

Examining the effect of feralization on craniomandibular morphology in pigs, *Sus scrofa* (Artiodactyla: Suidae)

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Received 15 June 2020; revised 2 September 2020; accepted for publication 7 September 2020

Feralization is the process by which domestic animals return to the wild and produce self-sustaining populations. It is often considered as a model in understanding the permanence of morphological changes associated with domestication; however, it is still unclear how much the release of anthropogenic selective pressures affects domestic traits. Here, we assessed the influence of feralization on the domestic morphological traits acquired through selective breeding using craniomandibular differences in shape and size between populations of feral pigs, wild boar and domestic pigs, using landmark-based geometric morphometrics. Our results suggest that numerous cranial and mandibular traits associated with domestication still exist in feral specimens, corroborating that domestication-induced changes in the shape of morphological elements are broadly maintained in feral populations. This is not the case for size variations, however, as the cranium is significantly smaller in feral pigs than in domesticated breeds, which could be due to the selective pressures associated with founding events. Our exploratory study, therefore, underlines the complexity of feral population history, the intricate influence of variations in genetic diversity, and novel selection pressures in the morphology of these groups. Future studies will need to expand the sample to take into account the diversity of morphotypes.

ADDITIONAL KEYWORDS: cranium – domestication – mandible – wild boar.

INTRODUCTION

Feralization is the process by which formerly domesticated populations become established in the absence of purposeful anthropogenic propagation—escaping their previously restricted environments

(Gering *et al.*, 2019b)—and has sometimes been considered as the reverse of domestication (Henriksen *et al.*, 2018). Feral populations are distinguished from their domesticated ancestors by the withdrawal of intentional anthropogenic efforts to support their reproduction, deeply modifying the selective pressures associated with predation, foraging requirements and mate competition (Johnsson *et al.*, 2016; Gering *et al.*, 2019b). Despite its potential as a model to explore rapid evolutionary changes, when the

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natural selection regime is altered, feralization has received little attention compared with domestication (Henriksen *et al.*, 2018). Yet, it is often considered as a model to understand the nature and permanence of associated changes it (Price, 2002; Zeder, 2012). In addition, the study of feral specimens provides ideal natural experiments to assess whether morphological changes fostered by multigenerational selection in captivity persist in the wild, or are simply individual plastic responses to captive environments (O'Regan & Kitchener, 2005; Harbers *et al.*, 2020).

Previous studies on the imprint of domestication which included feral populations, considered that these changes are deep-rooted and possibly irreversible (Price, 2002; Zeder, 2012). This assessment was mainly based on brain size studies, in which feral animals showed no signs of regaining the brain mass of wild populations once they had been returned to “wild” habitats (Kruska & Röhrs, 1974; Birks & Kitchener, 1999; Kruska, 2005). However, several analyses have highlighted the morphological changes associated with feralization. The relative size of several brain regions in feral pigs (*Sus scrofa*) from the Galapagos Islands differed significantly from that of domestic specimens by having a smaller diencephalon and medulla oblongata as well as a larger cerebellum (Kruska & Röhrs, 1974). Morphological changes associated with feralization have also been described in Australian dingoes (*Canis lupus dingo*), where brain size was found to be larger than in domestic dogs of similar body size (Smith *et al.*, 2018). Finally, the cranium of feral American minks (*Mustela vison*) is smaller, with a longer palate and larger postorbital constriction, when compared to domestic specimens (Lynch & Hayden, 1995).

It is therefore currently unclear whether feralization results in noticeable morphological changes in populations which are no longer subject to intentional anthropogenic pressures, particularly in the understudied ectocranial elements (Gering *et al.*, 2019b). For this reason, we studied the skull (i.e. cranium and mandible) of feral pigs, as these animals are among the most successful feral animals in geographical regions that are well outside their ancestral natural range [e.g. Australia, New Zealand and America (Gering *et al.*, 2019a)]. We focused on Australian feral populations as there is no evidence that wild boar and domestic pigs were present on the continent before the arrival of Europeans at the end of the 18th century (Pullar, 1953); thus there could have been no introgression with wild or domestic populations (Gongora *et al.*, 2004). To assess the impact of feralization, the shape and size of the skull of Australian feral pigs were compared to those of wild boar, as well as populations of pigs from Landrace and modern industrial breeds. We used three-dimensional

