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Wild boar *Sus scrofa* Linnaeus, 1758 dental variability in two areas of the Iberian Peninsula

Variabilidad dental en el jabalí *Sus scrofa* Linnaeus, 1758 en dos áreas de la península ibérica

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Abstract

The skulls and mandibles of 182 wild boars from the Western Pyrenees (WP) and the Middle Ebro Valley (MEV), Aragon, Spain, were assessed for dental variability. We evaluated whether there were differences in the frequency and age and sex distribution between areas, and whether any differences might be related to their environments (acquired) or were heritable (congenital). Variability included hyperdontia and hypodontia (more or fewer teeth than is normal), persistence (presence of deciduous teeth in adults), rotation and malposition (teeth deviations from the vertical or horizontal axes, respectively), diastema (abnormal space between two teeth), injuries, tooth loss, and tartar. Acquired variability such as tartar and injuries were significantly more frequent in the WP, which might have been due to differences in diet between the areas (e.g., in WP, rooting was considerable). Among the congenital, the areas differed significantly in the frequency of diastema, which might have been a hereditary characteristic in the MEV. Overall, the incidence of rotations (100%) and malposition (90%) were high, which suggests that these are characteristics of the dentition, rather than abnormalities. Among the congenital, diastema (and the frequently associated hypodontia) was the most common, which we interpret as an incipient adaptation towards a reduction in the number of teeth as a response to a shift to a predominantly vegetarian diet.
Keywords: Dentition, environment, foraging behavior, Suidae.

Resumen

Se evaluó la variabilidad dental de los cráneos y mandíbulas de 182 jabalíes del Pirineo occidental (PO) y del valle medio del Ebro (VME), Aragón, España. En concreto si había diferencias en la frecuencia y distribución por edad y sexo entre áreas, y si las diferencias podían estar relacionadas con sus hábitats (adquiridas) o eran hereditarias (congénitas). La variabilidad incluía: hiperdontia e hipodontia (más o menos dientes de lo normal), persistencia (presencia de dientes temporales en adultos), rotación y malposición (desviaciones de los dientes de los ejes vertical u horizontal, respectivamente), diastema (espacio anormal entre dos dientes), lesiones, pérdida de dientes y sarro. La variabilidad adquirida como el sarro y las lesiones fueron significativamente más frecuentes en el PO, lo que podría deberse a diferencias en la dieta entre las áreas (por ejemplo, en el PO el alimento subterráneo conseguido a partir de las hozaduras fue más importante que en el VME). Entre las congénitas, las áreas diferían significativamente en la frecuencia de diastema, que podría ser una característica hereditaria en el VME. En general, la incidencia de rotaciones (100 %) y malposición (90 %) fue alta, lo que sugiere que éstas son características de la dentición, más que anomalías. Entre las congénitos, el diastema (y la hipodontia frecuentemente asociada) fue la más común, lo que interpretamos como una incipiente adaptación hacia una reducción en el número de dientes como respuesta a un cambio a una dieta predominantemente vegetariana.
Palabras clave: Ambiente, comportamiento alimentario, dentición, Suidae.

Introduction

Mammal dentition has been studied in ecology, functional morphology, palaeontology, and systematics (Paglarelli 2003). Changes in dental formula, tooth morphology, and tooth lose are often associated with the environment, diet, and behaviour (Rodríguez-Cuenca 2003). Phenotypic variability is the result of genotypic and environmental factors (Miles & Grigson 1990). For instance, within a species, teeth can differ in number, size, and position. Variations can be small, common, but if they are rare, they are anomalies, even if this distinction is arbitrary (Miles & Grigson 1990). The teeth that are lost through evolution tend to be in marginal positions (Paglarelli 2003).

Dental variability, normally considered anomalies, are congenital (genetic or congenital) and acquired, caused by the environment (Feldhamer 1982, Vigal & Machordom 1987), and provide information on health, consanguinity (Garzón 1991), and feeding habits. Anomalies have been studied in ungulates such as red deer *Cervus elaphus* Linnaeus, 1758 by Metch *et al.* (1970), Feldhamer (1982), Kierdorf (2001); roe deer *Capreolus capreolus* (Linnaeus, 1758) by Jackson (1975), Kierdorf (2001) and Iberian wild goat *Capra pyrenaica* Schinz, 1838 by Vigal & Machordom (1987), Fandos *et al.* (1993), Gómez-Olivencia *et al.* (2013).

Research on the genus *Sus* has focused on tusk anomalies (Kierdorf *et al.* 2004a, Konjevic *et al.* 2006), the effect of diet on the occurrence of malformations and anomalies in domestic pigs (Tonge & McCance 1965, 1973), comparisons of domestic pigs and wild boar (Feldhamer & McCann 2004), archaeology (Zinoviev 2009, Binois *et al.* 2014), and wild boar populations (Abaigar 1990, Miles & Grigson 1990, Garzón 1991, Horwitz & Davidovitz 1992).

