RESEARCH ARTICLE

How Changes in Functional Demands Associated with Captivity Affect the Skull Shape of a Wild Boar (*Sus scrofa*)

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Abstract
The process of animal domestication is a key evolutionary transition in human history, within which the control of wild populations is considered a crucial first step. Yet, phenotypic changes associated with animal captivity remain challenging to document. Here, we investigated the craniofacial changes in wild boar (*Sus scrofa*) associated with a lifetime of growth in captivity under conditions of controlled mobility and diet. Using three-dimensional landmark-based geometric morphometrics, we assessed cranial and mandibular size and shape differences between captive and wild-caught wild boar, their link with masticatory forces, and how these plastic changes relate to traits selected in domestic pigs. We observed shape divergence associated with greater masticatory forces in captive wild boar (e.g., wider zygomatic arches, more upright mandibular rami, and reduced gonial angle) corroborating the fundamental role of biomechanical loading and constructional constraints in the skull shape changes associated with captivity. Despite their resemblance with domestic traits, these localised plastic changes follow a different phenotypic trajectory, suggesting that they did not contribute to the setup of the craniofacial morphology of current domestic breeds. A parallel increase of masticatory force in captive wild boars and domestic pigs may explain this phenotypic convergence but needs to be further explored.

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Introduction

Domestication is an ongoing process of intensification of human-animal interactions (Vigne 2011, 2015) and an evolutionary process of adaptation to anthropogenic ecological niches (Larson and Fuller 2014; Lord et al. 2020). Identifying the mechanisms responsible for the emergence of domestication is crucial to understand its role in the trajectories of human societies over the last 10,000 years (Zeder 2018) and the emergence of humans as a new evolutionary selective force (Erlandson and Braje 2013; Smith and Zeder 2013). The initial morphological changes associated with the first steps of the response of animal populations to anthropogenic environments, prior to the emergence of selected breeds, are largely unknown and therefore remain to be identified.

The control of the behaviour of wild animals, where they are removed from their natural habitat and moved into an anthropogenic environment, is generally considered as a catalyst for most of animal domestication processes (Vigne 2015; Zeder 2015). Here, we explore whether such environmental constraints can leave an anatomical print, i.e. morphological changes induced specifically by captivity, on the craniofacial musculoskeletal system beyond the phenotypic variation range observed in animals in their natural habitat. Next, we assess whether these plastic responses to captivity contribute to the phenotypic variation of selected pig breeds.

We focused on craniofacial modifications since most elements of this structure are used as markers to identify domestic animals (Arbuckle 2005; Kleisner and Stella 2009; Wilkins et al. 2014). Moreover, in addition to studies on postcranial structures (Harbers et al. 2020; Morimoto et al. 2011; Panagiotopoulou et al. 2019), the effects of captivity in mammals have often been explored for the skull (Hartstone-Rose et al. 2014; O'Regan 2001; Selvey 2018). The influence of the control of wild animals on plastic changes in the cranium and the mandible has however rarely been explored. The prevailing role of mechanical loading in shaping craniofacial morphology is well known (Cornette et al. 2015; Fabre et al. 2018; Herring and Lakars 1982; Paschetta et al. 2010). Therefore, we hypothesized that a lifetime in captivity would induce changes in the functional demands on the skull of a wild animal, due to changes in feeding and stereotypic behaviours in an anthropogenic environment. To assess the impact of a lifetime growth in a captive artificial environment on the skull and masticatory muscles of an ungulate, we used an experimental approach focusing on wild boar. To control for genetic and geoclimatic factors that could drive skull variation we collected weaned wild boar piglets from a genetically homogenous population and raised them in a captive anthropogenic environment close to their initial habitat (100 km away). In this experimental farm, the piglets were separated in two groups where their natural foraging behaviour was suppressed (100 m² stall with no possibility of foraging) or drastically limited (3000 m² pen with limited possibility of foraging due to the lack of space.) and where they were given processed dry food pellets developed to feed pigs in captivity. The second objective of this study was to define how and whether the craniofacial plastic changes associated with captivity are related to the phenotypes of domestic selected breeds. Specifically, we investigated whether the plastic changes associated with captivity include morphological features present in the long-term domesticated populations of pigs.

Materials and Methods

Experimental Design

The first two groups (Online Resource 1) consisted of wild boar from the DOMEXP project: a multidisciplinary experiment aiming to assess the effect of captivity on the musculoskeletal system (https://anr-domexp.cnrs.fr/). To experimentally test if mobility reduction induced a plastic response of on the shape of the skull in a wild ungulate, we relied on a control population of wild boar living in a 100,000 m² fenced forest in Urciers (France). From this population, we sampled 24 piglets that were divided into two groups of 12 specimens of equal sex ratio (6 males and 6 females). These groups were raised from 6 to 24 months at the Zoological Reserve of La Haute Touche (France) in two different contexts of mobility reduction: an indoor stall of 100 m² ('captive wild boar exp – stall' group) and a 3000 m² wooded pen ('captive wild boar exp – enclosure' group). These space restrictions represent respectively a reduction of 99.9% and 97% of the range of the control population and do not allow the captive specimens to performed the average daily distances measured in free populations of wild boar (Palencia et al. 2019; Russo et al. 1997). The stall offered no possibility of foraging while in the wooded pen this possibility was limited due to the lack of space. We supplied individuals from both groups with processed dry food pellets including 15.5% of raw proteins adapted for domestic pig diet.

Comparative Wild Boar Samples

In addition to the two captive groups, we also sampled 5 adult specimens from the initial free-ranging herd to serve as a control group (Online Resource 1; 'wild-caught wild boar – control' group). They were genetically homogenous to the captive groups allowing us to control for genetic variation. These specimens were wild-caught between 1

and 18 years of age. These specimens are from a wild boar farm, where human interaction is intentionally kept to a minimum in order to ensure that the behaviour of the wild boar remains as natural as possible. They are free to forage for food in the woods. In addition to the specimens of the DOMEXP project, we incorporated other free-ranging specimens. They include 9 French wild boar (Online Resource 1; 'wild-caught wild boar – France' group) from the forests of Chambord (54,400,000 m^2; Harbers et al. 2020) and Compiègne (150,000,000 m^2, Harbers et al. 2020) from the same geographic and climatic environment than the specimens from the DOMEXP project, i.e. temperate central France. Like most wild boar in Western Europe, these free ranging specimens had an omnivorous diet consisting mostly of vegetable foods, e.g. acorns, roots, crops (Schley and Roper 2003).

