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Cranial muscle architecture in wild boar: Does captivity drive ontogenetic trajectories?

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Abstract

The jaw system in mammals is complex and different muscle morphotypes have been documented. Pigs are an interesting group of animals as they are omnivorous and have a bunodont crushing dentition. Moreover, they have interacted with humans for over 10,000 years and grow nearly two orders of magnitude in size. Despite being a model system for studies on cranial form and function, data on the growth of the jaw adductor muscles are scant. Moreover, whether captivity impacts the growth and architecture of the jaw adductors remains unknown. Based on dissection data of the jaw adductors of 45 animals ranging from less than 1 kg to almost 100 kg, we show that muscle masses, muscle fiber lengths, and cross-sectional areas scale as predicted for geometrically similar systems or with slight negative allometry. Only the fiber length of the lateral pterygoid muscle grew with slight positive allometry. Animals raised in captivity in stalls or in an enclosure were overall very similar to wild animals. However, some muscles were larger in captive animals. Interestingly, variation in bite force in captive animals was well predicted by the variation in the size of the superficial masseter muscle relative to the overall jaw adductor mass.

KEYWORDS

bite force, captivity, muscle, ontogeny

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1 | INTRODUCTION

The mammalian masticatory system is anatomically and functionally complex, with a tremendous diversity in the relative size of the different components, their orientation and line of action, and their architecture (Ercoli et al., 2023; Gaspard, 1971; Herring, 2007; Schumacher, 1961; Turnbull, 1970). Important in this respect is the direction of pull of the muscles as this will determine their contribution to both movement and the generation of bite force (Herring, 1993). Moreover, the architecture of the jaw adductors in mammals is subjected to trade-offs with highly pennate muscles producing greater force but allowing less stretch, which may in turn impact the excursion of the jaw and thus gape (Herring & Herring, 1974). However, these constraints are partly circumvented by the complex architecture of jaw adductors like the masseter where some parts are characterized by vertically oriented longer fibers allowing more stretch and excursion, and other parts are pennate with shorter fibers more suited for force production during the power stroke (Herring, 1980).

Among mammals, suids are an exceptional model due to the diversity of their masticatory system and the decades of work by Herring et al. providing a detailed overview of the form and function of their jaw apparatus (e.g., Anapol & Herring, 1989, 2000; Herring et al., 1980, 1985b; Herring et al., 2001; Herring & Wineski, 1986). Suids have bunodont cheek teeth and specialize in grinding mastication associated with their omnivorous diet (Herring, 1985a). They have a suinomorph muscle morphotype with a laminar zygomatico-masseteric complex with well-developed layers and a moderately to well-developed pterygoideus medialis (Ercoli et al., 2023). Moreover, pigs have bilateral occlusion and muscle activation associated with their fused symphysis (Herring et al., 2001). Pigs have a long history of association with humans and were domesticated between 9500 and 8000 BCE in the Near-East (Price & Hongo, 2019). These pigs arrived in Western Europe around 5400 BCE and hybridized with European wild boars (see overview in Cucchi et al., 2023). In mammals, changes in feeding behavior in captivity often induce functional responses resulting in shape differences in the skull and mandible (Hartstone-Rose et al., 2014). Yet, in wild boar these changes are different from the morphological changes induced by recent intensive selective breeding (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021;Neaux et al., 2022).

The masticatory muscles comprise the major loading on the skull and consequently influence its growth (Herring, 2007). As such a captive environment can be expected to impact the growth and architecture of the cranial muscles driving the observed variation in cranial and mandibular morphology as was demonstrated in a study using wild boar raised in captivity (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021). Although the basic arrangement of the masseter was shown to be similar in all age classes, fascicle length did decrease with age relative to muscle mass (Herring & Wineski, 1986). Interestingly, the contraction patterns were simpler in infant pigs and increased in complexity with the increasing anatomical complexity observed in older animals (Herring, 1985a; Herring & Wineski, 1986). These changes go hand in hand with a change in fiber type composition. Whereas the masseter in neonates is mostly composed of fast twitch fibers, in adults the masseter comprises up to 30% slow-twitch fibers (Anapol & Herring, 2000). Finally, it has been shown that in pigs the masseter increases faster in mass and force than the digastric muscle associated with the transition from infant suckling to adult mastication (Anapol & Herring, 1989).

However, most of the studies on the pig jaw system and its functional properties have used Göttingen minipigs, a breed of domestic miniature pigs reaching an average adult size of around 35 kg only (McAnulty et al., 2012). Given the truncated growth of these animals the patterns observed may not be universally applicable to wild boar, which can grow up to more than 100 kg. Using a large data set on the jaw muscles of 45 wild boar from France, we explore the postnatal scaling of the mass, fiber length, and cross-sectional area of the jaw adductors. We specifically test predictions of a geometric similarity scaling model where muscle mass increases proportional to body mass, cross-sectional area to body mass to the power 0.66, and fiber length to body mass to the power 0.33. As our data set consists of both wild animals and animals raised in captivity, we further test whether animals raised under captive conditions differ in their jaw muscle architecture as has been suggested previously (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021). Finally, we provide the first bite force data for wild boar and ask ourselves which muscle traits best explain the observed variation in bite force.