Wild boar has a difiodont dentition, with brachiodont and bunodont teeth, that is adapted to omnivory. Permanent dentition appears within 2.5 years (44 teeth, I3/3 C1/1 P4/4 M3/3) (Matschke 1967, Boitani & Mattei 1992). Permanent canines emerge between 7 months (Matschke 1967) and 10 months (Boitani & Mattei 1992), and grow continuously in males and up to 2 years in females (Fernández-Llario & Mateos-Quesada 2003).

The aim of this study was to determine the type and frequency of dental variability in wild boar living in two neighbouring areas in Iberia. We evaluate whether any differences might be related to sex, age, teeth type or skull part and side (maxilla, mandible and left, right). We discuss the possible influence of environment or congenital factors on dental variability. We will talk of variability, rather than anomalies, as its frequency in many cases are high.

Material and methods

Study areas

Wild boar has a continuous distribution throughout the study areas since at least the 1960s (Gortázar *et al.* 2000) (Fig. 1). The study area in the Western Pyrenees (WP) was 78,197 ha, a third of which was forest, and elevation ranged from 800 m to 2,450 m, although hunting battues occurred in the forests between 800 m and 1600 m, only, because alpine pastures occur at elevations above the timberline. The topography was rugged with significant differences in vegetation because of differences in slope, elevation, and orientation. Mixed forests predominated. The landscape had been extensively modified by human activity, but rural abandonment has allowed the forest to recover. The most common forest species were, in decreasing order, Scots pine *Pinus sylvestris*, beech *Fagus sylvatica*, white oak *Quercus cerrioides*, and fir *Abies alba*, and there was some holm oak *Quercus ilex*. White oak and holm oak were present at low elevations. Scots pine predominated at all elevations.

Figure 1. Study areas: 1 Western Pyrenees, 2 Middle Ebro Valley © EuroGeographics for the administrative boundaries.

Beech formed the elevation limit of the forest in most of the area, together with mountain pine *Pinus uncinata*. Fir was interspersed among the Scots pine and beech forests. The average density of wild boars was 3.3 km^2. The study area is transitional between the Atlantic and the sub-Mediterranean regions, and has high ecological diversity. The average annual precipitation at 1,400 m is approx. 1,550 mm (Herrero 2003).

The Middle Ebro Valley (MEV) is an irrigated agricultural land along approximately 100 km of the Ebro River, where it meets the Gállego River. The main crops were maize *Zea mais*, wheat *Triticum sativum*, barley *Hordeum vulgare*, and alfalfa *Medicago sativa*, and there were fruit trees and vegetables. The area is semiarid and offered limited shelter and food for wild boar population. MEV is a densely populated area close to a medium-large city like Zaragoza (Fig. 1), and wild boar density is less than 1 indiv/km^2. Human density is of 320 km^{-2}, contrasting with the 10 km^{-2} of WP. Riparian habitats occur along the river. The climate is continental and sub-arid. Average annual precipitation in the study period was 329 mm, and the minimum absolute temperature in the same period was -15.2 ºC. Frosts are frequent in winter, as are fog and high winds, which contribute to the aridity of the area. The soil is sandy and easily excavated (Herrero 2003).

In the WP, the wild boar diet mainly consisted of plant matter from the aerial parts of forest plants. Beechnuts, acorns from white oak and holm oak, and bracken *Pteridium aquilinum* roots were the most abundant and frequent items in the diet and represented 70.7% of the total volume. Roots were the alternative to hard mast (Herrero *et al.* 2005). The amount of animal matter in the diet was small but was consumed frequently and consistently throughout three hunting periods. Crop damage in the area was minimal because of the abundance of forest fruits, alternative natural foods, and the mosaic of forest (Herrero *et al.* 2005). In the MEV, wild boars fed mainly on crops, particularly maize *Zea mays*. Other components of the diet that were of agricultural origin included wheat *Triticum sativum*, barley *Hordeum vulgare*, and alfalfa *Medicago sativa*, which were the alternatives to maize between harvest and seeding, which was the basis of seasonality in diet (Herrero *et al.* 2006).

In their second semester of life and after two years of age, sows in the MEV were heavier than were those in the WP. In both areas wild boar did not differ in litter size, ovulation rate, or intrauterine mortality, but did differ in fetal sex ratio, which was skewed towards males in the MEV. Pregnancy in the first year of life was frequent in the MEV and exceptional in the WP. Lifespan was lower in the MEV (6 years) than it was in the WP (11 years). Population structure differed between the two areas; the WP had a higher proportion of older animals and the MEV had a higher proportion of young ones. In the WP and the MEV, 59% and 75% were <24 months of age, respectively. That difference might have been because of differences in food quality and abundance, and shelter availability, which has led to differences in agricultural damage, growth, productivity, hunting pressure, and longevity (Herrero *et al.* 2008).

