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Hugo Harbers

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Hugo HARBERS

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Identification des marqueurs morphofonctionnels du processus de domestication en archéozoologie : approche tridimensionnelle de la variation endostructurale de la diaphyse humérale et de la forme du calcanéus

sous la direction de :

Dr. Thomas CUCCHI, CR, UMR 7209 CNRS - MNHN, Directeur de la thèse

devant le jury :

Pr. Marcelo SANCHEZ-VILLAGRA, Paläontologische Institut Zürich, Rapporteur

Pr. Joris PETERS, Institut für Paläoanatomie München, Rapporteur

Dr. Rose-Marie ARBOGAST, DR, UMR 7044 UniStra, Membre du jury

Pr. Roberto MACCHIARELLI, UMR 7194 CNRS - MNHN, Membre du jury

Dr. Lionel GOURICHON, UMR 7264 CEPAM, Membre du jury

Dr. Jean-Denis VIGNE, DR, UMR 7209 CNRS - MNHN, Membre du jury

Dr. Anthony HERREL, DR, UMR 7179 CNRS - MNHN, Membre du jury

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RÉSUMÉ

L'étude de la domestication peut nous apporter des informations capitales à la fois sur notre histoire et le développement de nos sociétés, mais également sur l'évolution des espèces et les processus biologiques qui ont mené à la diversité des formes vivantes actuelles. On peut synthétiser le processus de domestication en deux étapes : la mise en relation entre la potentielle espèce domestique et l'Homme, puis son adaptation évolutive à la vie avec l'Homme au fil des générations. Ainsi pour étudier la domestication il est nécessaire pour les archéologues de trouver des traces de ces deux étapes dans les restes archéologiques. Bien que l'adaptation évolutive laisse un grand nombre de marqueurs morphologiques qui nous permettent d'étudier sans peine la domestication une fois qu'elle est bien amorcée, la mise en relation en revanche ne laisse que très peu de traces.

Cette thèse vise à identifier et caractériser deux marqueurs du contact entre un animal et l'Homme : les conséquences morphologiques osseuses de la croissance en captivité sur le calcanéus et l'humérus chez le sanglier (*Sus scrofa*). Ces éventuels marqueurs serviront à développer de nouvelles méthodes pour détecter les premières étapes du processus de domestication chez le sanglier en contexte archéologique. L'hypothèse testée est que le changement de comportement d'un individu dont la mobilité est réduite peut laisser une empreinte observable et mesurable dans la morphologie osseuse. Cette thèse fait partie du projet ANR DOMEXP de domestication expérimentale dans laquelle des sangliers ont été élevés en captivité pendant deux ans et scannés tout au long de leur croissance pour étudier l'impact de la captivité sur leur anatomie osseuse.

Nos résultats montrent que la captivité induit une réponse morphologique plastique pour les deux marqueurs, et l'application de ces deux méthodes sur des suinés du Néolithique a montré que la morphologie des suinés d'Europe de l'Ouest a changé au cours du Néolithique, ce qui pourrait être considéré comme la conséquence de l'arrivée d'un nouveau système de gestion basé sur un contrôle accru des populations. De plus la présence de spécimens de petite taille évoque la possibilité d'une trajectoire commensale. Ces résultats pourraient être complétés par des approches isotopiques et génomiques afin de fournir une vision plus complète de cette période.

ABSTRACT

The study of domestication can provide us with valuable information both on our history and the development of our societies, but also on the evolution of species and the biological processes that have led to the diversity of living forms today. The domestication process can be synthesized in two stages : the contact between the potential domesticated species and the human ecosystem, then its evolutionary adaptation to life within the human environment over the generations. Thus to study domestication it is necessary for archaeologists to find traces of these two stages in archaeological remains. Although evolutionary adaptation leaves a large number of morphological markers that allow us to study domestication without difficulty once it is properly initiated, the process of the early interactions on the other hand, leaves very few traces.

This thesis aims to identify and characterize two markers of early process of domestication : the morphological skeletal consequences of growth in captivity in wild boar (*Sus scrofa*) on the calcaneus and humerus. These potential markers will be used to develop new methods to detect the early stages of the domestication process in wild boar in an archaeological context. The hypothesis being tested is that a change in the behavior of an individual with reduced mobility can lead to observable and measurable changes in bone morphology. This thesis is based on the DOMEXP ANR experimental domestication project in which wild boars were bred in captivity for two years and scanned throughout their growth to study the impact of captivity on their bone anatomy.

Our results show that captivity induces a plastic morphological response for both markers, and the application of these two methods on Neolithic suines showed that the morphology of Western European suines changed during the Neolithic, which could be considered as a consequence of the arrival of a new management system based on increased population control. Moreover, the presence of small specimens evokes the possibility of a commensal trajectory. These results could be complemented by isotopic and genomic approaches in order to provide a more complete picture of this period.

TABLE DES MATIÈRES

	Page
Remerciements	1
Résumé	4
Abstract	5
Table des matières	6
Table des figures	10
Liste des tableaux	12
1 Introduction	13
Préambule	14
1.1 Évolution et Domestication	14
1.1.1 Évolution des espèces	14
1.1.2 Définition biologique d'un animal domestique	15
1.1.3 Définition anthropologique d'un animal domestique	16
1.1.4 Trajectoires de domestication	16
1.1.5 Syndrome de domestication	19
<i>Aparté historique 1 L'expérimentation sur le renard argenté</i>	<i>19</i>
1.2 Identification de la domestication en contexte archéologique	21
1.2.1 Marqueurs archéologiques habituels	21
1.2.2 Génotype, Phénotype, Plasticité phénotypique et Norme de réaction	23
1.2.3 Protocole expérimental	24
1.2.4 Plasticité osseuse	26
1.2.5 Morphométrie géométrique	27
1.2.6 Cartographie de l'épaisseur corticale	28
1.2.7 Mise à l'épreuve des nouvelles méthodes : Application archéologique	31
<i>Aparté historique 2 Domestication du cochon et diffusion en Europe</i>	<i>32</i>
1.3 Structure de la thèse	33

Références	34
2 The mark of captivity :	
plastic responses in the ankle bone of a wild ungulate (<i>Sus scrofa</i>)	44
Abstract	45
2.1 Introduction	46
2.2 Material and methods	47
2.2.1 Experimental design	47
2.2.2 Comparative collection	47
2.2.3 Calcaneus three-dimensional models	49
2.2.4 Three-dimensional shape and centroid size variables	49
2.2.5 Life-history dataset	49
2.2.6 Muscle force estimates	49
2.2.7 Available area for locomotion	49
2.2.8 Statistical analyses	51
<i>Size, shape and life traits covariation in captive and wild-caught wild boars</i>	51
<i>Comparing plastic size and shape response to captivity with changes induced by artificial selection</i>	51
2.3 Results	51
2.3.1 Plastic responses to captivity in wild boars	51
2.3.2 Comparing plastic response to captivity in wild boars to artificial selection signal in domestic pigs	52
2.4 Discussion	53
2.4.1 Plastic response to captivity	53
2.4.2 Captivity and change in muscular function	54
2.4.3 Plastic versus selective changes	56
2.5 Conclusion	56
References	56
3 Investigating the impact of captivity and domestication on limb bone cortical morphology :	
an experimental approach using a wild boar model (<i>Sus scrofa</i>)	59
Abstract	60
3.1 Introduction	60
3.2 Material and methods	61
3.2.1 Experimental design	61
3.2.2 Comparative collection	62
3.2.3 Humerus 3D models	62
3.2.4 Bone volume	62
3.2.5 Morphometric mapping of the humeral cortical thickness	63
3.2.6 Standardization	64
3.2.7 Life history dataset	64
3.2.8 Muscle force estimates	64
3.2.9 Statistical analyses	64
<i>Size, shape and life trait covariations in wild-caught and captive wild boars</i>	64
<i>Comparing plastic size and shape response to captivity with changes induced by artificial selection</i>	64
3.3 Results	65