Domestic Pig Samples

Free-ranging specimens included 5 Corsican pigs (Online Resource 1; 'free-ranging domestic pigs – Corsican breed' group) aged between 14 and 18 months. These pigs were bred according to the traditional extensive herding practice in Corsica where pigs can roam freely in large areas of maquis forest (2,000,000 m^2; Harbers et al. 2020) to access natural resources for their diet (Molenat and Casabianca 1979). We also compared wild boar with long-term domesticated populations of pigs raised with a strong mobility reduction. They include pig 13 Landraces (Online Resource 1; 'captive domestic pigs – Landraces' group) and 6 intensively selected domestic pig breeds (Online Resource 1; 'captive domestic pigs – intensive breeds' group). All these domestic specimens were reared in stalls and were aged between 1 and 9 years.

Skull Form Data

We used 94 homologous landmarks and 193 semilandmarks placed on three-dimensional (3D) surfaces to describe the cranial and mandibular shape (Fig. 1; Online Resource 2). We digitized the anatomical landmarks and semilandmarks using the IDAV Landmark v3.0 software (Wiley et al. 2005). To assess the relationship between cranial shape, mandibular shape, and muscle force, we dissected 26 specimens (11 from the 'captive wild boar exp – stall' group, 11 from the 'captive wild boar exp – enclosure' group, two from the 'wild-caught wild boar – control' group, and two from the 'wild-caught wild boar– France' group).

Muscle Force Data

We collected the mass and the fibre length for seven masticatory muscles: masseter superficialis, masseter profundus, temporalis, anterior zygomaticomandibularis, posterior zygomaticomandibularis, pterygoideus medialis, and pterygoideus lateralis (Fig. 2). The muscles were weighed to the nearest gram and muscle fascicle length was measured with calipers. We computed the muscle physiological cross-sectional area (PCSA), defined as the cross-sectional area perpendicular to the fibre direction at 'optimal' fibre length (Morse et al. 2005). The PCSA is a representation of the maximum isometric force a muscle can produce (Moore et al. 2013). It is computed as muscle mass divided by the product of fibre length and muscle density (Alexander and Vernon 1975). We used a density of 1.06 g/cm^3, the average density of mammalian skeletal muscle (Segal et al. 1986).

Data Analyses

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 semilandmarks were slid along the tangent of the curves minimizing bending energy (Gunz and Mitteroecker 2013). They were superimposed with the 'true landmarks' using a generalized Procrustes superimposition (Rohlf and Slice 1990), implemented in the gpagen 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 performed Procrustes ANOVA with permutation procedures to quantify allometry, with size computed as the decimal logarithm of CS (log CS; Collyer et al. 2015), using the procD.allometry function of 'geomorph'. We tested the difference in log CS and in PCSA between all groups with a pairwise test and visualized it with box plots. Pairwise comparisons were performed using the function procD.lm included in 'geomorph'. We evaluated the significance of shape differences between groups by performing a Procrustes ANOVA on aligned Procrustes coordinates. To visualize the multivariate ordination of the aligned specimens, we performed a between-group PCA (bgPCA) using the package 'Morpho' (Schlager and Jefferis 2016) using the groups defined previously. The bgPCA provides a projection of the data onto the principal components of the group means, resulting in an ordination of the shape variables between the group means. The new axes are orthogonal and can be computed even when the per group data matrices are not of full rank. This method performs well when the number of observations in each group is smaller than the number of variables (Boulesteix 2005; Mitteroecker and Bookstein 2011). The use of bgPCA has recently been questioned (Cardini et al. 2019) but the use of Procrustes ANOVA on aligned Procrustes coordinates allows an evaluation of the significance of shape differences between groups independent of the bgPCA. Deformations are represented at $+2$ and -2 standard deviations
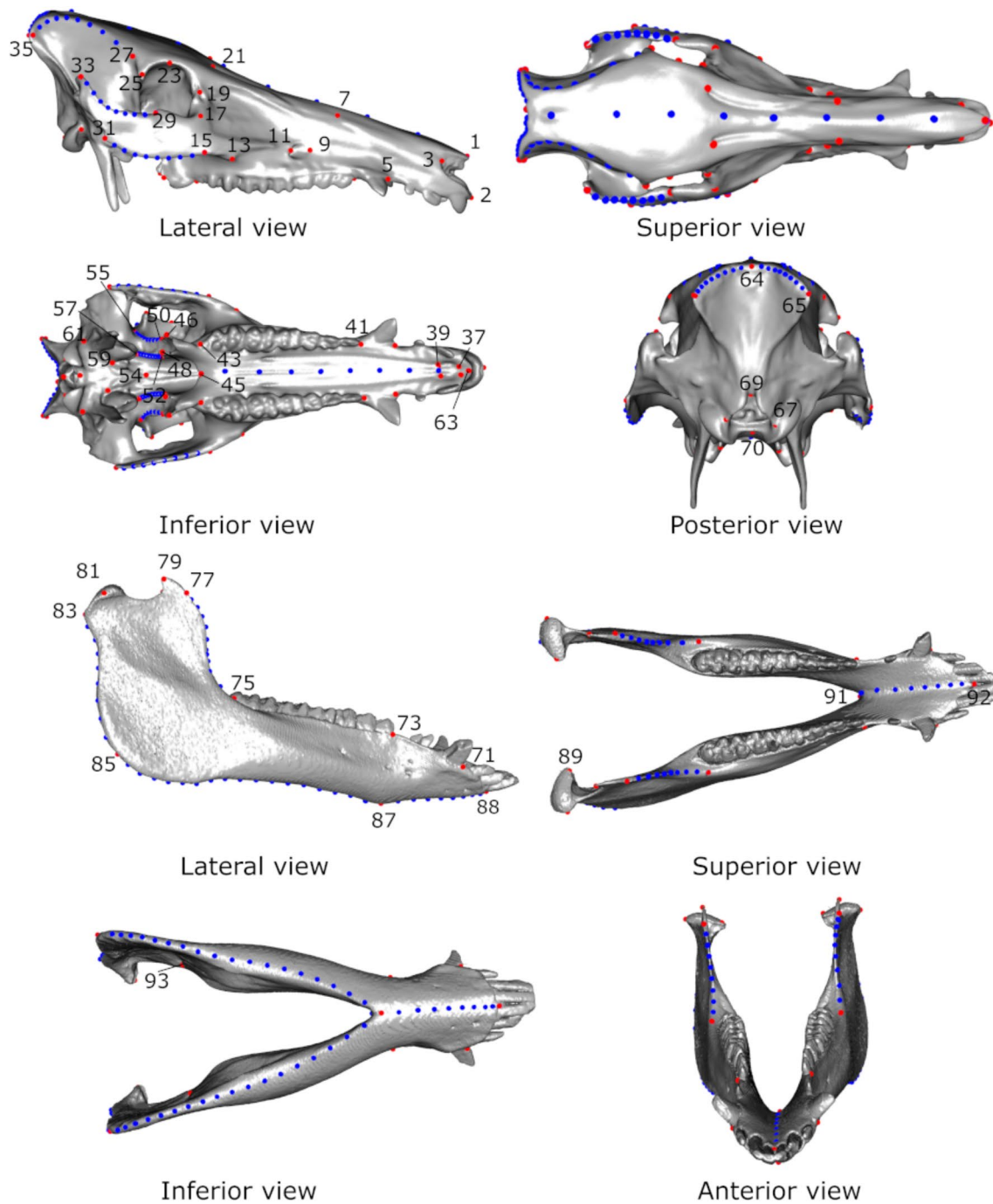
Fig. 1 Wild boar (*Sus scrofa*) cranium and mandible showing the homologous landmarks (red) and semilandmarks (blue) used in the study. For clarity sake, only right and midsagittal landmarks are numbered on the figure (Color figure online)