Material

Crania and mandibles (n=182, 7,916 teeth) were from the zoological collection of the Instituto Pirenaico de Ecología from the Consejo Superior de Investigaciones Científicas (IPE-CSIC). Those from the WP came from hunting battues (1990-1993) and those from the MEV came from culling to prevent crop damages (1994-2000) (Herrero 2003). In 23 samples, the M3 had not erupted (Table 1).

Methods

To confirm whether there were significant differences between areas and between the sexes in the number of individuals that were affected by dental variability, we used the χ^2 test. In addition, we evaluated whether there were differences in the frequency of the type of teeth that was affected by a given variability considering the side (left or right), bone (maxilla or mandible), and sex.

Specimens from the two areas did not differ in age and sex distributions (χ^2, $p>0.05$), although significantly (χ^2, $p<0.05$) more of the WP specimens were of animals that were 6-8 years old (Table 1). Therefore, for each of the variabilities that were correlated with age, the analysis was limited to individuals that were 5 years old or younger.

Dental variability consisted in (i) hyperdontia (increase in the number of teeth) (ii) hypodontia (decrease in the number of teeth), (iii) persistence (of deciduous teeth in adults), (iv) rotation (deviation on the vertical axis), (v) malposition (deviation on the horizontal axis), (vi) diastema (space between two teeth that should not be present (mandible,

Table 1. Age and sex of wild boar from the Western Pyrenees and the Middle Ebro Valley. Age was estimated following Boitani & Mattei (1992) until 145 weeks of age (average ± 95% confidence interval for the mean) and Matson's lab determination http://matsonslab.com/ from age 3 years and above.

Age	Western Pyrenees WP		Middle Ebro Valley MEV		
	Males	Females	Males	Females	Total
87 (±3) weeks	8	5	4	6	23
107 (±3.7) weeks	1	12	4	3	20
127 (±7.4) weeks	10	13	1	3	27
145 (±12.9) weeks	18	10	6	8	42
3-5 years	12	22	1	6	41
6-8 years	5	15	0	2	22
9-10 years	2	5	0	0	7
Total	56	82	16	28	182

P_2-P_1, P_1-C, C-I_3) or absence of diastema where it should be present (maxillae, P^1-C, C-$I^{3)}$ (Miles & Grigson 1990), (vii) damage caused by trauma or caries (viii) tooth loss, and (ix) tartar, which could have low, medium, or high deposition (In Annex images of the dental variabilities are shown).

Age was calculated based on dental eruption until 145 weeks of age (Boitani & Mattei 1992) and tooth cement layers from 3 years of age and older (Matson's Lab http://matsonslab.com/). Teeth rotation angles were calculated on photographs and assigned to one of the following categories: 0º-15º, 15.01º-30º, 30.01º-45º, 45.01º-60º, and >60º.

To confirm the normality of the data, we used the Spearman Correlation Test and the Kolmogorov-Smirnov Test.

Results

Among the 182 maxilla and mandibles, the variability included rotation (100%), malposition (90%), damage (73.1%), hypodontia (30.2%), diastema (21.4%), loss (3.3%), persistence (2.2%), and hyperdontia (1.6%). All hyperdontia were in WP females (n=3), and one had two of the four cases. Three cases were in the maxilla and one was in the mandible. Fifty-five specimens had hypodontia, of which 22 (40%) were in one tooth and 33 (60%) were in two teeth. Hypodontia was mainly in the mandible (96.6%) and the P_1 (95.5%).

Rotation of at least one tooth (n= 824) was present in all specimens, range= 1-11 teeth/specimen, average= 6 (SD= 2.2)], and most (97.5%) were in the premolars. In the maxilla, rotation occurred in all of the teeth and, in the mandible, all except P_1 were affected. The frequency of rotation was similar in the mandible (45.4%) and the maxilla (54.6%). Most (75.3%) had angles <15°; 21.6% between 15.01°- 30°, 2.4% between 30.01°- 45°, 0.4% between 45.01°-60º, and 0.5% > 60º. The majority (66.7%) of the most infrequent rotations (45.01°-60° and >60°) occurred in the incisors.