2 | MATERIALS AND METHODS

2.1 | Experimental sample

The experimental population 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 m^2 fenced forest in Urciers. From this population, we sampled 24 piglets that were divided into two groups of 12 specimens of equal sex ratio (six males and six females). These groups were raised from 6 to 24 months at the Zoological Reserve of La Haute Touche in two different contexts of mobility reduction: an indoor stall of 100 m^2 (“captive wild boar exp—stall” group) and a 3000 m^2 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 roam 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. Of these experimental animals, 12 animals from the enclosure group and nine animals from the stall group were euthanized and subsequently used for dissections (Table S1). All animals were of known age but of the same age and as such this sample could not be used to explore age-related variation in muscle architecture.

2.2 | Comparative sample

In addition to the captive specimens, we also dissected four adult specimens from the initial free-ranging herd to serve as a control group ("wild-caught wild boar—control" group). These specimens are from a wild boar farm where human interaction is low and where animals freely forage for food. We further dissected 13 French wild boar from the forest of Chambord (54,400,000 m^2; Harbers et al., 2020), four animals from Pradat, and three very young specimens from the Eure (Table S1). These free ranging specimens have an omnivorous diet consisting mostly of vegetable foods, for example, acorns, roots, and crops (Schley & Roper, 2003). None of these specimens were of known age.

2.3 | Dissections

For each specimen we dissected the different cranial muscles including the digastric muscle, the superficial masseter, the deep masseter, the anterior and posterior parts of the zygomaticomandibularis muscle, the temporalis muscle, and the medial and lateral pterygoid muscles from fresh cadavers (Druzinsky et al., 2011, 2016; Figure 1). We weighed each muscle to the nearest 0.1 g on an electronic balance, cut the muscle along its line of action and measured the fiber length (in cm). We then calculated the anatomical cross-sectional area by dividing muscle volume by fiber length assuming a muscle density of 1.06 $g cm^{-3}$ (Mendez & Keys, 1960).

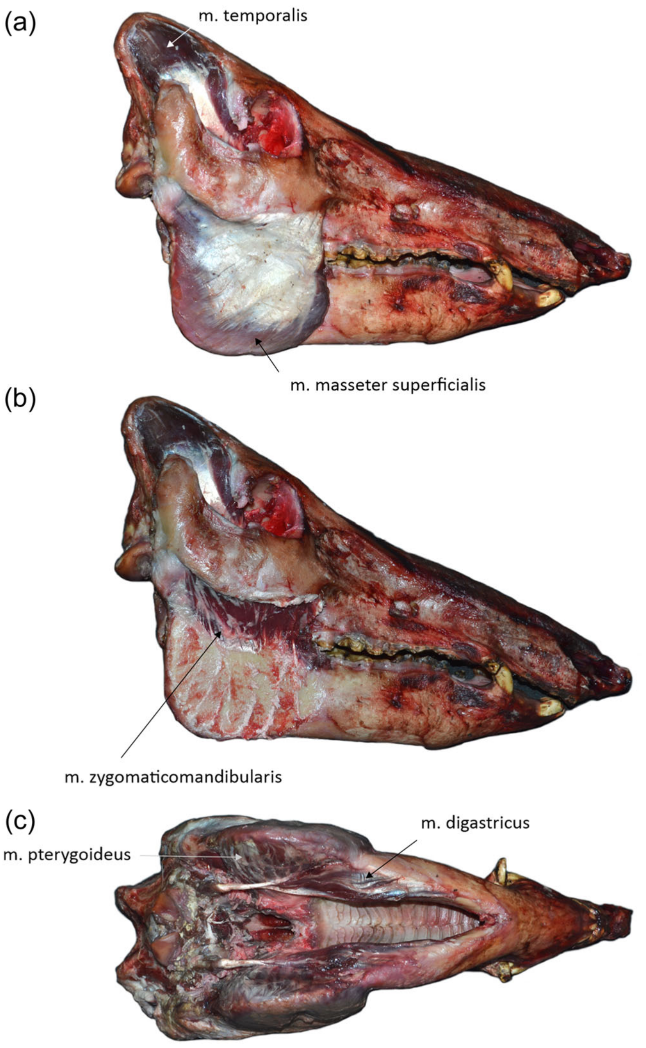

FIGURE 1 *Sus scrofa*, photographs of a dissection of a head illustrating the main jaw muscles. (a) Superficial lateral view after removal of the skin showing the temporalis and superficial masseter muscles. (b) Deeper lateral view after removal of the superficial and deep masseter muscles illustrating the zygomaticomandibularis. (c) Ventral view after removal of the skin, tongue, and associated muscles showing the position of the digastric and pterygoid muscles.

2.4 | Bite force

In vivo bite force data were recorded for 10 captive specimens that were later dissected. Two additional animals were included in the measurements but were kept alive at the end of the DOMEXP program. Four animals were reluctant to bite and were removed from the data set. We used a piezoelectric isometric Kistler force transducer (9311B; range ±5000 N; Kistler Inc.) connected to a charge amplifier (type 5058A5; Kistler Inc.; see Brassard et al., 2020; Herrel et al., 2002). The transducer was mounted in a custom set-up and fixed on a wooden stick and covered by several layers of cloth medical tape to protect the teeth of the wild boars and to provide grip. Animals were induced to move into a narrow cage with a wire mesh on the side. The transducer was passed through the mesh and animals readily bit the transducer. After one or two test bites animals quickly grabbed the transducer at the level of the premolar teeth and performed sustained bites. We performed three consecutive bite sessions for each animal and retained only the highest value for each individual. As the animals did not all bite at the same position on the transducer, we had to correct the recorded bite force for each trial by taking into account the distance between the location of the bite (using the imprints of the teeth on the tape) and the fulcrum.