of the principal components (Schlager and Jefferis 2016). We assessed the covariation between cranial and mandibular shape and muscle PCSA using partial least squares (PLS) analyses (Bookstein 1991; Rohlf and Corti 2000),

using the function two.b.pls from 'geomorph'. We performed Procrustes ANOVA analyses and bgPCA for wild boar and domestic pigs to contrast the plastic signal of
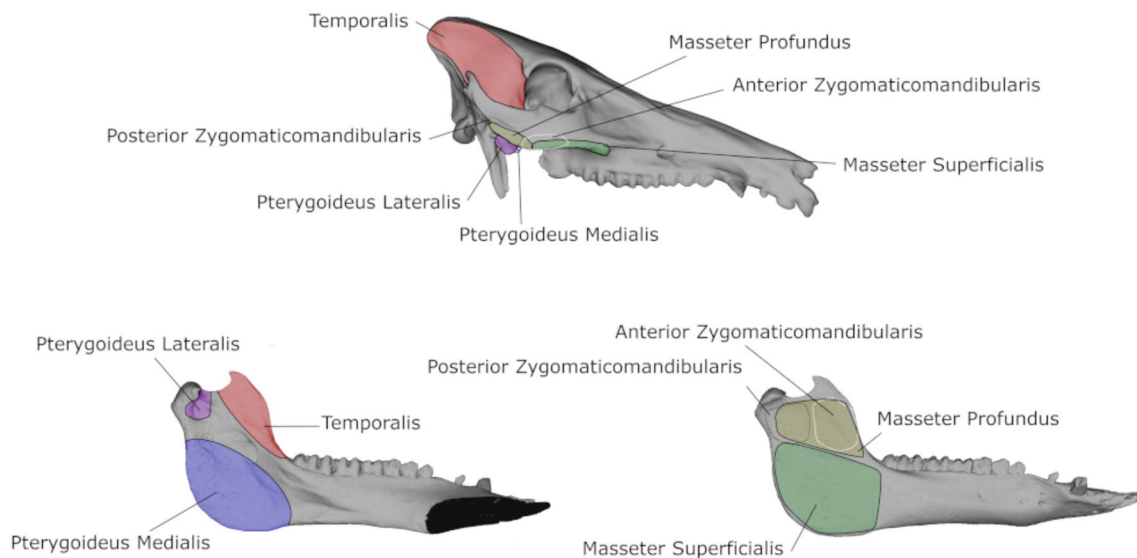
Fig. 2 Location of muscular insertions on a wild boar (*Sus scrofa*) cranium and mandible

captivity with the phenotypic changes induced by selective breeding in domestic breeds.

Results

Allometry

Allometry in wild boar was significant for the cranium ($p < 0.01$; 22.0% of the total variance) and the mandible ($p < 0.01$; 17.3% of the total variance), but the allometric slopes were different between the studied groups ($p < 0.01$). This absence of homogeneity of slopes prevented the calculation of common allometric directions and the estimation of the size-free residuals to investigate the allometry-free variation patterns (Klingenberg 2016). Allometry was reduced but still significant when the pig populations were included for the cranium ($p < 0.01$; 4.8% of the total variance) and the mandible ($p < 0.01$; 12.4% of the total variance).

Plastic Responses to Captivity in Wild Boar Skull

Pairwise comparisons of centroid sizes showed no clear influence of captivity on cranium size (Fig. 3; Table 1). Yet, captive wild boar ('captive wild boar exp – stall', 'captive wild boar exp – enclosure') mandibles show greater centroid sizes than wild-caught populations ('wild-caught wild boar – control', 'wild-caught wild boar– France').

Pairwise comparisons found significantly higher PCSA values in captive wild boar for the masseter profundus, the anterior zygomaticomandibularis, and pterygoideus lateralis (Fig. 4; Table 2).

There were significant pairwise differences in cranial shape between all groups except between the 'captive wild boar exp – stall' and 'captive wild boar exp – enclosure' groups (Table 3). The bgPCA on cranial shape clearly shows the main divergence from the captive to the wild-caught individuals along PC1 (63.3% of the total variance; Fig. 5a). The cranium shape changes associated with captivity (positive scores) involved a less concave cranium, less flared and narrower zygomatic arches, a lower external occipital protuberance, and a narrower nuchal crest with a less curved the temporal line. PC2 (27.6% of the variance) illustrated the separation of the wild-caught control from the other groups. The associated shape changes towards positive scores include a more concave and a mediolaterally larger cranium with more robust zygomatic arches and a greater angle between the parietal and the occipital.