Four specimens had persistence in the mandible, of which 80% were in the I_2. One specimen had two persistent teeth. The average number of damaged teeth was 3.2 (SD= 2.6), range= 1 (30.8%) to 16 teeth (0.7%), and the majority (68.2%) were in the mandible. The most damaged teeth totalling 82% were M_1 (34%), C (15.7%), M_2 (10.5%), I_1 (10.2%), and I_2 (11.2%). Average malposition was 3.9 (SD= 2,3), range= 1 (11%) to 16 teeth (0.6%), and most were in the mandible (74.8%). M_1 (25.6%) and I_3 (21.9%) were the teeth most affected.

Most (94.9%) of the diastema variability was separations between teeth. Only 5.1% of the anomalies were the absence of, which was present in the right hemimandible of one female (between P_1-P_2) and one male (between P_1-C_1) in the WP. Of those that had additional diastema, 37.8% had one and 62.2% had two; most (83%) were in the mandible and all involved the premolars. The absence of teeth from non-congenital causes (drop) occurred in six specimens, 66.7% in the maxilla, five from the WP (3.6% of that sample), and one from the MEV (2.3% of that sample). All specimens (n=182) had tartar accumulation (Table 2).

The correlations between variabilities (diastema and rotation, diastema and hypodontia, malposition

Table 2. Tartar accumulation in Iberian wild boar from the study areas.

Tartar accumulation	Western Pyrenees	Middle Ebro Valley	%
Slight	67	27	51.6
Medium	37	17	29.7
Abundant	34	0	18.7
Total	138	44	100

and damage, and damage and tartar) were calculated. For diastema, malposition, tartar, and damage, correlations were calculated for each age class to avoid having age as a confounding variable. In all cases, except for hypodontia and diastema, the correlation was non-significant (Rho Spearman, $p<0.05$) (Supplementary material, Table S1).

Considering individuals, with the exception of diastema, which was more common in the MEV (χ^2= 9.71; p= 0.002; Table S2), the frequency of variability did not differ significantly between the sexes and between areas. Within areas, with the exception of diastema, which was more common in WP males (χ^2=4.98; p=0.025) (Table S3), the frequencies of anomalies did not differ between the sexes.

Tartar deposition was influenced by age; therefore, the analysis was limited to individuals up to 5 years of age (n=153). There was significantly more deposition in the WP (χ^2= 11.7; p= 0.003) and in female specimens (χ^2= 6.8; p= 0.034). In the WP ($\chi^{2=}$ 6.2; p= 0.046), but not in the MEV ($\chi^{2=}$ 1.9; p= 0.17), females had significantly more deposition.

At the teeth level, 29.3% (n= 2,319) had some kind of variability; specifically, rotation (47.2%), malposition (27.6%), damage (18.1%), hypodontia (3.8%), diastema (2.6%), drop (0.3%), and hyperdontia and persistence (0.2%).

The bone (maxilla or mandible) and, to a lesser extent, area were the most significant correlates of variability. Rotations were more frequent in the maxilla, but the other anomalies were more frequently in the mandible and on the left side. Malposition was more common in males. Damages were most frequent in the WP and diastema was most frequent in the MEV. For hyperdontia, persistence, and loss, n<5; therefore, the χ^2 test was not applicable. Age was correlated with the frequencies of malposition, diastema, and damage; therefore, the analysis was restricted to individuals that were < 5 years of age (Table S4).

The distribution of variabilities was similar in the two areas and in the sexes. No difference between sexes was found in the MEV (χ^2, p>0.05). In the WP, diastema and malposition were more frequent in males than they were in females (χ^2, p<0.05) (Table S4). Hyperdontia, persistence, and drop were n<5; therefore, the χ^2 test was not applicable. The samples were for age up to 5 years in malposition, diastema and damage to avoid the age effect.

In both areas, hypodontia, malposition, and diastema were most frequent in the mandible. In the MEV, but not in WP, rotation was more frequent in the maxilla than it was in mandible. Damages did not differ between bones in the MEV, but were more frequent in mandibles from the WP (Table S5). Rotations occurred more frequently on the left side (Table S5).

Discussion

The permanent dentition of Iberian wild boar from two neighbouring areas had a high number and frequency of heritable and environmental dental variability. For this reason, we talk of variability, instead of anomalies, which is the term used normally in these cases. For some types of variabilities, the frequencies were in general similar to those reported in other studies. The analysis at the tooth level revealed patterns that were not detected in the analysis based on individuals.

Hyperdontia, hypodontia, persistence, and diastema are caused by genetic factors and are congenital (Miles & Grigson 1990). Damages, drop, and tartar are influenced by environmental factors. Rotation and malposition are influenced by both (Miles & Grigson 1990). Hypodontia and, to a lesser extent, hyperdontia and persistence, were the most common heritable variability.