3.3.1	Lifetime changes in humerus cortical thickness in wild boars associated with mobility reduction	65
3.3.2	Relative impacts of locomotor behaviour and selection in humerus cortical thickness	65
3.4	Discussion	66
3.5	Conclusion	69
	References	69
	<i>Erratum</i>	73
4	Pig domestication in Western Europe : assessing the impact of anthropogenic control over Early Neolithic <i>Sus scrofa</i> populations	74
4.1	Introduction	75
4.2	Material and methods	77
4.2.1	Comparative collection	77
4.2.2	Archaeozoological material and context	77
	<i>Mesolithic comparative collection</i>	79
	<i>Cyprus island</i>	80
	<i>Continental Western Europe</i>	80
	<i>Areas under Mediterranean influence</i>	81
4.2.3	Humerus cortical thickness topology and cross section area	82
4.2.4	Calcaneus three-dimensional shape and centroid size	83
4.2.5	Statistical analyses	83
4.3	Results	84
4.3.1	Humerus cortical thickness topography in modern and archaeological <i>Sus scrofa</i>	84
4.3.2	Variation in calcaneus size and shape in current and archaeological <i>Sus scrofa</i>	86
4.3.3	Predicting the level of anthropogenic pressure on population of <i>Sus scrofa</i> in Western Europe	90
4.4	Discussion	93
4.4.1	Methodological consideration	93
4.4.2	Revisiting the status of <i>Sus scrofa</i> remains from early Neolithic contexts in Cyprus and Western Europe	94
	<i>Cyprus island</i>	94
	<i>Continental Western Europe</i>	94
	<i>Early and middle Neolithic in the Mediterranean area</i>	95
	<i>Middle and late Neolithic in areas under Mediterranean influence</i>	95
	<i>On the low prediction rate of captive specimens</i>	95
4.4.3	Neolithisation and phenotypic diversification in Western Europe <i>Sus scrofa</i>	95
4.5	Conclusion and perspectives	96
	References	97
5	Conclusions et perspectives générales	104
	Préambule	105
5.1	Conclusions	105
5.1.1	Chapitre 2	105
	<i>Le comportement locomoteur d'un sanglier en captivité peut-il induire des modifications de conformation osseuse au-delà de la norme de réaction des sangliers sauvages ?</i>	105

	<i>À quel point ces modifications sont impactées par le lien fonctionnel entre os et muscles ?</i>	105
	<i>Comment ces modifications diffèrent-elles de celles induites par la sélection artificielle pratiquée chez le cochon au cours des 200 dernières années ?</i>	106
5.1.2	Chapitre 3	106
	<i>La réduction de la mobilité au cours de la croissance chez le sanglier peut-elle induire des variations mesurables dans la structure corticale des os des membres au-delà de la norme de réaction des sangliers sauvages ?</i>	106
	<i>À quel point ces modifications sont impactées par le lien fonctionnel entre os et muscles ?</i>	106
5.1.3	Chapitre 4	106
	<i>Quelles limites méthodologiques ont pu être mises en évidence par cette application archéozoologique ?</i>	107
	<i>Quelles nouvelles données ont pu être apportées par ce réexamen du statut des suinés du début du Néolithique en Europe occidentale ?</i>	108
5.2	Perspectives	110
5.2.1	Avenir du projet expérimental DOMEXP	110
5.2.2	Perspectives de l'analyse du calcaneus en morphométrie géométrique tridimensionnelle	110
5.2.3	Perspectives de l'analyse de la topographie de l'épaisseur corticale de l'Humérus	111
5.2.4	Avenir de l'évaluation de l'impact anthropogénique sur les populations archéologiques de <i>Sus scrofa</i> par l'étude de la forme des os et de la topographie de l'épaisseur corticale	112
	Références	113
	Annexes	117
	Rapports d'évaluation et corrections	131
	Rapport de Pr. Marcelo SANCHEZ-VILLAGRA	132
	Rapport de Pr. Joris PETERS	136
	Corrections	139
	1 Général	139
	2 Chapitre 1, Section 1.2.4, Plasticité osseuse	139
	3 Chapitre 3, <i>Erratum</i>	139
	Références complémentaires	140

TABLE DES FIGURES

Introduction	13
1.1 Diagramme synthétique du processus de domestication.	17
1.2 Vue d'ensemble des trajectoires et des symptômes du syndrome de domestication chez les animaux domestiques.	20
1.3 Diagramme du protocole expérimental DOMEXP.	25
1.4 Principe de la plasticité osseuse corticale.	25
1.5 Principe de la superposition procruste.	27
1.6 Protocole d'analyse de la topographie de l'épaisseur corticale de l'humérus.	29
1.7 Carte de la diffusion des populations Néolithiques en Europe à partir du proche-Orient. (D'après Tresset et Vigne, 2011)	31
Chapitre 2	44
2.1 The wild boar calcaneus in relation to the other bones and muscles of the leg.	50
2.2 Differences in calcaneus centroid size and body mass among captive-rearer and wild-caught wild boars.	52
2.3 Difference in muscle ACSA among captive-rearer and wild-caught wild boars.	53
2.4 Relationships between the calcaneus shape and body mass, available area, calcaneus centroid size and muscle ACSA.	53
2.5 Calcaneus centroid size variation.	54
2.6 Morphospace from CVA on calcaneus geometric morphometry.	55
Chapitre 3	59
3.1 Diagram of the different stages of the Morphometric mapping protocol.	63
3.2 Differences in body mass and bone volume among captive-reared and wild-caught wild boars.	65
3.3 Differences in muscle ACSA among wild caught and captive-reared wild boars.	66
3.4 PLS regressions between the humerus shaft cortical topography and life history traits and muscle ACSA.	67

3.5	Humerus bone volume variation.	67
3.6	Morphospace from CVA on humerus shaft cortical topography.	68
Chapitre 4		74
4.1	Geographical, chronological and archaeological context of the selected sites.	79
4.2	Variation in humerus cross section area in Mesolithic, Neolithic and current specimens.	85
4.3	Morphospace from LDA on humerus shaft cortical topography.	87
4.4	Calcaneus centroid size variation in Mesolithic, Neolithic and current specimens.	88
4.5	Morphospace from LDA on calcaneus geometric morphometry.	89
4.6	Summary of LDA probabilities, knn prediction, size cluster, and assumptions based on archaeozoological analyses.	91
4.7	Timeline of calcaneus centroid size and humerus cross section area for each period of each site in their chronological context.	93
Annexes		117
SI 4.2	131

LISTE DES TABLEAUX

Chapitre 2	44
2.1 Sample size and origin of the samples.	48
2.2 Anatomical definition of the 14 landmarks and 7 curves.	50
Chapitre 3	59
3.1 Sample origin and number of available specimens for the different parameters analysed in this study.	62
Annexes	117
SI 2.1	121
SI 2.2	122
SI 3.1	124
SI 4.1	130

CHAPITRE

1

INTRODUCTION

Préambule

Cette thèse a pour objectif d'identifier et caractériser les conséquences morphologiques osseuses de la croissance en captivité chez le sanglier, et à comprendre par quels phénomènes biologiques ces symptômes morphologiques sont engendrés. Ces symptômes serviront alors à développer de nouvelles méthodes pour détecter les premières étapes du processus de domestication chez le sanglier en contexte archéologique. Ces marqueurs morphologiques seront enfin appliqués à des séries archéologiques de *Sus scrofa* du Mésolithique au Néolithique final de l'Europe de l'Ouest afin d'apporter de nouvelles données sur l'histoire de la domestication du porc et du rôle de l'Homme sur l'évolution des populations de suinés en Europe.

Les prochains paragraphes de ce chapitre expliquent ce qu'est le processus de domestication et ce qui définit un animal domestique à la fois d'un point de vue biologique et anthropologique, quelles trajectoires peuvent amener les animaux à une domestication, quels sont les symptômes de la domestication, mais également quelles sont les différentes méthodes classiquement utilisées pour identifier la domestication sur des restes animaux trouvés en contexte archéologique et quelles sont leurs limites, quelle est l'hypothèse défendue dans cette thèse et quels protocoles expérimentaux et méthodologiques seront utilisés dans le cadre de cette thèse.

1.1 Évolution et Domestication

1.1.1 Évolution des espèces

Comme pour tous les animaux, le chien, le chat, le cochon et les autres animaux domestiques n'ont pas toujours existé. Ils sont le fruit d'un pan particulier du phénomène d'évolution des espèces : la domestication. Avant de voir en quoi la domestication se singularise de l'évolution, il est nécessaire de comprendre comment fonctionne l'évolution des espèces. Théorisée par Darwin (Darwin, 1859) puis Dobzhansky (Dobzhansky, 1937), Goldschmidt (Goldschmidt, 1940) et Mayr (Mayr, 1947) entre autres, la théorie de l'évolution repose sur trois constats :

1. *Variation*. Il existe une variabilité du phénotype entre les individus d'une même population. Autrement dit, tous les individus ont des caractéristiques différentes. Cette diversité est majoritairement provoquée par les mutations génétiques qui apparaissent aléatoirement chez les individus d'une génération à l'autre.
2. *Sélection*. Il existe une corrélation entre les caractères d'un individu et sa capacité à survivre et se reproduire : plus ses caractères sont en adéquation avec son écosystème actuel, plus ses capacités de survie et de reproduction sont élevées. Inversement, moins ses caractères sont en adéquation avec son écosystème actuel, plus ses risques de mourir et de ne jamais se reproduire sont élevés. C'est ce que l'on appelle la sélection naturelle.
3. *Héritabilité*. Les caractères sont au moins en partie héréditaires par les générations suivantes. Autrement dit un individu va avoir tendance à présenter des caractères similaires à ceux de ses parents.