We found significant pairwise differences in mandibular shape between all the groups except between the 'captive wild boar exp – stall' and 'captive wild boar exp – enclosure' groups and between the 'wild-caught wild boar – control' and 'wild-caught wild boar– France' groups (Table 3). The bgPCA performed on the wild boar mandible shape (Fig. 5b) differentiates wild-caught and captive specimens (PC1, 80.4% of variance). Along PC1, the shape change from wild-caught to captive consisted of a taller and more upright ramus, an anteroposteriorly shorter and taller corpus and reduced mandibular angle. The symphysis region is longer and narrower and, in dorsal view, the mandible global shape moves from a 'U shape' to a 'V shape'. The mandible shape change along PC2 is characterized by an anteroposteriorly shorter ramus where the coronoid process is significantly higher than the condyle, a
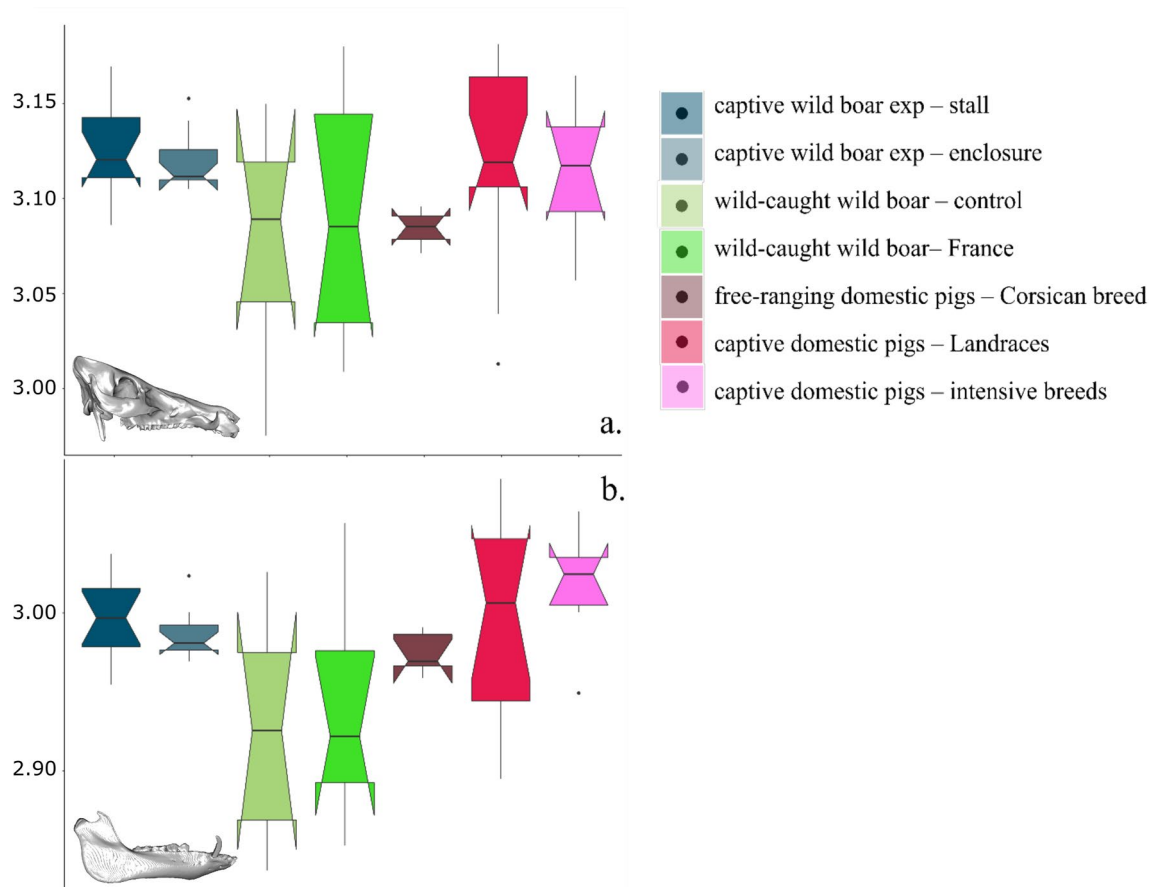
Fig. 3 Boxplot of centroid size for **a** the cranium and **b** the mandible. The boxes represent the interquartile range (IQR) accounting for 50% of the data, from t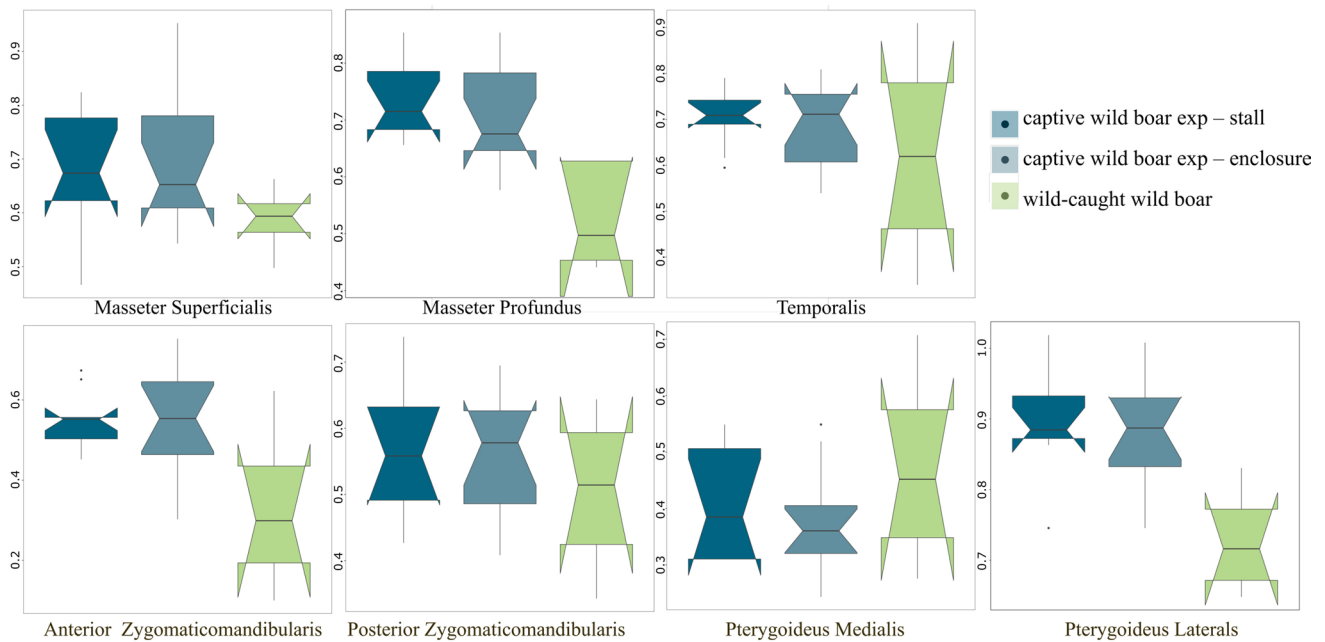he 25th percentile to the 75th percentile. The whiskers represent all the values within 1.5 times of the IQR. The horizontal lines in the boxes are the median and the notches display the 95% confidence interval of the median

Table 1 *p*-values of the pairwise ANOVAs of logarithm of centroid size (log CS) of the cranium and of the mandible between wild boar and pig groups

