characteristics

Skeletal muscle of domestic pigs indicates less maturity at birth and contains a lower number of myofibers when compared with wild-type pigs. Accelerated myofiber hypertrophy and protein accretion at the plane of transcription during postnatal growth produces the dominance of domestic pigs over wild-type pigs in skeletal muscle mass (Rehfeldt *et al.*, 2008).

Sus scrofa domestication is associated with a clear shift of skeletal muscle to fast-twitch glycolytic properties (Rehfeldt *et al.*, 2008). Evaluating fiber traits and glycolytic metabolites in muscle *Longissimus dorsi* of European wild boar, Pietrain and Meishan, Müller *et al.* (2002) found that Pietrain had the highest relative number of white fibers and the largest muscle fibers, while the wild boar presented the smallest muscle fibers. The R-value and lactate level of wild boar and Meishan were low, whereas Pietrain had high R-values and lactate levels. The glycogen level was highest in wild boar and lowest in Meishan.

Several antagonistic relations between fiber characteristics, muscle metabolites and performance traits for carcass and meat quality have been found (Müller *et al.*, 2002). Skewes *et al.* (2008) compared wild boar (chromosomal number 2n36) to phenotypically similar animals of 2n37 and 2n38 chromosomes (crossbreeds) with respect to live weight, carcass yield, meat yield, fat and weight of inner organs. The final live weight at 39 weeks of age of 2n36 animals was significantly lower in comparison with crossbreeds. Crossbreeds were heavier than wild boar (2n36). Similar live weight results were found by Weiler *et al.* (1998), Müller, *et al.* (2000), Vietes, *et al.* (2001) and De la Vega (2003). Andersson-Eklund *et al.* (1998) reported that the proportion of wild boar alleles in the genome of crossbreeds significantly influence the live weight.

Skewes *et al.* (2008) also found that wild boar showed the highest yields for most meat cuts compared to crossbreeds and differences between groups were most obvious for traits, calculated in relation to carcass weights. Additionally, the amount of mesenteric fat was higher ($P < 0.05$) in 2n37 > 2n38 > 2n36.

Muscle fiber studies found that *Gracilisis muscle* in wild boar is mainly composed of type I and IIa fibres (Weiler *et al.*, 1995; Ruusumen & Puolanne, 2004), especially in the light muscle (*Longissimus dorsi, Semimembranosus, Gluteus superficialis*) (Ruusumen & Puolanne, 2004), whereas type IIb fibres were leading in domestic pigs. Type I fibers tended to be the smallest fibers in domestic pigs, but were the largest fibers in wild boar (Weiler *et al.*, 1995). In domestic pigs, the cross sectional area of type IIb fibers is larger than the cross sectional area of type I and IIa fibers. In wild boars, the cross sectional part of all fiber types is analogous (Ruusumen & Puolanne, 2004).

Ruusumen & Puolanne (2004) also concluded that the average fiber cross sectional area is similar in the muscles of wild and domestic pigs, except in LD (*Longissimus dorsi*) and SM (*Semimembranosus*), where the average fiber cross sectional area in wild pigs is 25% smaller than in domestic pigs. The cross sectional area of type IIa fibers in the light SM and GS (*Gluteus superficialis*) of domestic pigs and the cross sectional area of both type I fibers and type IIA fibers in the light LD increase most with an increasing growth rate. Growth speed influences muscle fiber properties only in light muscles, not in dark muscles (Ruusumen & Puolanne, 2004). Andersson-Eklund *et al.* (1998) describes important quantitative trait loci (QTL) effects for composition and/or body percentage traits on chromosomes 2, 3, 4, and

8. The wild boar alleles give a shorter, less meaty carcass at an equal carcass weight. However, the wild boar allele of one of the QTL on chromosome 3 enlarged the *Longissimus muscle* area by 1.5 cm.

Weiler *et al.* (1995) identify giant fibers as a degeneration indicator only in domestic pigs and not in wild boar. Their presence, as well as the larger fiber size and the high proportion of type IIb fibers in domestic pigs, may be attributed to high concentrations of growth hormone.

From a commercial and processing point of view, wild boar meat has advantages over pork due to a more intense red coloration and smaller exudate losses. According to Marchiori & Felício (2003), these differences are associated to the slower and less extensive decline in pH and to a faster decline in temperature, which are due to wild boar genetics, management and feeding, resulting in older and less heavy animals at slaughter age.

In summary, wild boars have smaller and more numerous myofibers especially on type I and IIa with the type IIb being larger in pigs. Accelerated myofiber hypertrophy and protein accretion at the plane of transcription during postnatal growth produces the dominance of domestic pigs over wild-type pigs in skeletal muscle mass. The larger fiber size and the high proportion of type IIb fibers in domestic pigs, may be attributed to high concentrations of growth hormone. These results suggest there is a potential use of these traits as differentiation tool between wild boar, pig and their intercrosses.

5.2. Byproducts

In order to differentiate swine and wild boar in foods, Butschke (2004) developed several DNA analytic procedures such as PCR-RFLP, RAPD or sequences. By comparing samples and sequences, he sought to determine whether individual characteristics or group-specific markers could be used to differentiate swine from wild boar. Three specific genes, Tyrosinase, Immunoreceptor DAP10-Gen, and Melanocortin-1 were examined. Furthermore, a gene, two non-coding ranges and Introns, the Cytochrome b-gene, the D-loop-range and the repetitive range of the micro satellite S602 as well as Introns of the Immunoreceptor DAP10-Gens were analyzed. The DNA sequence comparisons showed a great homogeneity among genus *Sus scrofa* in comparison to the differences found between animals of different species. The sequence heterogeneity between all individuals is larger than amid wild boar and the domestic form. Thus, to differentiate the forms, several markers need to be applied. Butschke (2004) concluded that the most exact statement about the sample's identity can be made using the sequence of several DNA sections. Altogether, 14 markers that are suitable to distinguish forms were identified. Larson *et al.* (2005) could not distinguish swine DNA from wild boar. Nevertheless, Fajardo *et al.* (2007) through digestion of MC1R amplicons with the appropriate enzymes generated characteristic PCR-RFLP profiles that allowed discrimination among meats from wild and domestic swine specimens. The technique also enabled the detection of samples that yielded heterozygous profiles, suggesting hybrids resulting from wild boar and domestic pig breeding. In the opinion of Fajardo *et al.* (2007) the PCR-RFLP reported here, targeting the MC1R gene may be routinely applied to verify the correct labeling of game products. Nevertheless, there is a problem when applying this criterion to F2 animals resulting of crossbreeding (wild boar x pig) which can carry the homocigosis for E+ without being wild boar as stated also Marklund *et al.* (1998).

CONCLUSIONS

It is possible to differentiate wild boars from pigs and crosses by morphometric analysis of the skull, nevertheless it presents difficulties and is only applicable to dead animals. In live animals, at present there is no unique test for purity and it is strongly recommended to follow the step by step methodology which combines phenotype, karyotype and genomic analysis (Fig. 1).

The phenotypic analysis allows segregating individuals with evident characteristics of pig or crossbred but does not discriminate animals with wild boar appearance. The process should continue through karyotype. The European wild boar owns 2n36 karyotype and the domestic pig 2n38, its descendant's crosses gives animals with karyotypes 2n36, 2n37 and 2n38. Specimens 2n37 and 2n38 are descendants of domestic pigs or Asian wild boars, whereas individuals 2n36 are not necessarily pure wild boars. Finally, the discrimination must be complemented with homozygosity for the condition of E+ extension of gene MC1R and as well alleles II of gene KIT.

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