2.5 | Statistical analyses

We Log_{10}-transformed all data before analyses. We then regressed each Log_{10}-transformed variable (muscle mass, muscle fiber length, and muscle cross-sectional area) on Log_{10}-transformed body mass using the entire sample and tested whether the slope of the regression deviated from predictions of geometric similarity (slope for mass on mass = 1; slope of cross-sectional area on mass = 0.66; slope of length on mass = 0.33) and extracted the unstandardized

TABLE 1 Allometry of cranial muscle architecture.

	Slope	Intercept	*p*	R^2	95% CI	Allometry
Digastric mass	0.86 ± 0.029	−3.09 ± 0.13	<.001	0.96	0.81–0.92	-
Digastric fiber length	0.26 ± 0.017	−0.26 ± 0.076	<.001	0.85	0.23–0.30	-
Digastric ACSA	0.60 ± 0.028	−2.86 ± 0.13	<.001	0.92	0.55–0.66	
Sup. mass. mass	1.01 ± 0.027	−3.28 ± 0.12	<.001	0.97	0.96–1.06	
Sup. mass. fiber length	0.36 ± 0.015	−0.81 ± 0.067	<.001	0.93	0.33–0.39	
Sup. mass. ACSA	0.65 ± 0.032	−2.50 ± 0.15	<.001	0.91	0.59–0.71	
Deep mass. mass	1.03 ± 0.039	−3.42 ± 0.18	<.001	0.94	0.95–1.10	
Deep mass. fiber length	0.35 ± 0.019	−0.86 ± 0.085	<.001	0.89	0.32–0.39	
Deep mass. ACSA	0.67 ± 0.036	−2.59 ± 0.17	<.001	0.89	0.60–0.75	
ZMA mass	0.89 ± 0.033	−3.11 ± 0.15	<.001	0.94	0.82–0.95	-
ZMA fiber length	0.32 ± 0.027	−0.87 ± 0.12	<.001	0.76	0.26–0.37	
ZMA ACSA	0.57 ± 0.036	−2.27 ± 0.17	<.001	0.85	0.50–0.64	-
ZMP mass	1.07 ± 0.036	−3.92 ± 0.17	<.001	0.95	1.00–1.15	
ZMP fiber length	0.36 ± 0.022	−1.00 ± 0.10	<.001	0.86	0.31–0.40	
ZMP ACSA	0.72 ± 0.041	−2.94 ± 0.19	<.001	0.88	0.63–0.80	
Temporalis mass	1.02 ± 0.023	−3.16 ± 0.11	<.001	0.98	0.97–1.07	
Temporalis fiber length	0.30 ± 0.028	−0.39 ± 0.13	<.001	0.74	0.25–0.36	
Temporalis ACSA	0.71 ± 0.029	−2.79 ± 0.13	<.001	0.93	0.66–0.77	
Pt. medialis mass	1.05 ± 0.027	−3.36 ± 0.13	<.001	0.97	0.99–1.10	
Pt. medialis fiber length	0.39 ± 0.017	−1.03 ± 0.08	<.001	0.92	0.35–0.42	+
Pt. medialis ACSA	0.66 ± 0.031	−2.36 ± 0.15	<.001	0.91	0.59–0.72	
Pt. lateralis mass	0.82 ± 0.041	−2.82 ± 0.19	<.001	0.90	0.74–0.90	-
Pt. lateralis fiber length	0.35 ± 0.022	−0.96 ± 0.10	<.001	0.85	0.30–0.39	
Pt. lateralis ACSA	0.48 ± 0.045	−1.88 ± 0.21	<.001	0.73	0.39–0.57	-
Total adductor mass	1.00 ± 0.016	−2.44 ± 0.076	<.001	0.99	0.96–1.03	
Total adductor ACSA	0.64 ± 0.016	−1.60 ± 0.072	<.001	0.96	0.60–0.67	

Note: Table entries are the regression slopes ± the standard deviations, the intercepts of the regressions ± the standard deviations, the *p*-value, the proportion of variation explained, the 95% confidence intervals, and the direction of the allometry when present.

Abbreviation: Sup. mass., superficial masseter.

residuals. We considered that relationships were allometric when the predicted slope (1, 0.66, or 0.33) fell outside the 95% confidence limits of the regression slope on the experimental data. We next ran a factor analysis with varimax rotation on the residual data and extracted all factors with eigenvalues greater than one to explore the positioning of specimens in morphospace. Finally, we ran multivariate analyses of covariance on the Log_{10}-transformed data with Log_{10}-transformed body mass as our covariate to test for differences between experimental groups and wild caught animals and between males and females. However, as the effect of sex was not significant (Wilks' lambda = 0.606; $F_{18,21} = 0.76$; $p = .72$) this factor was subsequently removed from the analyses. To test what variables predicted variation in bite force we ran regressions with Log_{10}-transformed body mass and Log_{10}-transformed muscle architecture variables on Log_{10}-transformed bite force. Since none of the variables tested was a good predictor of bite force, we also calculated the relative proportion of each muscle group relative to the total adductor mass. We arcsin-transformed the proportion data and regressed them on bite force.