		CWB exp enclosure	WCWB control	WCWB France	FRDP Corsica	CDP Landraces	CDP intensive
Cranium	CWB exp stall	0.64	0.05	0.06	0.11	0.85	0.6
	CWB exp enclosure		0.09	0.13	0.19	0.92	0.86
	WCWB control			0.64	0.79	0.12	0.19
	WCWB France				0.89	0.16	0.29
	FRDP Corsica					0.23	0.31
	CDP Landraces						0.91
Mandible	CWB exp stall	0.61	**0.01**	**0.01**	0.43	0.95	0.47
	CWB exp enclosure		**0.03**	0.06	0.68	0.56	0.25
	WCWB control			0.7	0.16	**0.01**	**< 0.01**
	WCWB France				0.25	**0.02**	**< 0.01**
	FRDP Corsica					0.39	0.21
	CDP Landraces						0.51

Significant values (*p* < 0.05) are in bold

CWB captive wild boar, *WCWB* wild-caught wild boar, *FRDP* free-ranging domestic pigs, *CDP* captive domestic pigs

Fig. 4 Boxplot of PCSA for the 'captive wild boar exp – stall', 'captive wild boar exp – enclosure' groups, and a group including specimens from the 'wild-caught wild boar – control' and 'wild-caught wild boar – France' groups. 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

Table 2 *p*-values of the pairwise ANOVAs of muscle physiological cross-sectional area (PCSA) for the 'captive wild boar exp – stall', 'captive wild boar exp – enclosure' groups, and a group including specimens from the 'wild-caught wild boar – control' and 'wild-caught wild boar – France' groups

		CWB exp enclosure	WCWB
Masseter Superficialis	CWB exp stall	0.8	0.18
	CWB exp enclosure		0.10
Masseter Profundus	CWB exp stall	0.55	**0.01**
	CWB exp enclosure		**0.03**
Temporalis	CWB exp stall	0.81	0.30
	CWB exp enclosure		0.36
Anterior Zygomaticomandibularis	CWB exp stall	0.95	**0.01**
	CWB exp enclosure		**0.01**
Posterior Zygomaticomandibularis	CWB exp stall	0.96	0.36
	CWB exp enclosure		0.34
Pterygoideus Medialis	CWB exp stall	0.80	0.18
	CWB exp enclosure		0.10
Pterygoideus Lateralis	CWB exp stall	0.65	**< 0.01**
	CWB exp enclosure		**< 0.01**

Significant values ($p < 0.05$) are in bold

CWB captive wild boar, *WCWB* wild-caught wild boar

more squared symphysis region, and a greater mandibular angle.

Strong and significant covariation between cranium shape and PCSA was detected (r = 0.83; $p < 0.01$; Fig. 6a) and accounted for 80.2% of the total covariance. The three main muscles affecting the cranial shape are, in order of importance: the anterior zygomaticomandibularis, the masseter superficialis, and the masseter profundus. Specimens towards more positive values along the pair of axes are associated with a low PCSA for these muscles (Fig. 6) and a less concave cranium with less flared and narrower zygomatic arches, a less vertical occipital, a shorter distance between

Table 3 *p*-values of the pairwise MANOVAs of Procrustes coordinates of the cranium and of the mandible between wild boar groups

		CWB exp enclosure	WCWB control	WCWB France
Cranium	CWB exp stall	0.71	**0.01**	**< 0.01**
	CWB exp enclosure		**0.01**	**< 0.01**
	WCWB control			**0.02**
Mandible	WB exp stall	0.98	**< 0.01**	**< 0.01**
	WB exp enclosure		**< 0.01**	**< 0.01**
	WCWB control			0.31

Significant values (*p* < 0.05) are in bold

CWB captive wild boar, *WCWB* wild-caught wild boar

the zygomatic processes of the frontal, and a mediolaterally narrower nuchal crest. The correlation coefficient of PLS1 was also high and significant between mandible shape and muscle PCSA (r = 0.91; *p* < 0.01; Fig. 6b), accounting for 79.8% of the total covariance. Specimens positioned at the positive side of the axes are characterized by a low PCSA for the anterior zygomaticomandibularis and the masseter profundus associated with a shorter and longer corpus, and an increased value of the mandibular angle, i.e. a less upright ramus.

Comparing Plastic Response to Captivity in Wild Boar to Artificial Selection Signal in Domestic Pigs

Pairwise comparisons of centroid sizes found no significant difference in cranium size between wild boar and domestic pigs (Fig. 3; Table 1). However, the mandibles of wild-caught wild boar populations ('wild-caught wild boar – control', 'wild-caught wild boar– France') are smaller than those of captive pigs ('captive domestic pigs – Landraces', 'captive domestic pigs – intensive breeds') while experimental captive wild boars were not different from the captive pigs.

We found no significant (*p* > 0.05) pairwise differences among the wild boar groups in the cranium shape space (Table 4). There were significant differences among all groups except between the 'free-ranging domestic pigs – Corsican breed' and 'captive domestic pigs – Landraces' groups. For the mandible, there were no significant pairwise differences between the wild boar groups or between the 'free-ranging domestic pigs – Corsican breed' and 'captive domestic pigs – Landraces' groups (Table 4). There were, however, significant differences among all the other groups. The bgPCA for wild boar and domestic pigs was strongly dominated by PC1, accounting for 89.8% and 81.1% of the total variance for the cranium and mandible respectively (Fig. 7). For both structures, the PC1 was driven by the strong divergence between the wild boar phenotype toward negative scores and the industrial pig breeds toward positive scores, Landrace pigs being intermediate. For the mandible, PC2 mainly separates the captive wild boar from

the wild-caught wild boar. It is noteworthy that the plastic effect displayed on PC2 is different from the shape divergence between wild boar and pigs, displayed on both PC1s, as the two shape changes are located on different PCs. The cranium shape change from the wild to the highly selected domestic breeds along PC1 is 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, notably increasing the distance between the two zygomatic processes of the frontal. For the mandible, the divergence from wild to domestic animals was characterized by four main traits: (1) a taller and more upright ramus, (2) an anteroposteriorly shorter and taller corpus, (3) a reduced mandibular angle, and (4) a mediolaterally wider mandible, resulting notably in a wider symphysis region and an increase of the distance between the rami. The cranial shape change along PC2 involves three main shifts: (1) an anteroposteriorly longer cranium, (2) more robust zygomatic arches and (3) a parietal swept back forming a more acute angle with the occipital. The mandible shape change along PC2, from captive wild boar to wild-caught wild boar was characterized by (1) an increase of the corpus length, (2) a greater mandibular angle, and (3) a wider mandible in superior view.