(3D) landmark-based geometric morphometrics. This approach has been previously applied to explore the cranial shape and size variations of wild boar and pigs, providing clear evidence of significant differences between wild and domestic forms (Owen *et al.*, 2014; Evin *et al.*, 2017). Furthermore, the use of geometric morphometric methods to identify feral pig specimens in extant and archaeological populations has already been established for second and third molars (Evin *et al.*, 2015; Balasse *et al.*, 2016, 2018). In this exploratory analysis, we hypothesized that, in line with brain size (Kruska & Röhrs, 1974; Kruska, 2005), feral pigs would have craniomandibular morphology similar to that of domesticated specimens, indicating that domestication-induced changes are conserved in feral populations (Zeder, 2012).

MATERIAL AND METHODS

The dataset consists of 57 crania and 53 mandibles of adult *Sus scrofa* classified into five groups (Supporting Information, Appendix S1). The first group consisted of wild-caught feral pigs (‘Australian feral pigs’ group) from the Northern Territory of Australia. European and Asian domestic pigs were initially released on the continent by European settlers for meat consumption (Letts, 1962). European pigs were first brought with the settlement of Sydney in 1788 (Pullar, 1953). In the Northern Territory, pig populations from China were probably introduced by Chinese people during the Gold Rush (Pullar, 1950, 1953). Pigs were also imported to the Northern Territory from the islands of Timor in 1827 and Kisar in 1838 (Pullar, 1950, 1953). However, the precise origin of these populations is still uncertain due to scarce documentation (Gongora *et al.*, 2004). Some of these domestic pigs were then either released on purpose or escaped and established feral populations (Pullar, 1950; Izac & O'Brien, 1991). We compared these specimens with French wild-caught wild boar (‘Western European wild boar’ group), as well as German, Polish and French Landrace pigs, i.e. locally adapted breeds [‘European Landrace pigs’ group (Negri *et al.*, 2009)], including Corsican (‘U Nustrale’) pigs (‘Corsican pigs’ group), bred according to the extensive herding practice in Corsica where pigs roam freely in large areas of maquis shrubland (Molenat & Casabianca, 1979). In Corsica, pigs from centuries-old husbandry currently coexist with a cohort of wild populations of suids made up of wild boar, descending from feralized domestic populations introduced during the Neolithic (Vigne, 1992; Albarella *et al.*, 2006), feral pigs and hybrids from crossbreeding between pigs and wild boar (Richomme, 2009). The ‘U Nustrale’ breed was created to prevent the extinction of the traditional Corsican breed, due to crossbreeding with continental

Landraces from 1960 onwards and hybridization with the different wild populations of suids mentioned previously. This breed has a slender build body with a generally black coat colour. More importantly for our study, it is significantly larger than wild boar and its skull has a straight snout (Albarella *et al.*, 2007). The sample also includes the modern Berkshire industrial breed (Li *et al.*, 2014), a result of crossbreeding with Chinese and Siamese pigs for meat production.

We used 94 homologous landmarks and 196 semi-landmarks placed on 3D surfaces to measure the cranial and mandibular size and shape variations (Supporting Information, Appendix S2). This choice was guided by previous 3D landmark-based work on pigs and wild boar (Owen *et al.*, 2014; Evin *et al.*, 2017). We digitized the anatomical landmarks and semi-landmarks using the IDAV Landmark v.3.0 software (Wiley *et al.*, 2005). We performed all the analyses in the R environment (R Core Team, 2019). To remove variation related to their initial arbitrary position along the curves, the semi-landmarks were slid along the tangent of the curves, minimizing bending energy (Gunz & Mitteroecker, 2013). They were then superimposed with fixed landmarks using a generalized Procrustes superimposition (Rohlf & Slice, 1990), implemented in the *gpa* function of the package ‘geomorph’ (Adams *et al.*, 2019) to obtain a new set of shape variables (Procrustes coordinates) and the centroid size (CS). We tested whether shape differed among the studied groups while accounting for age and sex using a MANCOVA with 1000 permutations using *procD.lm* (‘geomorph’). We evaluated the significance of shape differences between groups by performing a Procrustes ANOVA on aligned Procrustes coordinates using *procD.lm*. We analysed the phenotypic similarity among the populations using a minimum spanning tree on the Euclidean distances of each group mean shape (Claude *et al.*, 2004) using *mst* in the package ‘APE’ (Paradis