Il en résulte qu'à chaque génération, la proportion dans la population de chaque caractère varie légèrement par rapport à la génération précédente. La proportion des caractères les moins adaptés à l'écosystème actuel baisse, et la proportion des caractères les plus adaptés augmente au fil des générations. Sur une courte échelle de temps, de l'ordre de quelques générations, cela peut se traduire par la fixation d'un caractère dans la population, c'est-à-dire que tous les individus de la population finissent par présenter ce caractère (microévolution). Sur une plus longue échelle de temps, deux populations d'une même espèce vivant dans des écosystèmes différents vont accumuler un grand nombre de nouveaux caractères différents en fonction de leur écosystème, jusqu'à ce que les différences entre les deux populations soient assez importantes pour les considérer comme deux espèces distinctes, c'est-à-dire deux populations qui ne sont plus interfécondes entre elles (macroévolution).

1.1.2 Définition biologique d'un animal domestique

Pour en revenir à la domestication, il s'agit d'un cas particulier d'évolution dans lequel les forces évolutives sont anthropogènes. Dans ce cas particulier, la population se retrouve en contact avec un anthropo-écosystème, c'est-à-dire un environnement créé ou modifié par l'Homme, dans lequel vivent des humains qui interagissent entre eux et avec l'environnement (Coppinger and Coppinger, 2001 ; Herre and Röhrs, 1990 ; Larson and Fuller, 2014 ; Lord et al., 2013 ; Vigne, 2015, 2011). Que ce soit quelques individus issus d'une population animale qui pénètrent cet anthropo-écosystème par eux-même, ou bien l'Homme qui les y introduit, cela va produire sur eux une cascade de phénomènes de deux types (Figure 1).

1. Des changements développementaux, qui interviennent dès l'entrée des individus dans le nouvel écosystème et se maintiennent tant que les individus y restent :
 - Un stress biomécanique lié à la diminution de la prédation, à l'augmentation de la disponibilité de la nourriture, à la diminution de l'espace disponible...
 - Un stress psychogénique, émotionnel et/ou comportemental lié aux densités élevées de population et à la réduction du nombre d'options disponibles en terme d'interactions sociales qui en découle.
 - Des changements de régime alimentaire liés aux nouvelles ressources offertes par l'anthropo-écosystème.
 - Des changements au niveau des maladies auxquelles sont soumis les individus, principalement liés aux fortes densités de population qui favorisent la transmission intra-spécifique, mais également à la proximité avec d'autres espèces domestiques qui favorise la transmission inter-spécifique des maladies.
2. Des changements génétiques et évolutifs, dont certains apparaissent directement liés au changement d'écosystème, et d'autres qui se mettent en place plus progressivement au cours de la succession des générations :
 - Un effet fondateur, c'est-à-dire une forte réduction de la variabilité génétique par rapport à la population sauvage, liée au nombre réduit d'individus qui ont rejoint l'anthropo-écosystème.
 - Une augmentation de la consanguinité qui découle directement de l'effet fondateur.

- Une augmentation de la dérive génétique qui découle également de l'effet fondateur. La dérive génétique étant un phénomène d'évolution aléatoire des fréquences de caractères dans la population, indépendamment de leur adéquation avec l'écosystème actuel, causée par le hasard des rencontres, des fécondations etc... Ce phénomène a lieu parallèlement à l'évolution classique par la sélection naturelle, mais ses effets sont d'autant plus importants que la population est petite (Kimura, 1968 ; Ohta and Kimura, 1969).
- Une augmentation de la sélection naturelle des caractères en adéquation avec la vie dans un anthropo-écosystème.
- Une diminution de la sélection naturelle des caractères en adéquation avec la vie dans un écosystème naturel.
- L'apparition d'une sélection artificielle, caractéristique de la domestication et exercée de façon consciente ou non par les Hommes en fonction de leurs préférences, de leurs besoins etc...
- Des effets corrélés à la sélection artificielle et la nouvelle sélection naturelle. En effet, beaucoup de gènes sont dit « pléiotropiques », c'est-à-dire qu'ils agissent sur plusieurs caractères. Ainsi la sélection d'un caractère peut, par effet pléiotropique, influencer d'autres caractères corrélés qui ne sont pas originellement ciblés par la sélection.

Tous ces phénomènes vont alors conduire à un isolement génétique de cette sous-population vis-à-vis du reste des populations de l'espèce, et à la sélection des individus dont les caractères sont les plus favorables à la survie et la reproduction dans cet environnement anthropogène et au contact de l'Homme. Ce processus d'isolement et de sélections naturelle et artificielle a des conséquences biologiques, à la fois comportementales et morphologiques. Ainsi, un animal domestique est un animal qui a colonisé un anthropo-écosystème et dont les caractères biologiques ont fini par être modifiés au fil des générations jusqu'à s'adapter à ce nouvel écosystème (Figure 1.1 page 17).

1.1.3 Définition anthropologique d'un animal domestique

La définition biologique de la domestication à l'avantage d'être précise, et à première vue sans équivoque. Cependant, elle souffre d'un défaut majeur : il s'avère que la colonisation du nouvel écosystème et l'apparition d'adaptations morphologiques sont toutes les deux des phénomènes continus, progressifs. En effet les interactions entre les populations animales et humaines forment un *continuum* qui va de la simple cohabitation sans réelle interaction, au contrôle total de tous les aspects de la vie d'un animal et son intégration dans la société comme dans le cas des animaux de compagnie. Il est ainsi très compliqué de tracer une limite sur ce *continuum* pour séparer les animaux sauvages des domestiques. Les anthropologues et les archéozoologues ont plutôt tendance à considérer le début de ce *continuum* comme étant le début du processus de domestication. Dans ce cadre, un animal commence donc à être considéré comme domestique dès que l'interaction entre l'Homme et l'animal commence à s'intensifier et avant même que des adaptations évolutives commencent à apparaître (Vigne, 2015, 2011) (Figure 1.1 page 17).

1.1.4 Trajectoires de domestication

Depuis une dizaine d'années, les archéozoologues se sont mis d'accord sur la conceptualisation de ces processus de domestication qui s'effectuent selon plusieurs trajectoires.