Discussion

Our results confirm that a lifetime of growth in a captive artificial environment affects the skull and masticatory muscles of wild boar. In terms of size, only the mandible increases in captivity. This difference is potentially explained by the multiplicity of functions the cranium must perform (e.g., vision, respiration, mastication, or brain protection), which affect cranial evolution (Lieberman 2011). In contrast, the mandible performs fewer functions and its morphology is more closely related to feeding behaviour (Anderson et al. 2014; Daegling and McGraw 2007; Taylor 2006).
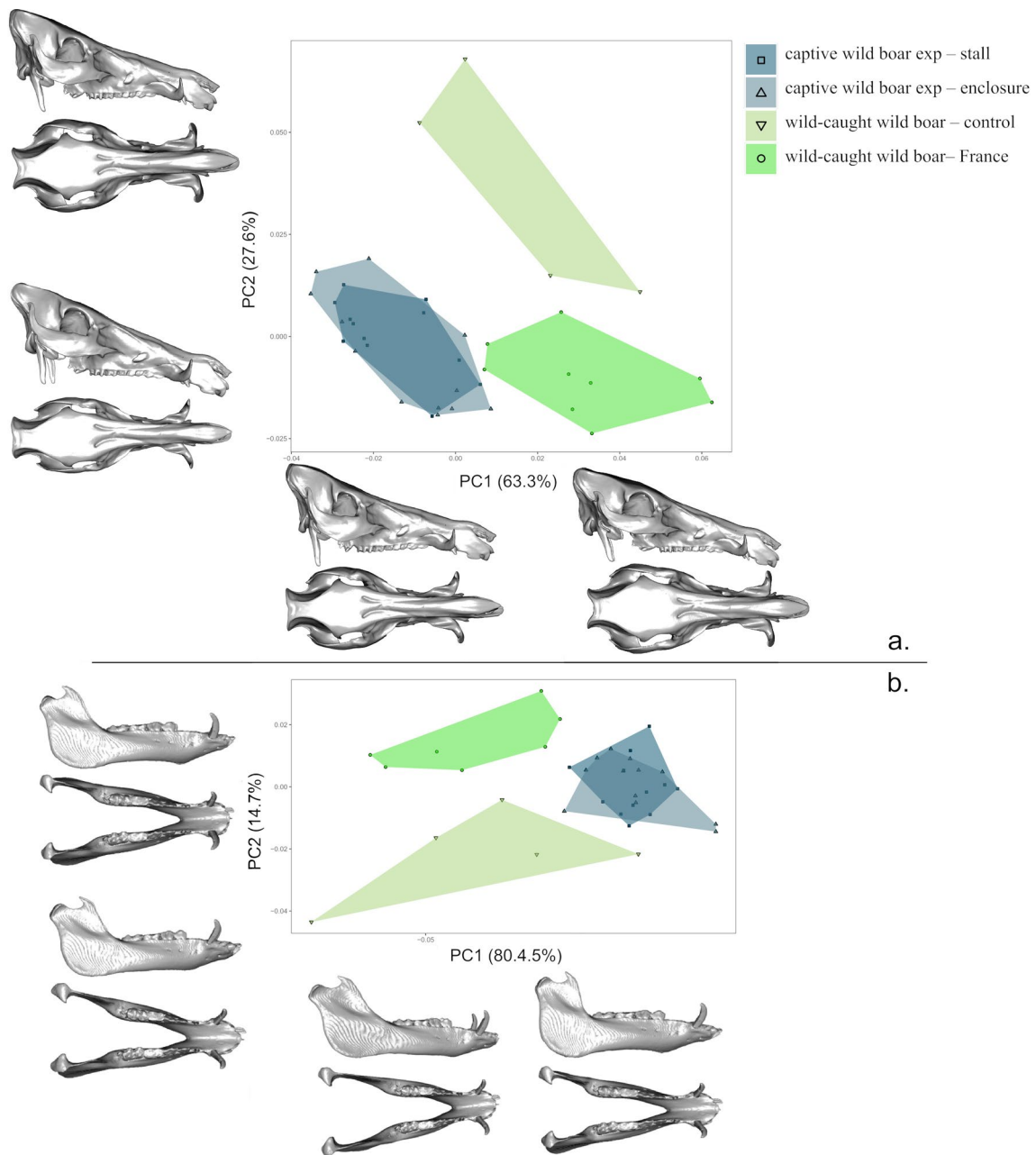
Fig. 5 Between-group principal component analysis for **a** the cranium and **b** the mandible for wild boar in the PC1–PC2 shape space. Shape changes are depicted in lateral and dorsal views

Our study shows that both cranial and mandibular shape are impacted by a lifetime growth in a captive artificial environment. These plastic skull changes associated with captivity are characterized by more flared and wider zygomatic arches, a more vertical occipital bone, more upright mandibular rami, an anteroposteriorly shorter corpus, and a narrower symphysis. Such observations have also been made in captive lions, tigers (Hartstone-Rose et al. 2014; O'Regan 2001; Zuccarelli 2004), and rhinoceros (Groves 1982). Our study of the covariation between skull shape

and masticatory muscles demonstrate that a prevailing part of described changes is possibly driven by larger muscles and greater masticatory forces in captive wild boar, supporting the hypothesis of Hartstone-Rose et al. (2014) that the masticatory muscles of captive animals are bigger. It also demonstrates that modifications in biomechanical loading or constructional constraints due to larger muscles in captivity produce an array of plastic changes in skull morphology. The main muscles covarying with skull shape are the anterior zygomaticomandibularis, the masseter profundus, and
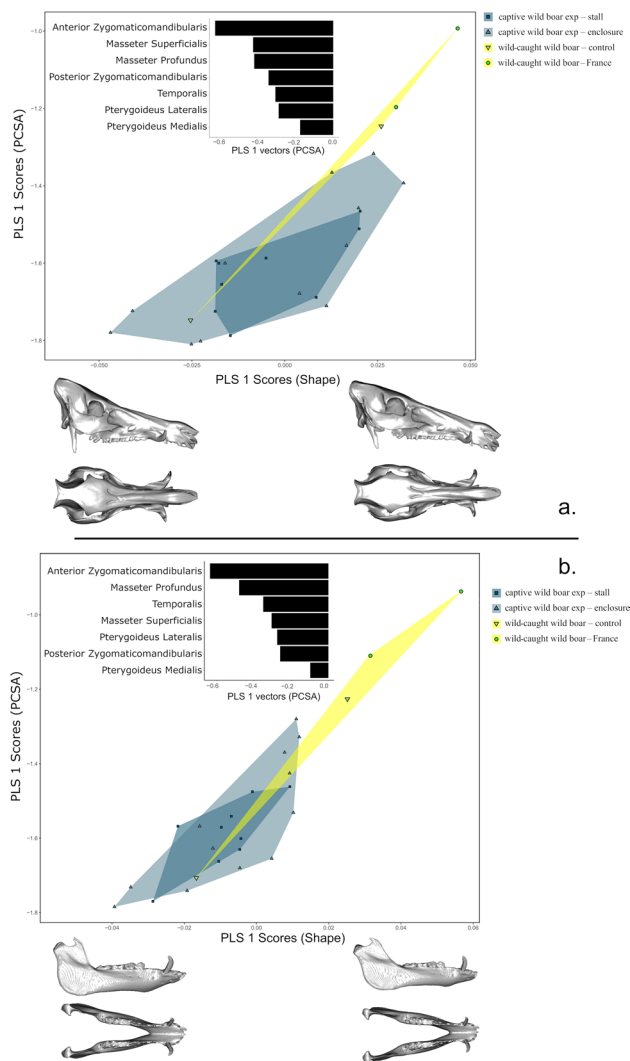
Fig. 6 First pair of partial least squares analysis axes (PLS1) between **a** cranial shape and physiological cross-sectional area (PCSA) of the masticatory muscles and **b** mandibular shape and PCSA. Shape changes are depicted in lateral and superior views. The histogram represents the muscle loadings associated with the cranial shape covariation