3 | RESULTS

Whereas the smallest specimen included in the study weighed only 800 g the largest animal included in the data set weighed 110 kg representing two orders of magnitude of variation in size.

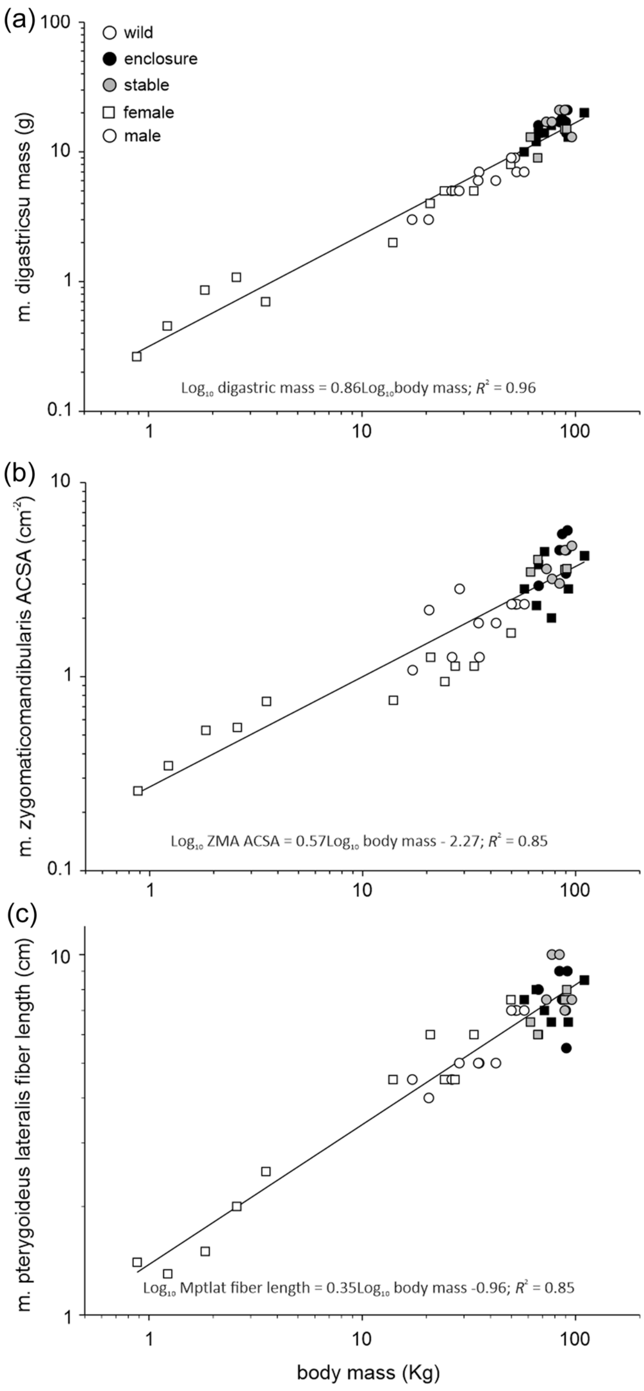

FIGURE 2 Scaling relationships of functional properties of some representative muscles: the mass of the m. digastricus (a), the anatomical cross-sectional area of the m. zygomaticomandibularis anterior (b), and the fiber length of the m. pterygoideus pars medialis (c). Indicated are the regression equations and the R^2 values. Squares represent females, circles males. Open symbols represent wild-caught wild boar, black symbols represent wild boar raised in an enclosure, and gray symbols represent wild boar raised in a stall.

TABLE 2 Results of the univariate analyses of covariance with Log10-transformed body mass as a covariate testing for differences between groups (stable, enclosure, wild).

Muscle	*F*	*p*
Digastric mass	6.66	.003
Digastric fiber length	1.39	.26
Digastric ACSA	6.66	.003
Sup. mass. mass	0.15	.86
Sup. mass. fiber length	1.02	.37
Sup. mass. ACSA	0.31	.73
Deep mass. mass	2.08	.14
Deep mass. fiber length	6.66	.003
Deep mass. ACSA	0.77	.47
ZMA mass	10.37	<.001
ZMA fiber length	0.38	.69
ZMA ACSA	5.15	.01
ZMP mass	0.36	.70
ZMP fiber length	2.34	.11
ZMP ACSA	0.07	.93
Temporalis mass	0.82	.45
Temporalis fiber length	2.52	.09
Temporalis ACSA	0.66	.52
Pt. medialis mass	5.39	.008
Pt. medialis fiber length	0.57	.57
Pt. medialis ACSA	5.73	.006
Pt. lateralis mass	4.18	.022
Pt. lateralis fiber length	2.99	.06
Pt. lateralis ACSA	6.25	.004
Total adductor mass	1.74	.19
Total adductor ACSA	0.41	.67

Note: Tables entries are the results of an ANCOVA with 2 and 41 degrees of freedom.

Abbreviation: Sup. mass., superficial masseter.