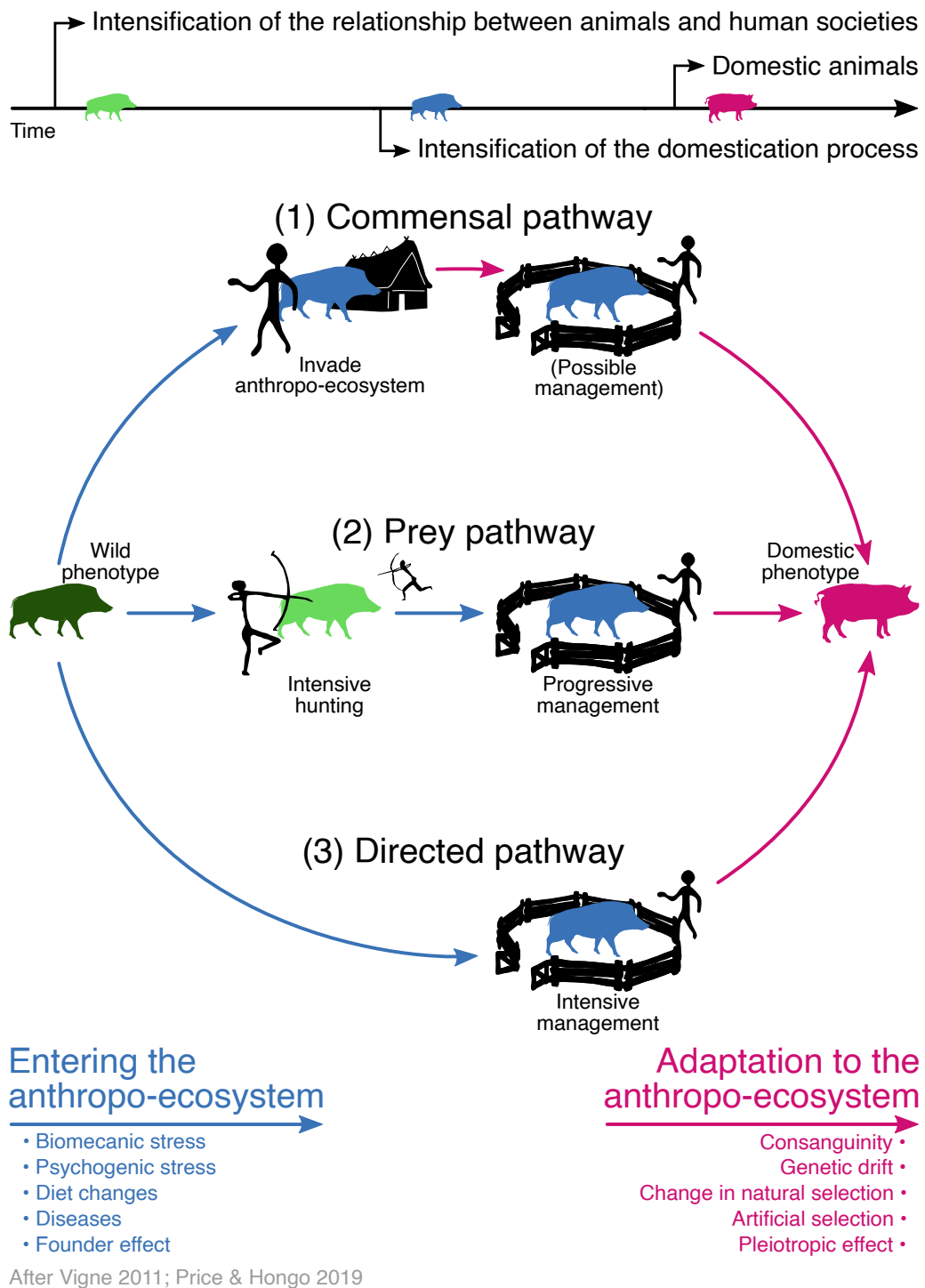


FIGURE 1.1 – Diagramme synthétique du processus de domestication.

Le diagramme représente les différentes trajectoires de domestication possibles, ainsi que les causes développementales et évolutives de l'émergence des phénotypes domestiques. La frise temporelle représente le début et l'intensification des trois phénomènes qui ont lieu : la relation entre l'Homme et l'animal, le processus de domestication, puis l'animal biologiquement domestique. Les flèches bleues représentent l'entrée dans l'anthropo-écosystème, et les flèches roses représentent l'adaptation à l'anthropo-écosystème. (D'après Vigne, 2011 ; Price and Hongo, 2019)

Ces trajectoires représentent les différentes façons pour un animal d'intégrer l'anthropo-écosystème, en fonction de la relation entre l'Homme et la futur espèce domestique (Hulme-Beaman, 2014 ; Larson and Burger, 2013 ; Price and Hongo, 2019 ; Vigne, 2011 ; Zeder, 2012) (Figure 1.1 page 17).

1. *La trajectoire commensale.* Le commensalisme consiste en une interaction avantageuse pour l'espèce en voie de domestication, mais neutre pour l'Homme (ou bien légèrement désavantageuse pour l'Homme, on parle alors de commensalisme parasitique) : l'espèce en voie de domestication va alors être attirée par les avantages proposés par la vie au contact de l'Homme, et s'y adapter en l'absence d'exploitation de l'animal par l'Homme (Price and Hongo, 2019 ; Zeder, 2012). C'est par exemple probablement le cas pour le loup (*Canis lupus*), dont certains individus auraient été attirés près des campements humains pour fouiller dans les déchets, jusqu'à s'adapter à ce mode de vie (Coppinger and Coppinger, 2001 ; Morey, 1994). C'est d'ailleurs historiquement la toute première voie de domestication qui a été empruntée il y a 17 000 à 15 000 ans par le loup (calibrated : cal BP) (Larson et al., 2012). C'est également la trajectoire empruntée par la souris (*Mus musculus*) attirée par les réserves alimentaires, ou bien le chat (*Felis sylvestris*), attiré par les autres petits commensaux comme les souris (Cucchi et al., 2020). Il est également possible que le porc (*Sus scrofa*) ait été domestiqué via cette trajectoire, attiré comme le loup par les déchets produits par les communautés humaines (Ervynck et al., 2001 ; Zeder, 2012).
2. *La trajectoire de prédation (ou chasse intensive).* La prédation consiste à chasser le plus souvent des individus ciblés en fonction de leur âge ou de leur sexe pour optimiser la quantité et la qualité des ressources recherchées comme la viande ou d'autres produits animaux (Price and Hongo, 2019 ; Zeder, 2012). Cette trajectoire de domestication a été empruntée par la plupart des animaux de bétail, comme le mouton (*Ovis aries*), la chèvre (*Capra hircus*) (Peters et al., 2005 ; Zeder, 2009, 2008, 2006a, 2006b ; Zeder and Hesse, 2000) ou la vache (*Bos taurus*) (Helmer et al., 2005) en Eurasie ; le lama (*Lama glama*) et l'alpaga (*Vicugna pacos*) en Amérique du Sud (Mengoni Gonalons and Yacobaccio, 2006 ; Wheeler et al., 2006) ; ou bien plus récemment le renne (*Rangifer tarandus*) (Baskin, 1974 ; Gordon, 2003 ; Mirov, 1945). Les proies sont domestiquées graduellement en augmentant le contrôle sur la population, en passant d'une stratégie de gestion du gibier pour en augmenter sa disponibilité, à une vraie gestion de troupeau, puis à un élevage contrôlé et rationalisé (Zeder, 2012). Cette voie de domestication semble s'être déroulée relativement lentement sur des centaines ou des milliers d'années, puisque les premiers changements morphologiques sur les restes osseux ont été détectés longtemps après les premiers indices d'une augmentation des interactions entre l'Homme et l'animal (Zeder, 2012).
3. *La trajectoire dirigée* consiste en une domestication rapide et intentionnelle d'un animal par une population humaine qui maîtrise déjà des animaux domestiques, et qui utilise ses connaissances acquises pour obtenir une nouvelle ressource ou un nouveau service à travers le nouvel animal convoité (Zeder, 2012). L'Homme contrôle alors la reproduction, l'alimentation, la mobilité, la structure sociale et l'écologie de la population animale (Price and Hongo, 2019). C'est par exemple le cas du cheval (*Equus caballus*), probablement domestiqué pour servir de monture et aider à la chasse, pour la traction ou le transport de ressources, en plus de la

viande, les peaux, le lait . . . (Olsen, 2006). C'est également la voie empruntée par les ânes (*Equus asinus*), les chameaux (*Camelus bactrianus*), les dromadaires (*Camelus dromedarius*), principalement pour le transport de ressources, mais également le vison (*Mustela vison*) ou le chinchilla (*Chinchilla lanigera*) pour la fourrure.

4. En plus de ces trois voies principales il existe des voies plus anecdotiques, qui peuvent être assimilées à des trajectoires dirigées, comme l'apprivoisement chez les éléphants d'Afrique et d'Asie (*Loxodonta africana* et *Elephas maximus*), le faucon pèlerin (*Falco peregrinus*) (Zeder, 2012), ou l'expérimentation chez le renard argenté (*Vulpes vulpes*) (Belyaev et al., 1985 ; Trut et al., 2009 ; Trut, 1999).

1.1.5 Syndrome de domestication

Aparté historique 1 L'expérimentation sur le renard argenté

URSS, 1959. Pour démontrer l'origine génétique du syndrome de domestication, et surtout montrer que la sélection de traits comportementaux seuls peut entraîner tous les symptômes du syndrome, Dimitri Beliaïev lance un programme de sélection artificielle contrôlée sur une population de renards argentés (*Vulpes vulpes*) originaire du Canada et historiquement élevée pour la fourrure. Il choisit comme critère de sélection la distance de fuite, c'est-à-dire la distance à laquelle un humain peut s'approcher avant de produire un comportement de fuite chez le renard, et s'applique à sélectionner pour la reproduction les individus qui ont la plus petite distance de fuite, génération après génération. Une sélection drastique a été appliquée, autorisant seulement 4 à 5% des mâles et 20% des femelles les plus dociles à se reproduire. (Trut, 1999)

40 ans et 30 à 35 générations plus tard, les descendants de cette lignée sélectionnés uniquement pour leur docilité présentent un comportement radicalement différent de la population d'origine et cherchent le contact avec les humains, mais surtout présentent un certain nombre de changements physiologiques et morphologiques à priori non-corrélés avec la distance de fuite comme des oreilles tombantes, une queue recourbée, une pelage tacheté ou marbré, et deux cycles de reproductions au lieu d'un par an. (Belyaev et al., 1985 ; Trut et al., 2009 ; Trut, 1999). Il est tout de même à noter que la population d'origine, en tant que population d'élevage pour la fourrure, était déjà habituée à la proximité avec l'Homme, et donc plus ou moins sélectionnée pour son apparence et sa docilité depuis le milieu du 19e siècle, ce qui remet en perspective la relative rapidité apparente du phénomène (Lord et al., 2020).