the masseter superficialis. Two of them (anterior zygomaticomandibularis and masseter profundus) also have a significantly higher cross-sectional area in captive wild boar when compared to wild-caught specimens. These muscles originate on the zygomatic arches and insert on the mandibular ramus or on the angle of the mandible, i.e. the structures displaying the most changes in our PCA analyses. This suggests that when these muscles increase in cross-sectional area, the associated zygomatic arch is more robust and the mandibular ramus is more upright and vice versa. These changes in cranial and mandibular morphology may be induced by modifications of biomechanical loading in the masticatory region or may be due to space constraints related to housing larger

muscles. Increased muscle activity results in the enlargement of attachment areas and bone remodelling in response to stress loads (Cornette et al. 2015; Dinu 2009; Wolff 1986). However, given that the muscles that most strongly covary with cranial and mandibular shape are positioned deep, space constraints seem the most likely hypothesis. This would suggest that captivity triggers developmental or functional pathways specifically impacting more medially positioned adductor muscles, subsequently impacting skull and mandibular shape (Dinu 2009; Wolff 1986).

The modification associated with a more anthropogenic environment, notably changes in foraging behaviours and increase in feeding behaviours, may explain this increase in muscle size. Indeed, these changes, provoking an extensive use of the masticatory muscles, may put a premium on those best placed to generate forces at low gape, i.e. the masseter and zygomaticomandibularis muscles, affecting their size, and in turn, skull size and morphology (Hartstone-Rose et al. 2014; Lieberman et al. 2004). This is in line the findings of Sella-Tunis et al. (2018) that humans with a high masticatory force display wider and a more vertical ramus associated with anteroposteriorly shorter corpus, and a smaller mandibular angle. These findings are also in line with our covariation results where these morphological features (i.e., vertical ramus and reduced mandibular angle) correspond to the captive specimens, i.e. the groups possessing the higher PCSA. Similarly, experimental studies on pigs shown that modification of feeding behaviour result in changes in mandibular (Ciochon et al. 1997) and temporomandibular joint (Lindsten et al. 2004) shape associated with alterations of the kinematic profile of jaw movement during chewing (Montuelle et al. 2020). This provides further support for the role of strain generated by mastication on muscles and jaw morphology. The reduction of foraging frequency could also modify the muscles in the neck region, exerting greater force on these areas of attachment, explaining the changes observed in the parietal and occipital bones of our captive specimens (Duckler 1998). Stereotypical behaviour may be another possible driver of these changes. Stereotypy is defined as a repeated, relatively invariant, sequence of movements with no obvious purpose (Fraser and Broom 1990, p. 307) particularly existing in captive animals. Oral stereotypical behaviours, such as repetitive bar biting and rooting are particularly present in pigs (Rhodes et al. 2005; Terlouw et al. 1991). Furthermore, several studies indicate that, in sows, stereotypical behaviours are more frequent in confined stalls than in more open areas (Arellano et al. 1992; Pol et al. 2000; Vieuille-Thomas et al. 1995). Duckler (1998) reported shape changes in the sagittal crest of the cranium in captive tigers possibly resulting from stereotypies. Moreover, Groves (1982) reported that the wider zygomatic arches, as it is the case in our analyses, could also be caused by stereotypies, after specimens of rhinoceroses had rubbed their cheeks

Table 4 *p*-values of the pairwise MANOVAs of Procrustes coordinates of the cranium and of the mandible between all groups

		CWB exp enclosure	WCWB control	WCWB France	FRDP Corsica	CDP Landraces	CDP intensive
Cranium	CWB exp stall	0.98	0.51	0.30	**< 0.01**	**< 0.01**	**< 0.01**
	CWB exp enclosure		0.46	0.34	**< 0.01**	**< 0.01**	**< 0.01**
	WCWB control			0.56	**0.03**	0.05	**< 0.01**
	WCWB France				**< 0.01**	**< 0.01**	**< 0.01**
	FRDP Corsica					0.41	**0.04**
	CDP Landraces						**< 0.01**
Mandible	CWB exp stall	0.99	0.17	0.08	**< 0.01**	**0.01**	**< 0.01**
	CWB exp enclosure		0.16	0.09	**0.01**	**0.01**	**< 0.01**
	WCWB control			0.68	**0.01**	**0.02**	**< 0.01**
	WCWB France				**< 0.01**	**< 0.01**	**< 0.01**
	FRDP Corsica					0.41	**< 0.01**
	CDP Landraces						**< 0.01**

Significant values (*p* < 0.05) are in bold

CWB captive wild boar, *WCWB* wild-caught wild boar, *FRDP* free-ranging domestic pigs, *CDP* captive domestic pigs

against the bars of the paddock. It is thus conceivable that an increase in stereotypical behaviours in captive specimens might explain some of the plastic morphological variations observed in our study, notably the more robust zygomatic arches of captive wild boar. We found very similar results for the two studied populations of captive specimens (i.e., in stall and in enclosure). We can hypothesize that, beyond a limit which remains to be defined, the changes provoke by a lifetime growth in a captive artificial environment do not increase when the available space is reduced.