The frequency and distribution of hypodontia were similar to those reported in other studies (Abaigar 1990, Garzón 1991, Feldhamer & McCann 2004). Bilateral P_1 absence is more frequent than is unilateral, and there is only one reported case in P^1 (Abaigar 1990). Feldhamer & McCann (2004) reported I_3 hypodontia. Horwitz & Davidovitz

(1992) did not observe hypodontia in P_1, but did find a high frequency of hypodontia in the I^3 (40%) in one of four populations, which they suggested was related to low heterozygosity, and was not an evolutionary trend as in the case of P_1.

Diastema (and the frequently associated hypodontia) was the most common congenital anomaly (Azorit *et al.* 2022), which we interpreted as incipient adaptation towards a reduction in the number of teeth in this species as a response to a predominantly vegetarian diet. Typically, teeth that are evolutionarily lost are on the margins of each dental series (Paglarelli 2003) and erupt after the other surrounding teeth (Peyer 1968 in Line 2003). In wild boar, the canines erupt before the P1 (Paglarelli 2003). The eruption pattern of P_1 and its marginal or isolated position relative to the other teeth, can contribute to its absence (Feldhamer & McCann 2004). That pattern of reduction is an evolutionary trend in Artiodactyla (Vigal & Machordom 1987); specifically, in Suinae and domestic pigs (Miles & Grigson 1990). That loss might allow an increase in the size and complexity of the M_3, with a larger chewing surface, and a reduction in the number of premolars. Tooth loss might indicate adaptation to grass and root crushing, which has been found in fossil Suinae (Harris & Cerlin 2002), and in extant mainly herbivorous species (Genov 1981). In any case, there is no consensus whether the P_1 is deciduous, without permanent successor, or permanent without a predecessor (Miles & Grigson 1990).

Typically, hyperdontia is most common in the premolars (Horwitzh & Davidovitz 1992, Liebl 2003, Zinoviev 2009) and, because wild boar has the original eutherian dental formula (44 teeth), hyperdontia is infrequent (Feldhamer & McCann 2004, Zinoviev 2009). The rare cases of hyperdontia are probably because of a duplication of a tooth, rather than the emergence of an ancestral tooth (Binois *et al.* 2014). In any case, the aetiology of supernumerary teeth is uncertain (Xiu-Ping & Jiabing 2011). Possibly, duplication is caused by the complete division of a tooth's root, hereditary, mutational, or affected by environmental factors (Wolsan 1984).

Evidently, both areas, with the exception of diastema, did not show patterns of congenital variability associated with tooth eruption that differed from those observed in other wild boar populations. The high frequency of diastema in the MEV suggests some genetic mechanism. The P1 and I3 are affected by diastema, and the whole area is hypervariable.

Age affects the frequencies of malposition, diastema, damage, tartar, and persistence. Diastema can be a result of the eruption of a tooth in an anomalous position (genetic factor) or a consequence of a periodontal disease (Towfighi *et al.* 1997). In the later, a higher frequency can be related to gingivitis and periodontitis, which occurs more frequently in old animals (Samuel & Woodall 1988).

Variability is more common in females in some cases (Abaigar 1990, Garzón, 1991). In our study areas, they were similar in the sexes, except for diastema and malposition, which was more common in males, and tartar, which was most common in females. Except for rotations, there were more in the mandible in our study than that of Feldhamer & McCann (2004), but Horwitz & Davidovitz (1992) found more in the maxilla. The mandible is the bone where the evolutionary process of dental formula modification is clearer, which is reflected mainly in hypodontia and diastema.

Domestic pig breeds or animals bred in captivity are prone to having dental variability because of their low heterozygosity (Miles & Grigson 1990), and reduction in facial cranial bone sizes (Zinoviev 2009), which can occur in isolated populations or in those that were founded from a small number of individuals.

Unfortunately, persistence and diastema have not been the subject of much study. In our study the incidence of rotations and malposition was high, which implies that these variabilities should be considered a characteristic of the dentition, rather than an abnormality, as it has been before.

Variation in teeth position is more strongly associated with environmental, rather than to genetic factors. Rotations appear to be related to dental crowding, which can have a genetic origin, such as cranium size or environmental factors such as a severe malnutrition (Miles & Grigson 1990).

Rotations, particularly in the premolars, are common in wild boar and other suids, but no other study has reported a frequency of >25% (Abaigar 1990, Miles & Grigson 1990, Horvitz & Davidovitz 1992, Feldhamer & McCann 2004). The fact that P_1 is separated from the other teeth by diastema and is the only premolar that had no rotations suggest that rotations are the consequence of a lack of space because of the large number of premolars, and that their eruption is after the P_1, M_1, and M_2 (Boitani

& Mattei 1992); e.g., in Sika deer *Cervus nippon* (Feldhamer 1982). That said, the correlation between hypodontia in P_1 and diastema between P_2 and P_3 was not associated with less rotation. In any case, the higher frequencies in our study compared to that in another (Vigal & Marchordom 1987) might have been the result of the way we reported rotation, which was not a normalized variable.