Concurrently, the total jaw adductor muscle mass ranged from 2.7 to 383 g, again spanning over two orders of magnitude. The largest adductor muscle was the temporalis muscle, which took up on average 24.7 ± 3.4% of the total adductor mass, followed by the medial pterygoid (21.0 ± 3.2%), the superficial masseter (17.2 ± 3.1%), and the deep masseter (15.0 ± 3.6%). The remaining muscles each take up a similar amount of the total adductor mass (zygomaticomandibularis pars anterior: 7.1 ± 2.5%; zygomaticomandibularis posterior: 7.8 ± 1.5%; pterygoideus lateralis: 7.2 ± 3.1%).

Our scaling analysis showed that most muscle architecture variables scaled as predicted for geometric similarity (Table 1). Negative allometry was observed for the mass and fiber length of the digastric muscle, the mass and cross-sectional area of the anterior part of the zygomaticomandibularis, and lateral pterygoid muscles (Figure 2). Thus, larger animals had relatively shorter digastric muscle

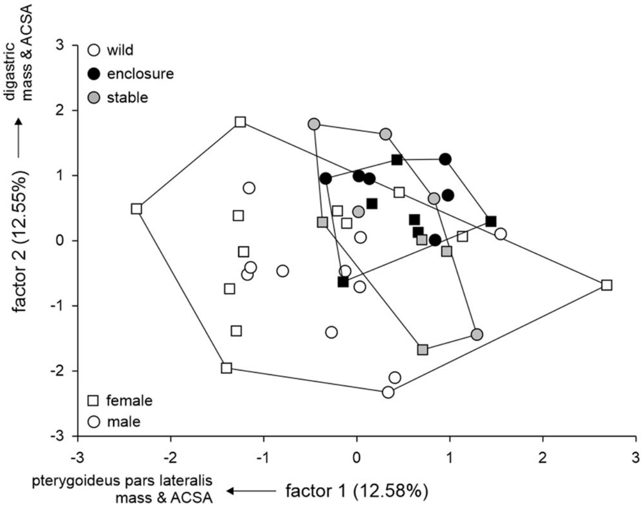

FIGURE 3 Graph illustrating the results of a factor analysis with varimax rotation performed on the residual muscle traits. Plotted are the individual specimens dissected. Note how wild animals tend to be different from captive animals in having a larger mass and anatomical cross-sectional area of the medial pterygoid muscle. Squares represent females, circles males. Open symbols represent wild-caught wild boar, black symbols represent wild boar raised in an enclosure, and gray symbols represent wild boar raised in a stall.

fiber lengths and smaller masses and cross-sectional areas of the anterior zygomaticomandibularis and the lateral pterygoid. Positive allometry was observed only for the fiber length of the medial pterygoid muscle showing that larger animals had relative longer fibers (Figure 2).

The MANCOVA detected significant differences in muscle architecture between the different groups (Wilks' lambda = 0.19; $F_{36, 48} = 1.72$; $p < .001$). The effect of body mass was also significant (Wilks' lambda = 0.10; $F_{18, 24} = 129.07$; $p < .001$). Subsequent univariate ANCOVAS showed that differences were significant for the mass and cross-sectional area of the digastric muscle, the fiber length of the masseter profundus, the mass and cross-sectional area of the zygomaticomandibularis pars anterior, and the mass and cross-sectional area of the pterygoideus pars lateralis and medialis (Table 2). Subsequent ANOVAs coupled to Bonferroni post hoc tests showed that wild was different from enclosure for the cross-sectional area of the digastric muscle with wild animals having smaller cross-sectional areas. The fiber length of the masseter profundus was also different between wild and enclosure with wild animals showing longer fibers. Wild animals were also different from both stable and enclosure animals in the mass of the anterior part of the zygomaticomandibularis muscle with captive animals having a significantly heavier muscle. Finally, the wild animals differed from the enclosure animals in having a larger cross-sectional area of the lateral pterygoideus muscle.

The factor analysis performed on the residual muscle architecture data extracted eight axes jointly explaining 82% of the variance in the data set (Figure 3). The first two axes explained only 25% and the first three axes only 37% of the variation in the data set (Table 3). Whereas the first axis was mainly negatively determined by the mass and cross-sectional area of the lateral pterygoid muscle, variation along the second axis was driven by variation in the digastric muscle mass and cross-sectional area. The third axis was mostly positively determined by the mass and cross-sectional area of the masseter profundus muscle (Table 3). When plotted the different groups in the morphospace determined by the first two factors wild animals appear clustered to the left of the first axis characterized by a larger mass and cross-sectional area of the lateral pterygoid, supporting the results of the statistical analysis.

The captive wild boar that participated in the bite force measures weighed on average 76.9 ± 14.8 kg and bit 753.9 ± 133.1 N ($N = 8$) at the level of the premolar teeth during unilateral biting. The highest force measured was 982.3 N for a female wild boar that weighed 57.3 kg. Variation in bite force was predicted well by the relative proportion of the superficial masseter only (R^2: 0.96; Figure 4). The larger the proportion of the superficial masseter relative to the total adductor mass, the higher the bite force (Figure 4).