The second objective of this work was to assess whether the plastic changes associated with captivity in wild boar include morphological features present in the long-term domesticated populations of pig breeds. Our results show that the size of the mandible is not significantly different between captive wild boar and domestic pigs while it is different between wild-caught wild boar and these two groups. The increase of the mandible size is both a plastic response to captivity in wild boar and an artificial selection signal in domestic pigs and may therefore be defined as a reliable phenotypic signature of the first steps of animal domestication (Lord et al. 2020). The phenotypic changes associated with captivity in wild boar resemble the differences observed in domestic forms (e.g., wide zygomatic arches, more vertical occipital bone, more upright mandibular rami) driven by the last 200 years of selective breeding. Yet, the captivity-driven plastic variation in the cranial and mandibular shape of wild boar follows an orthogonal direction (along PC2 on Fig. 7) to that of breeding selection in pigs (along PC1 on Fig. 7), which suggests that despite these resemblances, the skull variation produced by captivity has not contributed to the

domestic phenotype. This convergence needs to be further explored but one might hypothesize that it may be due to the large muscles displayed by domestic pigs, similar to those of the captive wild boar, as they were selected for meat production and early growth (Wilkinson et al. 2013).

Conclusion

Our study has demonstrated that changes in the functional demands during captivity can affect the skull shape of a wild ungulate during its lifetime. Differences in cranial and mandibular shape are located mainly in the zygomatic arches and in the mandibular rami, points of attachment of the masticatory muscles, corroborating the prevailing role of these muscles in skull shape changes associated with captivity. Changes in constructional constrains and modifications in foraging and feeding behaviours, as well as stereotypical comportments, are among the potential factors able to modify cranial and mandibular shape. The increase of the mandible size, as well as several phenotypic features (e.g., wide zygomatic arches, more vertical occipital bone, more upright mandibular rami), are plastic changes associated with captivity that can be used as proxy for early process of animal control in the archaeological record. These traits are also present in long-term domesticated population of pigs, but arise along a different phenotypic trajectory, suggesting that they do not contribute to the setup of the craniofacial morphology of current domestic breeds.
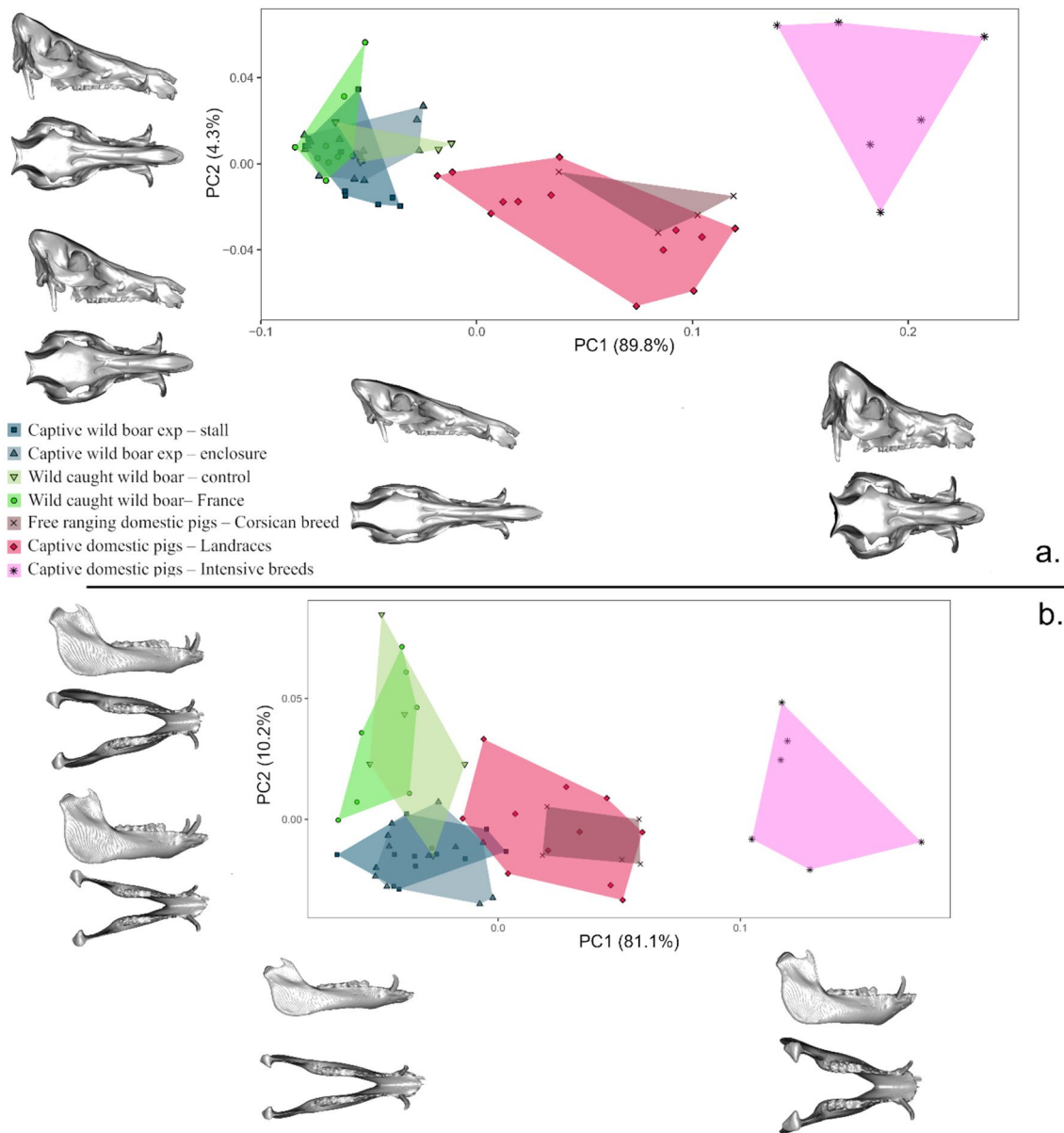
Fig. 7 Between-group principal component analysis for **a** the cranium and **b** the mandible wild boar and domestic pigs in the PC1–PC2 shape space. Shape changes are depicted in lateral and superior views

and RC, DN led the manuscript with scientific and editorial input from TC, AH, VD, RS, AH, GS and J-DV. All authors gave final approval for publication.

Data Availability The datasets generated during and analysed during the current study are available from the corresponding author on reasonable request.

Code availability The code used for this study is available at https://github.com/dneaux/captivity

Compliance with Ethical Standards

Conflict of interest The authors have no conflict of interest to declare.

Ethical Approval This experiment received ethics approval from the French Ministère de l'Enseignement Supérieur et de la Recherche (APAFIS#5353-201605111133847).

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