Laterality of the rotations might be a result of sidedness behaviour (Ströckens *et al*. 2012). As left rotations prevail, wild boars might be chewing more on the left side of their mouth, which has led to a higher frequency of rotations on this side because those teeth would be subject to more friction at their eruption.

We found significant differences in acquired variability such as tartar and injuries, which were most common in the WP, possibly because of differences in diet (Butler 1986 in Gual & Suárez 1996, Horwitz & Davidovitz 1992, Vilà *et al.* 1992,) and behaviour (Konjevic *et al.* 2006); in the WP, rooting is important but, in the MEV, it is rare (Herrero *et al.* 2008).

The correlations between damage and malpositions were not significant regarding areas because they do not occur concurrently. Tooth loss associated with periodontal diseases (Horwitz & Davidovitz 1992) and malposition (Kierdorf *et al*. 2004b).

The high frequency of damages in the mandible might have been a consequence of rooting because this bone is used as a shovel in searching for food underground. The M_1 was the most frequently damaged, probably, because it is the first permanent tooth to emerge (Boitani & Mattei 1992). Damages to tusks probably come from fighting, and experience small trauma during marking and rooting (Konjevic *et al*. 2006). We shouldn't dismiss also the possible traumatism caused by vehicle collisions during male dispersion. The search for underground food might have contributed to the high frequency of damages in the I_1 and I_2 in the WP (Herrero *et al*. 2005). The sexes did not differ in tooth damage, even though there are sex differences in a behaviour related to rooting, which suggests that the damages that males suffer was from marking trees and fighting other males.

Tartar levels differed between areas and the sexes. Hard food reduces tartar accumulation (Vosburgh *et al*. 1982). Eating ripe corn for several months a year in MEV (Herrero *et al.* 2008) could be the reason for a reduced tartar deposition. The high presence of tartar in females might have been associated with their higher energetic requirements related to gestation and piglet breed, which leads them to spending more time rooting.

The variabilities do not appear to reduce wild boar survival, which is very high in the WP, but low in the MEV because of hunting and culling (Herrero *et al*. 2008). The only exception might be tartar, which is associated with periodontal illness and can lead to bacteraemia, endocarditis, and liver and kidney diseases (Gual & Suárez 1996).

Conclusions

1. Hypodontia (decrease in the number of teeth) in wild boar seems to point towards an evolutionary reduction of its dental formula, which several authors have interpreted as an adaptation to an increasingly phytophagous diet.
2. The presence of diastemas (space between two teeth that should not be present) is significantly higher in Middle Ebro Valley individuals and may indicate a possible subpopulation character.
3. Hypodontia and diastemas (frequently associated anomalies) occur much more frequently in the mandible. The greater mobility and functional weight could exert greater selective pressure on this bone, resulting in a higher frequency of anomalies in general.
4. Rotation frequency (deviation on the vertical axis) is much higher in our sample compared to other previous studies, which could be because there is no clear methodology to assess dental rotations in this species.
5. Malposition (deviation on the horizontal axis) is more frequent in males and could be related to the continuous growth of the canines. This is the first work in which malposition has been described in a wild boar population.
6. Diet influences the appearance of damage and tartar on teeth and is more frequent in the Pyrenean subpopulation.
7. The abnormalities studied are not considered to limit or influence the survival of individuals with the exception of tartar, which can lead to serious diseases associated with excessive bacterial plaque in the mouth.

Elena Granados-Rigol analysed crania and mandibles of wild boar belonging to the IPE-CSIC collection. Juan Herrero gathered the samples and prepared the collection. All the samples came from legal hunts and cullings.

Ricardo García-González provided references and the knowledge to analyse dental variability. Alicia García-Serrano assisted in the data analysis. All the authors wrote the manuscript and agreed to its publication. No conflict of interest influenced our objectivity.

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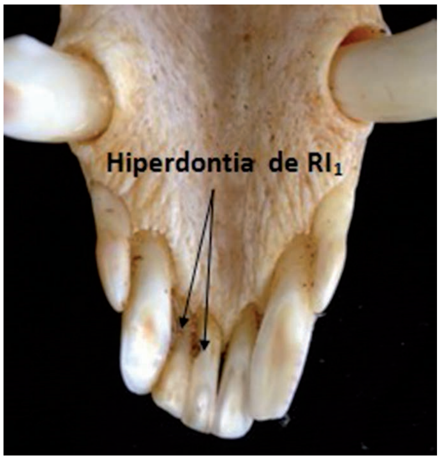
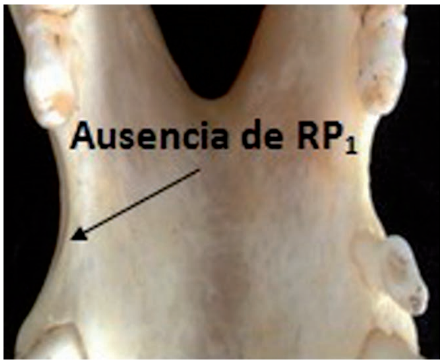
Annexe 1. Photographic images of the dental variability considered in this study (photos by Elena Granados).