En dépit des différentes trajectoires de domestication, des différentes espèces domestiquées, à différents endroits et différentes périodes, les adaptations biologiques liées à la domestication sont souvent étonnamment similaires. Le processus de domestication fait converger les caractères morphologiques et comportementaux vers la même direction générale, qu'on appelle le « syndrome de domestication » (Darwin, 1868 ; Ross-Ibarra et al., 2007 ; Wilkins et al., 2014). Ce syndrome inclus chez les mammifères une dépigmentation de la peau et la fourrure (Belyaev et al., 1985 ; Darwin, 1868 ; Gariépy et al., 2001 ; Trut

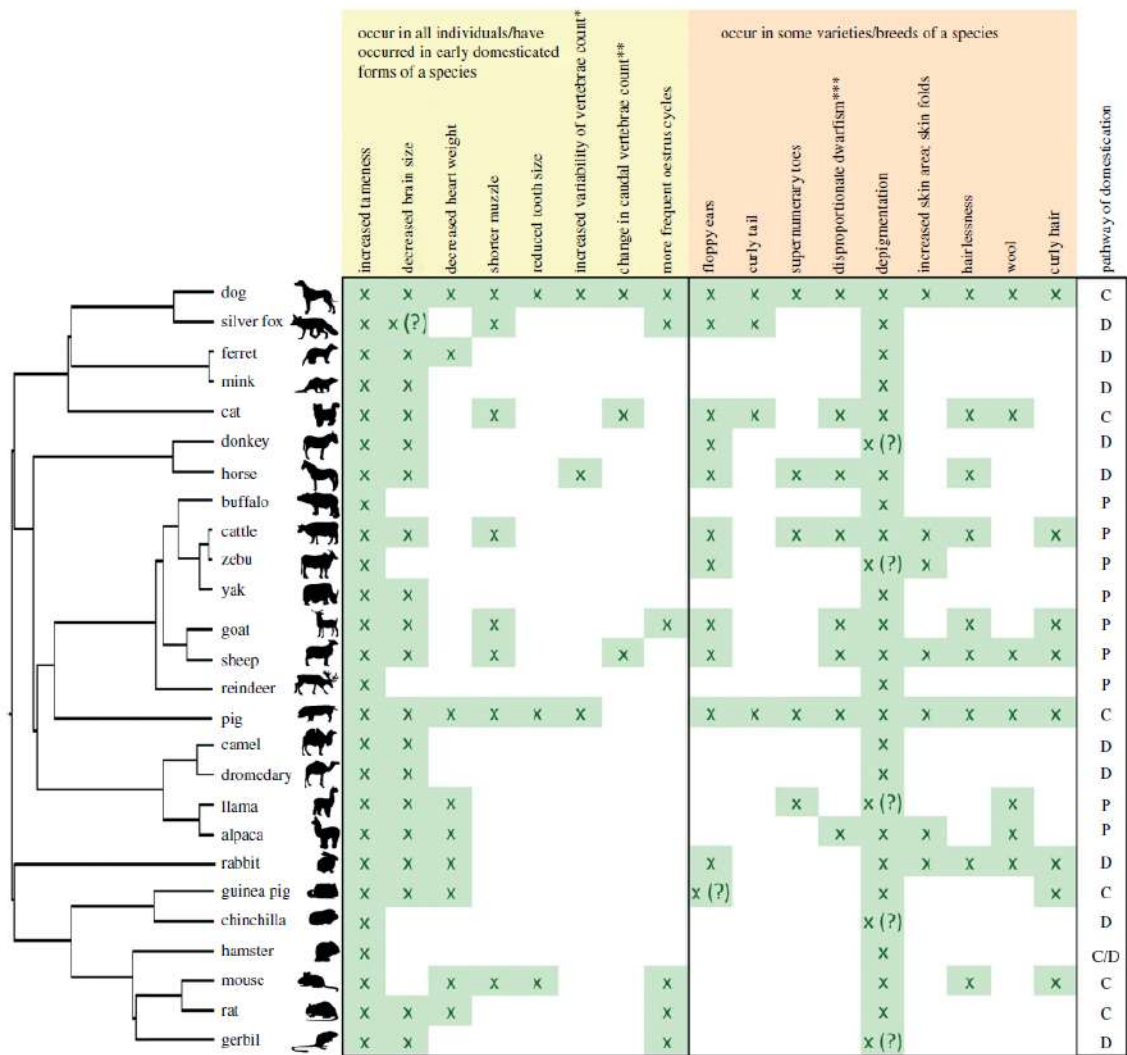


FIGURE 1.2 – Vue d'ensemble des trajectoires et des symptômes du syndrome de domestication chez les animaux domestiques.

L'arbre phylogénétique représente les liens de parenté entre les différentes espèces domestiques, et le tableau liste pour chacune de ces espèces quels symptômes elle présente et quelle est la trajectoire de domestication supposée. C = Commensale ; P = Prédation ; D = Dirigée ; * : thoracic, lumbar ; ** : increase or decrease ; *** : relatively short limbs. (D'après Sánchez-Villagra et al., 2016)

et al., 2009), les oreilles réduites et tombantes (Arbuckle, 2005 ; Belyaev et al., 1985 ; Darwin, 1868 ; Hemmer, 1990), un museau plus court (Clutton-Brock, 1999 ; Darwin, 1868 ; Zeuner, 1963), des dents plus petites (Clutton-Brock, 1999 ; Darwin, 1868), une queue recourbée (Darwin, 1868 ; Trut et al., 2009), une réduction de la boîte crânienne (Hemmer, 1990 ; Kruska, 1988, 2005), une plus grande docilité (Belyaev et al., 1985 ; Darwin, 1868), un cycle de reproduction plus rapide (Arbuckle, 2005 ; Darwin, 1868 ; Kruska, 1988, 2005 ; Trut et al., 2009), et une conservation des comportements juvéniles à l'âge adulte (Gariépy et al., 2001 ; Hare et al., 2012 ; Price, 1999 ; Trut, 1999). Ces traits ne sont pas forcément tous présents chez toutes les espèces domestiquées, mais sont largement répandus. Darwin considérait à son époque que les syndromes de domestication étaient des réponses environnementales mais il a fallu attendre les expérimentations de Belyaev pour démontrer une origine génétique de ces syndromes (Voir Aparté historique 1).

Des recherches complémentaires à la suite à cette expérimentation ont permis de montrer que la sélection des comportements dociles conduirait à un léger déficit de cellules dans la crête neurale pendant le développement embryonnaire, ce qui provoquerait directement ou indirectement la plupart des caractéristiques du syndrome de domestication (Sánchez-Villagra et al., 2016 ; Wilkins et al., 2014). En effet la crête neurale est à l'origine de certaines cellules des glandes surrénale, pituitaire, du thymus, de la thyroïde et parathyroïde (Bockman and Kirby, 1984 ; Kuratani and Bockman, 1990 ; Le Lièvre and Le Douarin, 1975 ; Maeda et al., 2016 ; Minugh-Purvis and McNamara, 2002 ; Varga et al., 2009), mais aussi de la zone du cerveau associée à l'apprentissage et à la récompense (Arons and Shoemaker, 1992 ; Richardson and Sieber-Blum, 1993), des cellules liées à la pigmentation du corps et de la tête, des poils, plumes, bec et cornes (Eames, 2005 ; Schneider, 2005), et enfin de toutes les cellules des os, tendons et cartilages de la tête. L'hypothèse d'un lien entre les cellules de la crête neurale et les symptômes du syndrome de domestication est donc raisonnable à envisager (Sánchez-Villagra et al., 2016). Cependant, un certain nombre d'études ont montré une absence de corrélation entre la docilité et l'apparence chez le chien et le rat (Albert et al., 2009 ; Baranowska Körberg et al., 2014 ; Hart, 1995 ; Linderholm and Larson, 2013 ; Stockard et al., 1941), ainsi qu'une origine fortement polygénique de la docilité chez le lapin (Carneiro et al., 2014 ; Sánchez-Villagra et al., 2016). Par ailleurs, la vision traditionnelle de la domestication ainsi que l'expérimentation sur le renard argenté de Belyaev et collaborateurs reposent sur un modèle de domestication via une isolation reproductive de la population captive vis-à-vis de la population sauvage et d'une sélection comportementale drastique. Or il a été montré, au moins chez le porc (Frantz et al., 2015), que les flux génétiques ont été maintenus tout au long du processus de domestication entre les populations domestiques et sauvages. Les flux génétiques qui viennent homogénéiser les génomes des deux populations font donc partie du processus de domestication et doivent être pris en compte au même titre que la sélection des traits domestiques chez les populations captives.