et al., 2004). To visualize the multivariate ordination of the aligned specimens, we performed Principal Component Analyses (PCA) using *plotTangentSpace* (‘geomorph’) on the groups defined previously. We computed shape deformations by warping the surface of one of the wild boar specimens at +2 and -2 standard deviations of the principal components using *plotRefToTarget* (‘geomorph’). We tested the difference in CS between groups with a pairwise test and visualized it with box plots using *procD.lm*.

RESULTS

We found significant cranial and mandibular shapes differences between the studied groups, respectively ($F = 17.48$, $P < 0.01$) and ($F = 13.41$, $P < 0.01$). We found a significant effect of age over cranial shape ($F = 4.91$, $P < 0.01$) but the studied groups did not show a common shape covariation with age (shape \times age: $F = 1.59$, $P < 0.01$). The effect of age over mandibular shape was not significant ($F = 3.77$, $P = 0.07$) nor was the effect of sex over cranial ($F = 2.33$, $P < 0.35$) and mandibular shape ($F = 3.46$, $P < 0.10$). We found significant ($P < 0.05$) pairwise differences of shape between all groups except between the ‘Australian feral pigs’ and ‘Corsican pigs’ groups, and the ‘European Landrace pigs’ and ‘Corsican pigs’ groups in the cranium shape space (Table 1). For the mandible, there were significant pairwise differences among all groups except between the ‘European Landrace pigs’ and ‘Corsican pigs’ groups. On the minimum spanning trees, the ‘European Landrace pigs’ and the ‘Corsican pigs’ groups were clustered and were the phenotypically closest to the ‘Australian feral pigs’ group for the cranium and for the mandible, respectively (Fig. 1). The PCA was strongly dominated by PC1, accounting for 58.2% and 41.6% of the total variance for the

Table 1. Pairwise ANOVA P -values of the Procrustes coordinates computed from the cranium and mandible. Significant values ($P < 0.05$) are in bold.

		Western European wild boar	European Landrace pigs	Corsican pigs	Berkshire pigs
Cranium	Australian feral pigs	< 0.01	0.01	0.07	0.02
	Western European wild boar		< 0.01	< 0.01	< 0.01
	European Landrace pigs			0.42	< 0.01
	Corsican pigs				0.03
Mandible	Australian feral pigs	< 0.01	< 0.01	0.01	< 0.01
	Western European wild boar		< 0.01	< 0.01	< 0.01
	Landrace pigs			0.51	< 0.01
	Corsican pigs				< 0.01