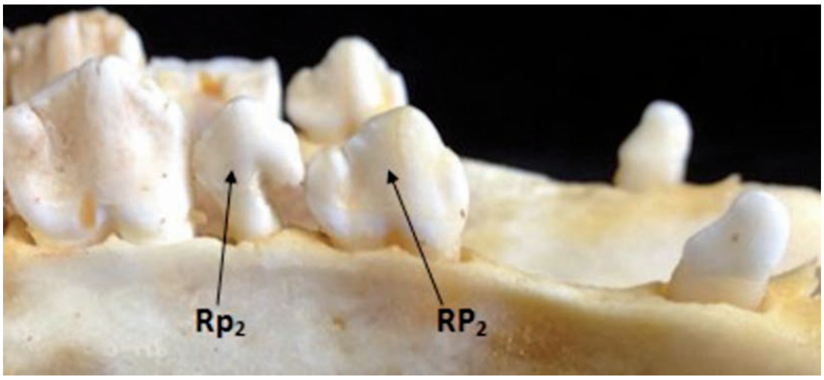
(i) Hyperdontia Hyperdontia of the left PM^2 and the right I_1.



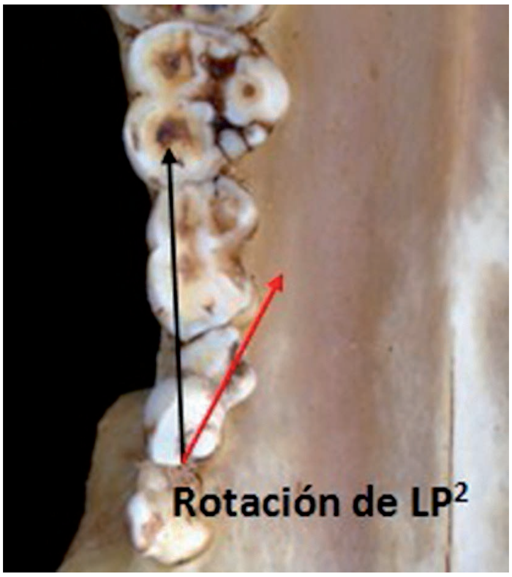
(ii) Hipodontya. Bilateral absence of PM_1. Also, this specimen presents an abnormal diastema between PM_2-PM_3 of the left side.



(iii) Persistence. Presence of the right I_2.



(iv) Rotation. In the first image, we can observe a deviation of the right PM^2 respect the longitudinal axis. The central photo shows a big rotation of the right PM^1 and the lower one the rotation of the left P^2.



(v) Malposition of the left and right M_1. It consists in teeth deviation respect the horizontal axis.

(vi) Diastema: abnormal gap between PM_2 and PM_3.

(vii) Damage: we can observe a the right M_1 affected by damage.

(viii) Tooth loss of RI_3.

(ix) Tartar.
Low deposition.

Moderate deposition.

High deposition.

Supplementary material. Tables of statistical analysis. Galemys, 34 A2 (2022).

Table S1. Correlations between anomalies. ns: no significant, p>0.05; *: significant, p ≤0.05 and **: very significant, p≤0.01.

Anomaly	Years old=1 N=23	Years old=2 N=89	Years old= 4 N=41	Years old=7 N=22	Years old=9 N=7
Diastema-Rotation	φ=-0.17; p=0.93 ns	φ=-0.13; p=0.22 ns	φ=-0.06; p=0.68 ns	φ=-0.23; p=0.31 ns	φ=-0.42; p=0.35 ns
Diastema-Hipodontia	φ=0.07; p=0.76 ns	φ=0.22; p=0.041*	φ=0.38; p=0.015 *	φ=0.61; p=0.003 **	φ=0.64; p=0.12 ns
Malposition-Damage	φ=0.05; p=0.83 ns	φ=0.52; p=0.63 ns	φ=-0.42; p=0.79 ns	φ=0.08; p=0.71 ns	φ=-0.26; p=0.57 ns
Malposition-Tartar	φ=0.01; p=0.95 ns	φ=-0.77; p=0.47 ns	φ=-0.18; p=0.25 ns	φ=0.17; p=0.45 ns	φ=-0.44; p=0.32 ns

Table S2. Dental anomalies of all wild boars according to sex and area (N = 182 individuals) ns: no significant, p>0,05; *: significant, p ≤0,05 and **: very significant, p≤0,01.