1.2 Identification de la domestication en contexte archéologique

1.2.1 Marqueurs archéologiques habituels

Parmi les manifestations morphologiques du syndrome de domestication, certaines sont visibles sur le squelette, et furent donc utilisées en contexte archéologique pour distinguer

les individus domestiques des sauvages, comme la réduction de la taille, le raccourcissement du museau, ou les dents plus petites.

On peut également citer la réduction du dimorphisme sexuel (i.e. différence de taille des éléments squelettiques entre mâles et femelles) lié à la perte de la sélection naturelle de la reproduction qui a été utilisée pour identifier les débuts de l'élevage des caprinés en Iran (Monchot et al., 2005) et des suinés à Chypre (Vigne et al., 2012, 2011, 2009). La divergence morphologique entre populations sauvages et domestiques liée à l'isolement génétique et à l'adaptation au milieu anthropogène a été utilisée pour identifier les débuts de la domestication des suinés en Chine grâce à l'utilisation de la morphométrie géométrique des formes dentaires (Cucchi et al., 2016, 2011). Cette approche s'est révélée très prometteuse en Chine car l'une des hypothèses est que les premières sociétés agricoles chinoises ont pratiqué un élevage des suinés très contrôlé dès le 7e millénaire AEC (Avant l'Ère Commune) avec peu de croisement avec les sangliers, contrairement à un mode plus extensif des premiers élevages porcins d'Europe (Cucchi et al., 2016). Cette approche fut également appliquée à l'exploration de l'émergence des races ovines en Asie du Sud-Ouest depuis le Néolithique à partir de la variation de la morphologie de l'astragale. Elle a permis de révéler des patrons de variation fortement liés au processus de divergence, lié à la sélection anthropogène depuis le Néolithique (Pöllath et al., 2019).

Cependant, ces modifications présentent certaines limites : les plus flagrantes se retrouvent sur le crâne qui, en dehors des dents, n'est pas la pièce osseuse la plus souvent retrouvée sur les sites archéologiques, mais surtout, ces modifications sont d'origine évolutive et apparaissent assez tardivement dans le processus de domestication, après plusieurs générations soumises à une sélection, elles sont donc peu utiles pour identifier le processus de domestication. Ces premières étapes ne peuvent pas être identifiées par des adaptations évolutives, nous devons plutôt nous focaliser sur les potentiels symptômes ou indices provoqués par l'augmentation des interactions entre l'Homme et l'animal à l'échelle d'une seule génération, avant même que se mette en place le processus de sélection.

Heureusement, les pièces osseuses retrouvées en contexte archéologique permettent de réaliser des analyses et observations pour nous aider à identifier ces indices. Ainsi, les méthodes d'estimation de l'âge de mort des animaux en contexte archéologique comme l'épiphyssation des os longs (Zeder, 2006a), le degré d'éruption dentaire (Zeder, 2006a) ou l'étude des anneaux de ciment dentaire (Gustafson, 1966 ; Stott et al., 1982) permettent de reconstituer des courbes d'abattage et d'en déduire des stratégies d'exploitation de la population animale, et donc son niveau d'interaction avec la société humaine. La recherche de symptômes de maladies peut également servir d'indice de la proximité avec l'Homme. En effet, cette proximité, couplée avec la proximité d'autres animaux domestiques, augmente fortement le risque de contamination inter-spécifique (Hoberg et al., 2001), tout en augmentant les chances pour un animal de survivre à une maladie (Bartosiewicz and Gál, 2013 ; Bendrey, 2014).

Les études sur les isotopes radioactifs peuvent nous renseigner sur le régime alimentaire des animaux, qui va potentiellement varier selon le degré d'interaction avec la société humaine (Balasse et al., 2018). En effet, les isotopes du Carbone peuvent être des indicateurs de la consommation de millet (Hu et al., 2009 ; Pechenkina et al., 2005 ; Wang et al., 2018), de poissons marins (Müldner and Richards, 2007) ou de glands et de faînes (Madgwick et al., 2012), et les isotopes de l'Azote peuvent être des indicateurs de la consommation de poissons marins (Matsui et al., 2005 ; Minagawa et al., 2005), de protéines animales (Ha-

milton and Thomas, 2012 ; Madgwick et al., 2012), ou de plantes issues d'un sol fertilisé (Bogaard et al., 2007 ; Styring et al., 2015, 2017), qui sont chacun des indicateurs d'un lien avec une société humaine.

Enfin, les analyses génétiques faites sur les restes osseux nous permettent de tracer les lignées domestiques au fil de leur diffusion au cours du temps (Irving-Pease et al., 2019 ; Larson et al., 2007).

Outre les méthodes précédemment citées, l'intensification de l'interaction entre l'Homme et l'animal pourrait être identifiée via l'impact de la réduction de la mobilité chez l'animal. En effet, la domestication implique dans la plupart des cas un contrôle accru de la population et une réduction de la mobilité (Zeder, 2012). Une étude des pathologies de l'astragale liées à la stabulation sur des séries de caprinés et d'ovin du Néolithique précéramique d'Asie du Sud-Ouest par l'équipe de Joris Peters a montré que des arthropathies localisées sur la face crâniale pouvait présenter des marqueurs très pertinents pour identifier les processus de domestication des caprinés au Proche Orient (Zimmermann et al., 2018).

Ainsi, l'hypothèse préalable de cette thèse est que le changement de comportement d'un individu sauvage qui entre sous contrôle de l'Homme peut laisser une empreinte observable et mesurable dans l'anatomie osseuse via la *plasticité phénotypique*, et que cette empreinte repousse les limites de la *norme de réaction* habituellement observée chez les populations sauvages.

1.2.2 Génotype, Phénotype, Plasticité phénotypique et Norme de réaction

Avant d'appréhender les concepts de plasticité phénotypique et de norme de réaction, il est nécessaire de comprendre un ensemble de notions interdépendantes sur lesquels ils reposent : l'ADN, le gène, l'allèle, le génotype et le phénotype. (Reece et al., 2012)

- *L'ADN*. Ce que nous transmettons d'une génération à l'autre via les cellules reproductrices (spermatozoïde et ovule) est une portion de notre matériel génétique, constitué d'ADN. C'est une très longue molécule présente chez tous les êtres vivants. Certaines parties peuvent être « décodées » dans nos cellules par la machinerie moléculaire, pour produire des protéines, qui serviront de « briques de base » pour façonner tout ce qui nous constitue et faire fonctionner tous les processus qui ont lieu dans notre corps.
- *Le gène*. Chaque portion de notre matériel génétique qui peut amener à produire une protéine est appelé un gène.
- *L'allèle*. Au cours de l'évolution peuvent survenir des mutations, des modifications aléatoires du matériel génétique, causées par divers facteurs. Ces mutations, si elles ont lieu sur un gène, peuvent conduire à produire une protéine différente de celle produite avant la mutation. Les deux versions du gène, celle non mutée et celle mutée, qui mènent à la production de deux protéines différentes sont appelées deux allèles du gène.
- *Le génotype* est l'ensemble des allèles des gènes portés par un individu. Chaque individu possède un génotype différent qui la caractérise dans une certaine mesure,

puisqu'il permet de produire toutes les protéines qui composent cet individu et font fonctionner ses processus biologiques.

- *Le phénotype*. En produisant les protéines qui constituent un individu, le génotype va contribuer à façonner l'ensemble de ses caractères observables, c'est ce qu'on appelle le phénotype. Ainsi la pigmentation de la peau, le groupe sanguin, la masse corporelle, la forme des os etc... constituent le phénotype d'un individu.

Or, le génotype seul n'est pas suffisant pour expliquer certains de ces caractères. Pour un même génotype, certains caractères peuvent varier : la pigmentation de la peau et la masse corporelle sont de bons exemples. Même s'ils ont une base génétique, ils peuvent être affectés respectivement par l'exposition au soleil et l'alimentation. Ainsi le phénotype est induit conjointement par le génotype et l'environnement.