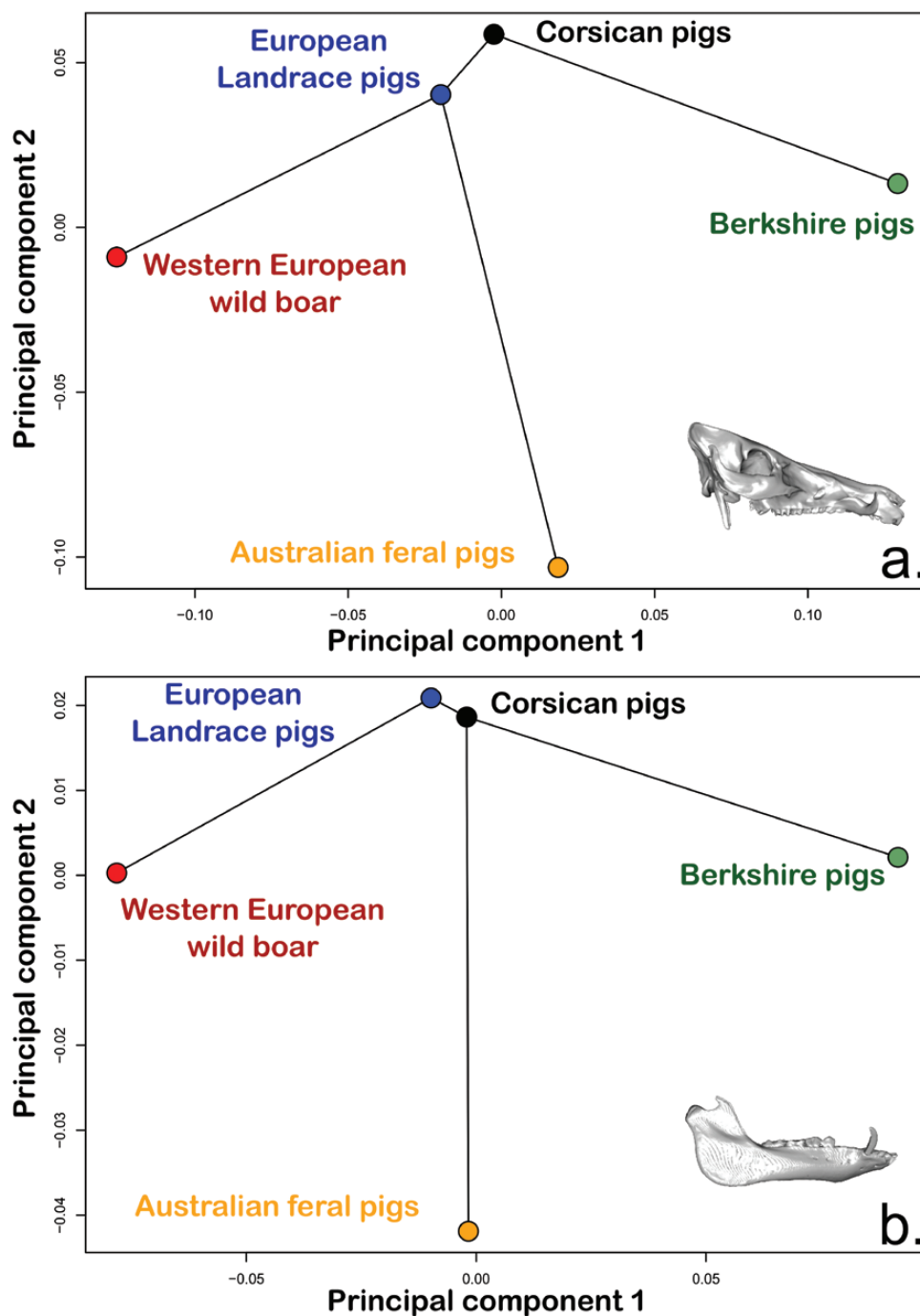


Figure 1. Minimum spanning trees of the Euclidean distances of each group mean cranial (a) and mandibular (b) shape space represented on the PC1-PC2 shape.

cranium and mandible, respectively (Fig. 2). For both the cranium and the mandible, PC1 was driven by the strong divergence between the wild boar phenotype towards negative scores and the Berkshire breed towards positive scores. Feral, Landrace and Corsican pigs show intermediate PC1 scores. For both elements, PC2 mainly separated feral pigs from Landrace and

Corsican pigs. The cranium shape changes from wild boar to the crossbred Berkshire pigs along PC1 were expressed by four traits: (1) a greater concavity and shortening of the parietal, frontal and nasal regions; (2) a wider zygomatic arch; (3) a more vertical occipital bone, becoming nearly perpendicular to the occlusal plane; and (4) a mediolaterally wider cranium. For the