4 | DISCUSSION

Our results showed that most muscles scaled isometrically or with slight negative allometry relative to overall body mass. The one exception was the fiber length of the medial pterygoid which scaled with positive allometry. When comparing our data to previously published data by Anapol and Herring (1989) we find that the scaling relationships of the mass of the masseter and the digastric muscle are nearly identical with slopes being only slightly steeper in minipigs. Thus, whereas the mass of the digastric scaled with slight negative allometry in wild boar it was isometric in minipigs (Table 4 and Figure 5). The mass of the masseter and its subdivisions scaled isometrically in both wild boar and minipigs. Interestingly, whereas muscle anatomical cross-sectional areas scaled isometrically for nearly all muscles, the tetanic tension of both the digastric and masseter muscles increased with strong positive allometry (Table 4; data from Anapol & Herring, 1989). In contrast bite force in wild boar scaled isometrically (Figure 5) suggesting a discrepancy between the scaling of maximal tetanic tension and muscle cross-sectional area and between maximal tetanic tension and bite force. The positive allometry for tetanic tension is unexpected as previous studies have shown that in older minipigs the masseter is composed of a greater proportion of slow-twitch fibers (Anapol & Herring, 2000). This, combined with differences in the jaw lever system during growth (see Figure 4 in Herring, 1985b) may help explain why bite force scaled as observed here. As the exact age of the wild-caught animals was unknown and as all DOMEXP animals were of the same age at the time of culling, we were unable to explore age-related growth patterns as done in other studies (Leonard et al., 2020). This would be an interesting avenue for further research.

As predicted, we observed some differences in the muscle architecture between wild animals and wild boar raised in captivity. Our results are similar to the results of Neaux, Blanc, Ortiz, Locatelli,

TABLE 3 Loadings of the factor analysis performed on the residual muscle architecture data.

	1	2	3	4	5	6	7	8
Eigenvalue	3.27	3.26	3.20	3.20	2.74	2.51	1.94	1.44
% variance	12.58	12.55	12.32	12.30	10.52	9.66	7.47	5.23
Res. digastric mass	0.014	**0.870**	0.112	0.075	0.056	0.201	−0.161	0.021
Res. digastric fiber length	−0.165	0.100	0.089	−0.060	−0.083	0.762	−0.189	0.170
Res. digastric ACSA	0.112	**0.836**	0.062	0.113	0.107	−0.248	−0.052	−0.080
Res. masseter sup. mass	−0.089	0.360	−0.047	**0.749**	0.120	−0.104	−0.176	0.303
Res. masseter sup. fiber length	0.024	−0.057	−0.163	−0.042	−0.130	**0.799**	0.253	0.062
Res. masseter sup. ACSA	−0.085	0.327	0.035	0.644	0.160	−0.451	−0.262	0.224
Res. masseter profundus mass	0.003	0.152	**0.864**	−0.109	0.320	0.026	0.070	−0.110
Res. masseter profundus fiber length	0.405	0.374	0.098	−0.301	0.315	0.404	0.105	−0.346
Res. masseter profundus ACSA	−0.207	−0.029	**0.881**	0.038	0.182	−0.181	0.021	0.060
Res. ZMA mass	0.730	0.151	0.354	−0.001	−0.273	0.280	0.006	0.077
Res. ZMA fiber length	0.055	−0.037	0.170	−0.087	−0.121	0.093	**0.875**	0.142
Res. ZMA ACSA	0.620	0.164	0.195	0.064	−0.157	0.184	−0.645	−0.035
Res. ZMP mass	−0.175	0.020	0.241	0.253	**0.833**	0.022	0.067	−0.007
Res. ZMP fiber lengh	−0.091	−0.346	0.028	0.239	−0.148	0.488	0.516	−0.049
Res. ZMP ACSA	−0.106	0.209	0.199	0.093	**0.823**	−0.250	−0.224	0.020
Res. temporalis mass	0.185	0.272	0.407	0.550	−0.150	0.267	0.204	−0.047
Res. temporalis fiber length	0.112	0.518	0.545	−0.383	−0.186	0.158	0.032	0.083
Res. temporalis ACSA	0.042	−0.275	−0.193	**0.808**	0.058	0.064	0.133	−0.117
Res. pterygoideus medialis mass	0.440	0.539	0.227	0.346	0.390	−0.028	0.006	−0.024
Res. pterygoidus medialis fiber length	−0.159	−0.026	0.009	0.116	0.084	0.193	0.159	**0.780**
Res. pterygoideus medialis ACSA	0.472	0.484	0.194	0.237	0.294	−0.132	−0.083	−0.454
Res. pterygoideus lateralis mass	**−0.815**	−0.016	0.264	−0.022	0.145	0.124	−0.024	0.237
Res. pterygoideus lateralis fiber length	0.275	0.047	0.086	−0.174	0.540	−0.257	−0.089	0.403
Res. pterygoideus lateralis ACSA	**−0.891**	−0.038	0.202	0.065	−0.131	0.241	0.021	0.022
Res. total adductor mass	0.114	0.415	0.633	0.497	0.343	0.122	0.064	0.102
Res. total adductor ACSA	−0.024	0.246	0.466	0.616	0.399	−0.215	−0.299	−0.149

Note: Bolded variables are variables with loadings greater than 0.7.