- *La plasticité phénotypique* est cette capacité pour un individu d'exprimer différents phénotypes à partir d'un même génotype en fonction de son environnement (Ghalambor et al., 2007; Sultan and Stearns, 2005). Cette plasticité phénotypique a d'ailleurs un rôle à jouer dans le processus d'évolution puisque la sélection naturelle s'applique sur le phénotype et non sur le génotype : les individus sont sélectionnés en fonction du phénotype qu'ils expriment et de son adéquation avec l'environnement actuel, et non en fonction de tous les phénotypes qu'ils auraient pu exprimer à partir de leur génotype. Autrement dit, ce sont les variations du phénotype générées par la plasticité qui sont sélectionnées, et donc la capacité à exprimer ce phénotype dans cet environnement qui est transmise d'une génération à l'autre (Nicoglou, 2014).
- *La norme de réaction* est l'ensemble des phénotypes qu'un génotype peut exprimer à partir de conditions environnementales différentes (Griffiths et al., 2000).

1.2.3 Protocole expérimental

Pour tester notre hypothèse, il est nécessaire de collecter des individus sauvages issus de différentes populations d'Europe occidentale afin de déterminer la norme de réaction supposée des sangliers sauvages, puis d'obtenir des individus dont on sait qu'ils ont grandi dans un contexte de mobilité réduite, et dont tous les autres paramètres sont contrôlés, notamment l'alimentation et la lignée génétique, afin de déterminer si leur morphologie a été soumise à une plasticité phénotypique suffisante pour étendre la norme de réaction au-delà de la norme initialement observée chez les sangliers sauvages.

C'est dans cet objectif qu'a été mené le projet de domestication expérimentale (ANR DOMEXP dirigée par T. Cucchi). Vingt-quatre marcassins de six mois, issus d'une population génétiquement homogène de sangliers d'élevage, ont été séparés en deux groupes homogènes (même sexe ratio, variabilités de poids, taille et dimension crânienne similaires) puis élevés dans deux conditions différentes de réduction de mobilité. Le premier dans un enclos arboré de 3000m² (0,3ha), le second dans une étable couverte de 100m² où les mâles et femelles sont séparés dans deux espaces de stabulation, avec en moyenne 4m² par individu. La zone d'alimentation d'un sanglier étant de 100ha, les deux conditions représentent bien une diminution de leur mobilité (Étienne, 2003). Le but de cette expérimentation est de tester l'effet de la captivité sur la croissance et la variation osseuse d'un modèle suidé : le sanglier. (Figure 1.3 page 25)

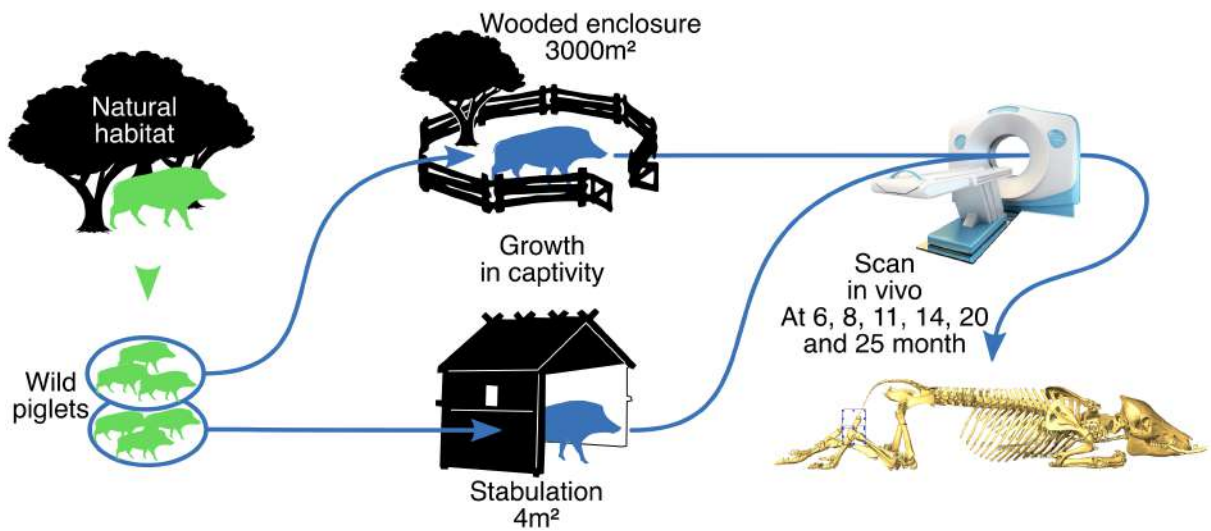


FIGURE 1.3 – Diagramme du protocole expérimental DOMEXP.

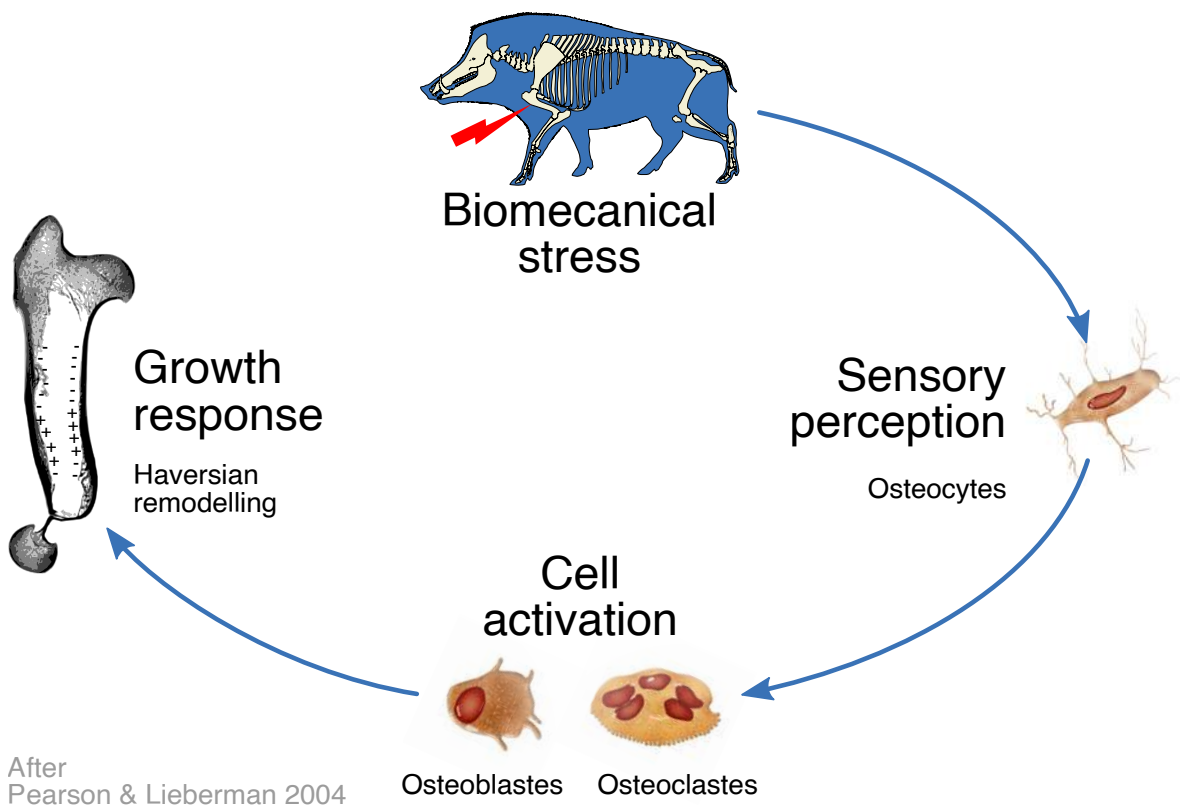


FIGURE 1.4 – Principe de la plasticité osseuse corticale.