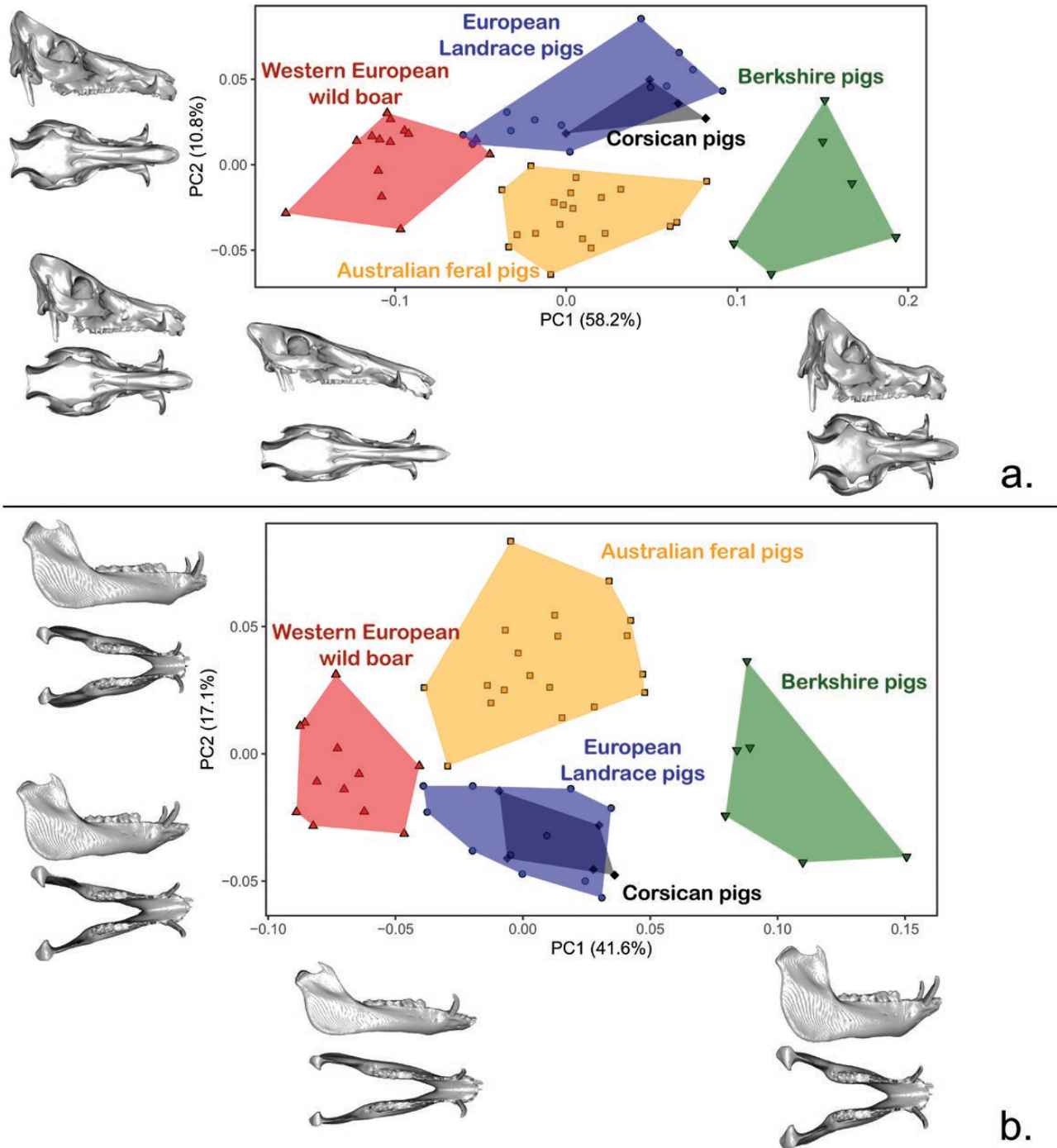


Figure 2. Principal component analyses for (a) the cranium and (b) the mandible in the PC1-PC2 shape space. Shape changes are depicted in lateral and dorsal views.

mandible, the divergence from wild boar to domestic pigs was characterized by four main traits: (1) a taller, larger and more upright ramus; (2) an anteroposteriorly shorter and dorsoventrally taller corpus; (3) a reduced mandibular angle; and (4) a mediolaterally wider mandible, resulting in a wider symphysis region

and an increase of the relative distance between the rami. The cranial shape changes from feral pigs to Landrace pigs along PC2 involved three main shifts: (1) an anteroposteriorly longer cranium, notably in the nasal and maxillary regions; (2) more robust zygomatic arches; and (3) a parietal swept back forming a more