Anomaly	Sex	Area
Hypodontia	χ^2=0; p=1; ns	χ^2=0.78; p= 0.4; ns
Rotation	χ^2=0.01; p=0.9; ns	χ^2= 0.003; p= 0.96; ns
Malposition	χ^2=0.05; p=0.82; ns	χ^2= 0.00; p=1; ns
Diastema	χ^2=3.04; p=0.08; ns	χ^2= 9.71; p= 0.002; **
Damage	χ^2=0.04; p=0.8; ns	χ^2= 0.63; p= 0.4; ns

Table S3. Dental anomalies comparison between WP (n=138) and MEV (n=44). ns: no significant, p>0.05; *: significant, p ≤0.05 and **: very significant, p≤0.01.

Anomaly	Sex	
	WP	MEV
Hypodontia	χ^2=0.15; p=0.7; ns	χ^2=0.17; p=0.68; ns
Rotation	χ^2=0; p=1; ns	χ^2=0; p=1; ns
Damge	χ^2=0.27; p=0.61; ns	χ^2=0.5; p=0.48; ns
Malposition	χ^2=0.09; p=0.7; ns	χ^2=0.07; p=0.8; ns
Diastema	χ^2=4.98; p=0.025; *	χ^2=0.16; p=0.7; ns

Table S4. Factors affecting dental anomalies in wild boar < 5 years old at the dental level (n=6,640). ns: not significant; *: significant, p ≤0.05; **: very significant, p≤0.01 and ***: highly significant p≤0.001.

Anomaly	Sex	Bone	Laterality	Area
Hypodontia	χ^2=0; p=1 ns	χ^2=76.41; p=2.3x10^{-18} ***	χ^2=1.14; p= 0.2 ns	χ^2=2.25; p= 0.1 ns
Rotation	χ^2=0.19; p=0.7 ns	χ^2=9.32; p=2.2x10^{-3} **	χ^2=23.67; p=1.1x10^{-6} ***	χ^2=0.98; p= 0.3 ns
Malposition	χ^2=8.87; p=0.002 **	χ^2=105.86; p=7.9x10^{-25} ***	χ^2=0.03; p=0.85 ns	χ^2=2.41; p=0.12 ns
Diastema	χ^2=3.57; p=0.058 ns	χ^2=23.14; p=1.5x10^{-6} ***	χ^2=1.14; p=0.28 ns	χ^2=11.02; p=0.9x10^{-4} ***
Damage	χ^2=0.05; p=0.82 ns	χ^2=39.2; p=3.8x10^{-10} ***	χ^2=0.08; p=0.77 ns	χ^2=25.40; p= 4.6x10^{-7} ***

Table S5: Distribution of dental anomalies of wild boar between areas. For hypodontia and rotation: N (WP) = 6020 teeth; N (MEV) = 1896 teeth. For malposition, diastema and damages: N (WP) = 4832 teeth; N (MEV) = 1808 teeth. ns: not significant; *: significant, p ≤0.05; **: very significant, p≤0.01 and *** : highly significant p≤0.001.

Anomaly	Sex		Mandible/maxille		Laterality	
	POA	VME	POA	VME	POA	VME
Hypodontia	χ^2=0.27; p=0.6; ns	χ^2=0.63; p=0.42; ns	χ^2=57.07; p<0.001; ***	χ^2=19.59; p<0.001; ***	χ^2=1.33; p=0.25; ns	χ^2=0.04; p=0.85; ns
Rotation	χ^2=0.16; p=0.69; ns	χ^2=0.43; p=0.51; ns	χ2=0.17; p=0.68; ns	χ^2=31.81; p<0.001; ***	χ^2=18.77; p<0.001; ***	χ^2=4.92; p=0.02; *
Malposition	χ^2=5.93; p=0.015; *	χ^2=2.41; p=0.12; ns	χ^2=76.38 ; p<0.001; ***	χ^2=29.55; p<0.001; ***	χ^2=0.24; p=0.62; ns	χ^2=1.18; p=0.28; ns
Diastema	χ^2=6.65; p=0.01; **	χ^2=0.16; p=0.7; ns	χ^2=10.8; p=0.001; ***	χ^2=12.46; p<0.001; ***	χ^2=0; p=1; ns	χ^2=2.46; p=0.12; ns
Damage	χ^2=0.56; p=0.45; ns	χ^2=2.48; p=0.11; ns	χ^2=38.46; p<0.001; ***	χ^2=1.88; p=0.17; ns	χ^2=0.25; p=0.62; ns	χ^2=0.21; p=0.65; ns