Laurens, et al., (2021) who used the same data set to explore how captivity impacts the cranial system in wild boar. However, in the Neaux, Blanc, Ortiz, Locatelli, Laurens, et al. (2021) study variation in body size was not considered in the analyses. Here, we show that differences persist irrespective of variation in body size. Different from that study, our result suggest that the differences were greatest between animals raised in an enclosure and wild animals with animals raised in a stall being intermediate. Interestingly wild animals had a greater anatomical cross-sectional area of the lateral pterygoid muscle. This muscle has a dual function in jaw opening and the stabilization of the jaw joint, at least in rhesus macaques (McNamara, 1973). Given the diversity of oral behaviors in wild boar such as rooting in addition to feeding (Erdtmann & Keuling, 2020) stabilization of the jaw joint may be particularly important in wild animals. Moreover, wild animals had longer fibers in the deep masseter compared to animals raised in an enclosure. Longer fibers will allow a greater excursion and may promote gape. This may again be associated with a greater diversity of foods and food types eaten by the wild animals compared to captive ones. In contrast, captive animals had a larger anterior zygomaticomandibularis muscle mass as was shown previously (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021). This was suggested to be due to an increase in feeding behavior, especially feeding on small pellets and an increase in stereotypical behaviors like bar biting or cheek rubbing (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021). Finally, enclosure animals had a greater digastric cross-sectional area suggesting they have a more

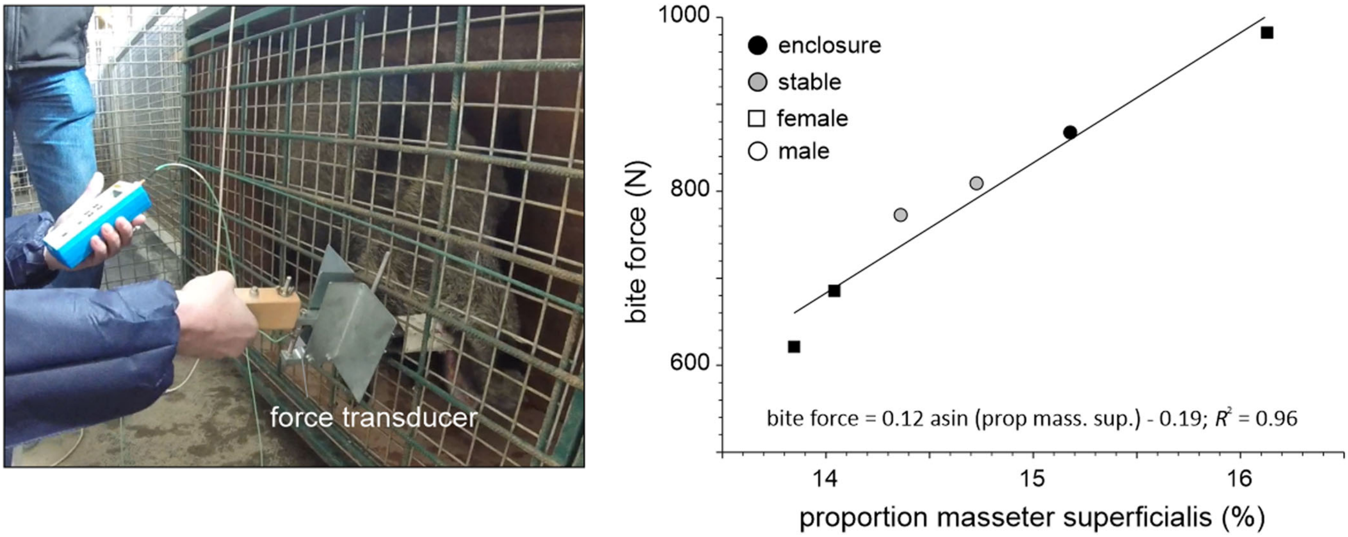

FIGURE 4 Illustration of the set-up used to measure bite forces in captive wild boar (left). To the right is plotted variation in bite force in function of body mass. The slope, intercept, and % variation explained are also indicated on the graph. Squares represent females, circles males. Black symbols represent wild boar raised in an enclosure, and gray symbols represent wild boar raised in a stall.

TABLE 4 Scaling relationships for minipig data from Anapol and Herring (1989).

	Slope	Intercept	*p*	R^2	95% CI	Allometry
Digastric mass	0.90 ± 0.08	−3.24 ± 0.29	<.001	0.90	0.74–1.07	
Digastric force	1.07 ± 0.13	−3.87 ± 0.49	<.001	0.84	0.79–1.35	+
Sup. mass. mass	1.11 ± 0.08	−3.21 ± 0.31	<.001	0.93	0.93–1.28	
Sup. mass. force	1.18 ± 0.12	−3.46 ± 0.44	<.001	0.88	0.93–1.43	+

Note: Whereas muscle mass scaled isometrically, muscle force scaled with positive allometry.

Abbreviations: CI, 95% confidence interval; Digastric, m. digastricus; Sup mass., superficial masseter.

forceful jaw opener muscle. Why this could be remains elusive at this point and remains to be understood.