acute angle with the occipital. The mandible shape changes along PC2 from Landrace and Corsican pigs to feral pigs were characterized by: (1) a longer ramus; (2) an increase of the corpus length; and (3) in dorsal view, a global shape moving from a 'V shape' to a 'U shape' associated with a shorter and wider symphysis region. Pairwise comparisons of centroid sizes showed no significant differences in cranium size except between the 'Australian feral pigs' and 'European Landrace pigs' groups, the latter being bigger (Table 2; Fig. 3). We found no significant pairwise differences in mandibular shape among all the groups except between the 'Western European wild boar' and 'European Landrace pigs' groups and the 'Western European wild boar' and 'Berkshire pigs' groups, European Landrace and Berkshire pigs being larger.

DISCUSSION

Our results confirmed that most morphological traits of feral pigs' skulls are similar to those of European Landrace pigs. For both the cranium and the mandible, feral pigs are significantly different from other populations, with the exception of Corsican pigs for the cranium. The absence of a significant effect of sex and a limited effect of age on cranium shape suggest that these similarities are not due to sexual or ontogenetic dimorphism. We must stress however that the relatively small sample and large number of variables in our studies could have biased these results (Thiese *et al.*, 2016). The main axis of cranial and mandibular shape variation is driven by the strong divergence between wild boar and the industrial Berkshire breed, accounting for an increase in breeding selection associated with a shortening of the snout and a widening of the skull. Along this gradient of cranial change due to the latest domestication process, feral,

Landrace and Corsican pigs have an intermediate position, in agreement with previous studies exploring cranial variability in wild boar and domestic pigs (Owen *et al.*, 2014; Evin *et al.*, 2017). The phenotypic similarities in both the cranium and the mandible between the 'Australian feral pigs' and the 'European Landrace pigs' from both continental Europe and the Corsican island suggests that numerous cranial and mandibular traits associated with the selective breeding of the last 200 years of the domestication process are still present, despite 200 years of feralization as in the Australian example. This is in line with the assessment that domestication-induced changes are generally conserved in feral populations (Zeder, 2012), suggesting that feralization affects morphological elements to a smaller degree than domestication (Henriksen *et al.*, 2018). The process of feralization is often associated with the founder effect, as generally only a part of a domesticated population becomes established in the "wild" (Gering *et al.*, 2015). This founder effect, inducing a low level of initial genetic diversity, may explain the relative stability of domestication-induced changes in feral populations. Along the second axis of the shape space, feral pigs were separated from Landrace and Corsican pigs, showing that these populations are not morphologically similar even though they share numerous traits. It is challenging to decipher whether these differences are due to the feralization process, to the founder effect or to distinctions in their ancestral populations, as Australian feral pigs possibly descend from European and Asian domestic pigs, while the Landraces from our sample were exclusively European (Letts, 1962).

We found significant cranium size reduction in Australian feral specimens compared to European Landraces but a similar size range with Western European wild boar and Corsican pigs. These results disagree with the hypothesis that feral pigs display

Table 2. Pairwise ANOVA *P*-values of the centroid size (CS) computed from the cranium and mandible. Significant values (*P* < 0.05) are in bold.

		Western European wild boar	European Landrace pigs	Corsican pigs	Berkshire pigs
Cranium	Australian feral pigs	0.50	0.01	0.70	0.08
	Western European wild boar		0.07	0.97	0.21
	European Landrace pigs			0.22	0.89
	Corsican pigs				0.35
Mandible	Australian feral pigs	0.07	0.23	0.88	0.07
	Western European wild boar		0.01	0.19	< 0.01
	European Landrace pigs			0.47	0.52
	Corsican pigs				0.21

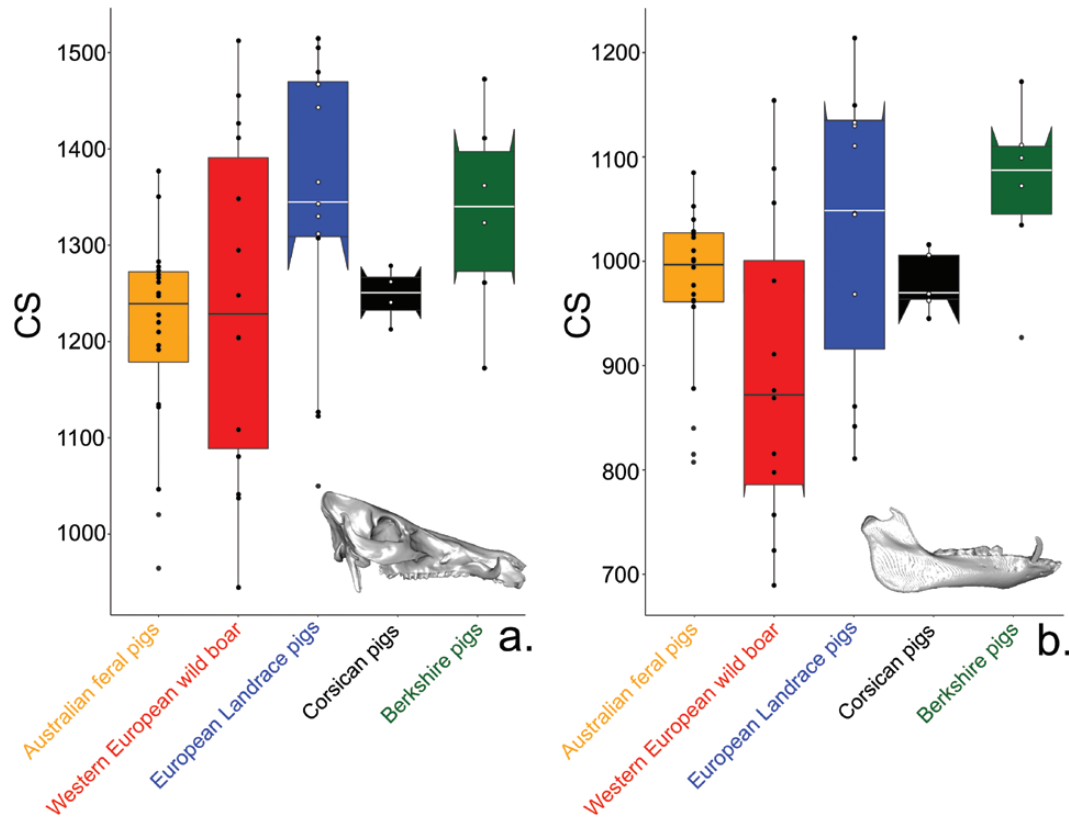


Figure 3. Boxplots of centroid size (CS) for (a) the cranium and (b) the mandible. The dots are the values of CS for each specimen. The boxes represent the interquartile range (IQR) accounting for 50% of the data, from the 25th percentile to the 75th percentile. The whiskers represent all the values within 1.5 times of the IQR. The horizontal lines in the boxes are the median and the notches display the 95% confidence interval of the median.

skull sizes similar to those of domesticated populations based on the observations in pig brain size where feral and domestic populations show no significant differences (Kruska & Röhrs, 1974; Kruska, 2005). These previous observations are, however, misleading, as they are based on the relative relationship between brain size and body size in a taxa where the selection for body growth during domestication is significant (Henriksen *et al.*, 2018). The difference in cranial size between feral and domesticated specimens in our study is potentially explained by the high selective pressures undergone by feral populations settling in new habitats (Gering *et al.*, 2019b). Indeed, the mortality of Australian feral pigs is high, from 15 to 50% between age cohorts (Giles, 1980), especially from starvation, drought (Groves *et al.*, 1989; White, 2008), and predation by dingoes and feral dogs (Morrant *et al.*, 2017). This reappearance of strong selective pressures once returned to the “wild” can explain this cranial size reduction, as high selective pressure, especially predation, can induce a decline in the mean size of individuals (Kotler *et al.*, 1988; Ohlberger *et al.*, 2019). Indeed, the body of Australian feral pigs

has been described previously as smaller and leaner than that of domestic pigs (Choquenot *et al.*, 1996). However, we observed no significant differences in mandible size between feral pigs and the other studied populations. This similarity between feral and domestic populations matches a previous study in the house mouse (*Mus musculus domesticus*) which found no significant mandibular variations between commensal and feral specimens (Souquet *et al.*, 2019). The fewer functions performed by the mandible when compared to the cranium (Lieberman, 2011), limiting the impact of selective pressures, may explain this similarity.