Neither body mass nor muscle mass or cross-sectional area were good predictors of bite force in our data set. This is possibly because all animals were adults rendering variation in bite force across individuals low. Yet, the proportion that the superficial masseter took up relative to the total adductor mass was an excellent predictor of bite force. This suggests that the superficial masseter is an important contributor to bite force and that variation in this muscle specifically rather than overall variation in muscle mass or cross-sectional area is important. Our bite force measurements for captive wild boar were significantly lower, however, than previous estimates for feral pigs or peccaries (Sicuro et al., 2021) despite being heavier, on average. It is unlikely that we underestimated bite force due to unilateral biting on the transducer as pigs have a fused symphysis (Lee et al., 2019) allowing the transfer of muscle force from the balancing to the working side. Although captive conditions may impact the use and the development of the jaw closer muscles, our results for the muscle data showed that wild animals only had a greater cross-sectional area of the lateral pterygoid muscle compared to wild ones. The overall summed cross-sectional area, likely a good proxy for bite force, did not differ between captive and wild specimens. However, the feral pigs studied in Sicuro et al. (2021) are likely derived from domestic breeds, which likely differ in muscle mass and architecture compared to the wild boar studied here. Indeed, when inspecting the scaling of masseter muscle mass between minipigs (domestic breed) and wild boar it becomes apparent that minipigs have a larger masseter mass for their size (Figure 5). Moreover, in our study animal were biting at the level of the premolars, more anteriorly on the tooth row than in the study by Sicuro et al. (2021). As bite force decreases with the distance of the bite point to the fulcrum this may explain the lower forces observed here. One final possibility is that the pigs in our study bit at larger gapes than the animals in the Sicuro et al. (2021) study. Indeed, in that study the device introduced in the mouth had a diameter of 16.5 mm whereas the total distance between the bite plates in our study was closer to 42 mm. As bite force is known to decrease with gape (Dumont & Herrel, 2003) this may further help explain the observed differences.

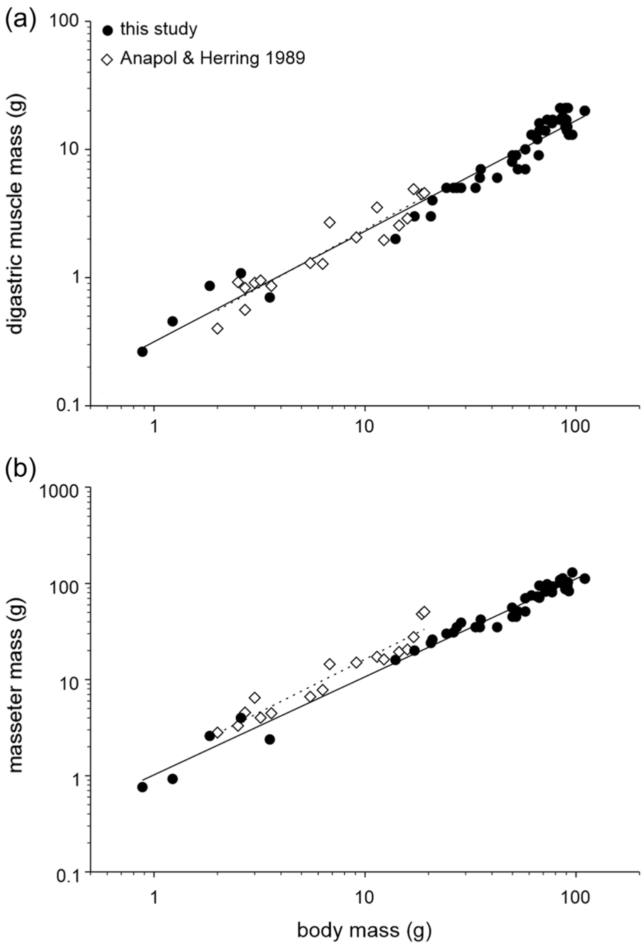

FIGURE 5 Plot of data collected in this study with the data from Anapol and Herring (1989) for the digastric and masseter muscles (a). Note that the scaling of muscle mass is isometric for both wild boar and the minipigs from Anapol and Herring (1989). However, minipigs have a larger masseter muscle for a given body size compared to wild boar (b; see Table 4).

5 | CONCLUSION

Our data show that the jaw muscle system in wild boar grows largely isometrically with larger animals being scaled-up versions of smaller ones. This is reflected in the scaling of muscle mass, fiber length, muscle anatomical cross-sectional area, and bite force. Unexpectedly, the variation in the proportion of the superficial masseter to the overall adductor muscle mass was an excellent predictor of variation in bite force. We observed some differences in the muscle architecture between wild animals and animals raised under captive conditions with animals raised in outdoor enclosures being most different. Differences in feeding behavior and nutritional quality likely underpin these differences, yet remain to be investigated further.

AUTHOR CONTRIBUTIONS

Anthony Herrel: Conceptualization (lead); data curation (equal); formal analysis (equal); investigation (equal); visualization (lead); writing—original draft (lead); writing—review and editing (lead). **Yann Locatelli**: Project administration (supporting); resources (equal); writing—review and editing (supporting). **Katia Ortiz**: Project administration (supporting); resources (equal); writing—review and editing (supporting). **Jean-Christophe Theil**: Investigation (supporting); methodology (supporting); writing—review and editing (supporting). **Raphaël Cornette**: Investigation (supporting); writing—review and editing (supporting). **Thomas Cucchi**: Data curation (lead); funding acquisition (lead); investigation (supporting); project administration (lead); writing—review and editing (supporting).

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DATA AVAILABILITY STATEMENT

Data are available in article (supplementary material).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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