Interestingly, non-significant differences in their cranial shape and measures of similarities in mandibular shape suggest that Australian feral pigs are phenotypically closer to the Corsican pigs breed than the European Landraces suggesting that beyond a common history of anthropogenic selection, these two populations could share a common ecomorphological signature. Even if many domestication-induced variations are broadly maintained in feral populations (Zeder, 2012), these two populations share the possibility

to roam freely while having undergone (feral pigs) or are currently undergoing (Corsican pigs) anthropogenic pressures. This raises the question of the influence of both captivity and anthropogenic environments on the phenotype. The impact of these factors on the shape of feral and domestic individuals should be further explored in future studies (Harbers *et al.*, 2020).

Our study constitutes a first exploratory work supporting the hypothesis that changes associated with the breeding selection of the last 200 years of domestication are likely irreversible (Price, 2002; Zeder, 2012). These tentative results will need to be expanded further using a greater set of data. Indeed, extant domestic pigs display a huge diversity of phenotypes worldwide and Australian feral pigs from the Northern Territory descend from both European and Asian domestic pigs (Letts, 1962). Our sample of Western European populations may therefore have covered a limited morphological range in comparison with the large array of phenotypes of domesticated pigs, especially for those populations from which Australian pigs may derive their ancestry. Furthermore, a distinctive South-East Asian haplotype has been associated with the earliest movement of pigs across the Wallace Line, first into Wallacea, and then into Near and Remote Oceania (Larson *et al.*, 2005, 2007; Dobney *et al.*, 2008). As some pigs introduced into the Northern Territory were from the Wallacean Region [e.g. Timor and Kisar Island (Pullar, 1950, 1953)], it is likely that they included some of these so-called ‘Pacific pigs’. In addition, our dataset includes extant populations, representing the extreme end of the domestication process and morphologically different (at least for the Landrace and Berkshire pigs) from Old World specimens prior to the 18th century (Albarella & Payne, 2005; Albarella *et al.*, 2005; Cucchi *et al.*, 2011). Finally, there are also important morphological differences in wild boar across Western Europe to Eastern Asia (Albarella *et al.*, 2009; Evin *et al.*, 2015), while wild boar from our sample are exclusively French. Therefore, our dataset does not take into account all the variability of wild boar shape and size. Future studies will need to include a greater and more diverse sample in order to take into account the complex and mixed heritage of the Australian material, as well as the overall diversity of the populations of pigs and wild boar used to define the domestic and wild morphotypes, respectively.

CONCLUSION

Australian feral pigs display skull shape traits fairly similar to those of European Landraces, both continental and insular. This result corroborates the strong residual

imprint of the selective breeding of the last 200 years of domestication in the phenotype of feral animals (Zeder, 2012). Our exploratory study underlines the complexity of feral population history, shaped by variations in genetic diversity and novel selection pressure, and clarifies that feralization cannot be considered as a mere reversal of domestication (Gering *et al.*, 2019b).

ACKNOWLEDGEMENTS

We thank the CIRE platform at INRAE (Hans Adriansen, Frédéric Elbout, Christian Moussu and Luc Perrigouard), CT teams from the Leibniz-IZW in Berlin (Guido Fritsch and Juliane Kühne), the University Hospital Halle/Saale (Silvio Brandt) and Anthony Herrel and Vincent Debat for fruitful discussions. We thank the reviewers, Antoine Souron, Julien Claude and Keith Dobney, for their constructive comments that have contributed to improve the quality of the manuscript. We thank Jill Cucchi for copy editing. This research was funded by ANR, through the Domexp Project (ANR-13-JSH3-0003-01) LabEx ANR-10-LABX-0003-BCDiv in the programme ‘Investissements d’avenir’ ANR-11-IDEX-0004-02, programme Emergence SU-19-3-EMRG-02, Muséum national d’Histoire naturelle (Paris), and CNRS INEE.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Groups and specimens used.

Appendix S2. Digitization and definitions of landmarks.