(D'après Pearson et Lieberman, 2004)

1.2.4 Plasticité osseuse

En ce qui concerne notre étude, ce sont les os qui vont montrer une certaine plasticité et se remodeler en fonction des contraintes exercées par les forces extérieures (Marcus, 2002 ; Pearson and Lieberman, 2004). Dans le cas de la domestication, le nouvel environnement engendre deux principaux changements :

- Un changement d'alimentation, qui pourrait induire des modifications au niveau de l'appareil masticatoire. En effet des aliments plus robustes vont induire chez le cochon une augmentation de l'activité musculaire masticatoire, ainsi que de la durée et de l'amplitude du cycle de mastication (Herring, 1977, 1976), mais également plus de variabilité individuelle dans les mouvements alors que les aliments moins robustes induisent des mouvements plus stéréotypés (Montuelle et al., 2018). Cependant, une étude qui s'est penché sur les conséquences morphologiques de ces modifications comportementales n'a pas pu démontrer d'impact sur l'épaisseur ou la densité de l'os cortical de l'arc zygomatique, auquel s'attachent les muscles masticateurs, ni sur les éléments du neurocrâne (Franks et al., 2016). Ces études nous permettent d'ailleurs de mettre en évidence le fait que toutes les structures ne sont pas forcément plastiques, certaines peuvent être surtout contrôlées génétiquement, mais également que parfois la plasticité n'impacte pas les caractères eux même, mais plutôt la variabilité de ces caractères.
- Une limitation de l'espace disponible et donc une réduction de la mobilité et de l'ensemble du répertoire locomoteur d'un animal interagissant avec l'environnement de son habitat naturel. Ce qui induirait en cascade : une modification des comportements locomoteurs, puis un ajustement de la musculature provoquant un stress biomécanique sur le squelette, puis un remodelage osseux suite aux stimulations musculaires, et enfin une modification de la morphologie et la structure des os qui découle de ce remodelage. (Figure 1.4 page 25)

D'après ce que l'on sait de la plasticité osseuse, on peut s'attendre à observer des modifications osseuses à trois niveaux.

1. Au niveau de la morphologie externe de l'os : l'os peut s'adapter aux nouveaux stimuli exercés par les muscles et les autres os avec lesquels ils sont articulés en devenant plus ou moins robuste, plus ou moins courbé, avec des structures osseuses plus ou moins prononcées etc... (Hammond et al., 2010 ; Marcus, 2002 ; O'Regan and Kitchener, 2005 ; Pearson and Lieberman, 2004)
2. Au niveau de la topographie de l'épaisseur corticale de la diaphyse : la diaphyse des os longs est parsemée d'enthèses, qui sont les points d'ancrage des muscles. Étant donné que l'augmentation globale des stimulations musculaires au cours de la vie engendre un épaissement global de la diaphyse (Carter et al., 1996 ; Ehrlich and Lanyon, 2002 ; Kilbourne and Hutchinson, 2019 ; Niinimäki, 2012 ; Pearson and Lieberman, 2004 ; Scheidt et al., 2019), on peut prendre pour hypothèse que l'épaisseur de la diaphyse augmente au niveau des enthèses où la stimulation augmente, et s'amincit au niveau des enthèses où la stimulation diminue.
3. Au niveau de la microstructure trabéculaire des métaphyses et épiphyses : la modification des stimulations musculaires perturbe l'uniformité du stimulus mécanique

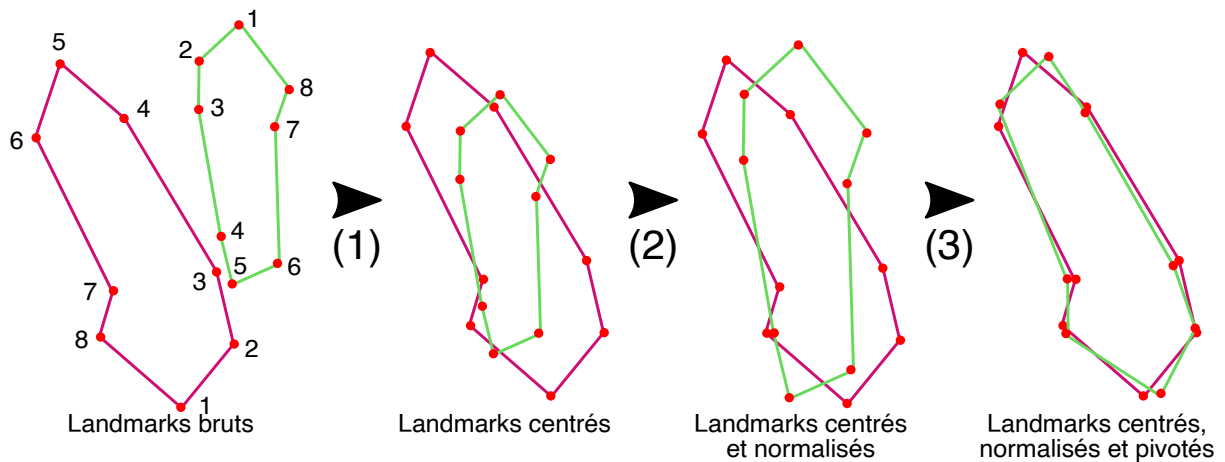


FIGURE 1.5 – Principe de la superposition procruste.

Les points rouges représentent les points repères, ou landmarks. Chaque landmark est présent sur chaque spécimen. Le tracé rose et le tracé vert représentent chacun un spécimen différent.

sur les trabécules. Certaines trabécules sont alors plus contraintes que d'autres, entraînant une formation osseuse sur les zones où les contraintes ont augmenté, et une résorption osseuse sur les zones où les contraintes ont diminué. Il en résulte des modifications morphologiques des trabécules (Adachi et al., 1997; Tsubota et al., 2002).

Dans le cadre de cette thèse, seules les déformations aux niveaux de la morphologie externe et de la topographie de l'épaisseur corticale seront étudiées, en raison des contraintes temporelles mais surtout techniques. En effet l'étude de la microstructure trabéculaire demande des moyens techniques beaucoup plus coûteux puisqu'elle nécessite de passer tous les ossements au scanner micro-CT, tandis qu'un scanner médical est suffisant pour étudier les deux autres niveaux structurels.

Pour étudier les déformations au niveau de la morphologie externe des os, nous nous sommes focalisés sur le calcaneus, et pour celles au niveau de la topographie de l'épaisseur corticale sur l'humérus. Ces choix ont été faits pour deux raisons. La première raison, de type morphofonctionnelle, est que ces deux os sont fortement impliqués dans la locomotion, et sont donc susceptibles d'être impactés en priorité par un changement de comportement locomoteur. La seconde raison, de type taphonomique, est que ce sont des os particulièrement compacts et robustes (pour l'humérus, au moins sa partie distale), ce qui leur assure une conservation relativement bonne en contexte archéologique, et nous permet d'avoir une certaine quantité de restes à analyser.

1.2.5 Morphométrie géométrique

Pour décrire la morphologie externe des os de façon précise et quantitative, nous allons utiliser la morphométrie géométrique. Concrètement, cette méthode consiste à identifier sur l'os un certain nombre de points de repère anatomiques, qu'on appellera ici *landmarks*, que l'on va pouvoir retrouver sur chacun des spécimens, puis d'extraire leur position relative les uns par rapport aux autres, c'est-à-dire leur information spatiale, leurs coordonnées cartésiennes. Ainsi, la morphologie de chaque os devient caractérisée par l'ensemble des

coordonnées de ses *landmarks* et peut être analysée statistiquement et comparée avec les autres (Cucchi et al., 2015).

Chaque *landmark* doit être homologue sur tous les spécimens, c'est-à-dire correspondre à la même structure biologique pour permettre une comparaison. Un *landmark* peut être de trois types en fonction de son niveau d'homologie (Bookstein, 1991) : le type I correspond aux structures biologiques ponctuelles bien définies localement, comme une intersection entre des lignes de suture, c'est celui dont l'homologie est la plus forte ; le type II correspond aux maximum de courbure, aux extrémités etc... ; le type III correspond aux *landmarks* dépendant de la position d'autres *landmarks*, comme le milieu entre deux autres *landmarks*, ce sont des *landmarks* non-homologues.

Une fois identifiés, les *landmarks* caractérisent la forme de l'os, que l'on peut décomposer en deux variables : la taille et la conformation. Là où les méthodes de morphométrie classique utilisent la forme comme un tout, la morphométrie géométrique permet de séparer les deux variables, et de les étudier indépendamment, ainsi que d'étudier leur interaction, c'est-à-dire comment la taille et la conformation s'influencent mutuellement. Pour cela, on réalise une superposition procruste (Goodall, 1991 ; Rohlf and Slice, 1990), qui permet de standardiser les coordonnées des *landmarks* en trois étapes (Figure 1.5 page 27) :

1. Une translation permet d'aligner tous les spécimens sur le centre de gravité pour éliminer les informations de position
2. Une normalisation permet de mettre tous les spécimens à la même échelle et supprimer les informations de taille en divisant leurs coordonnées par leur taille centroïde
3. Et enfin une rotation pour supprimer les informations d'orientation en minimisant la somme des carrés des distances entre tous les *landmarks*.

On obtient alors d'une part des variables de conformation pure : les coordonnées procrustes issues de la superposition procruste ; et de l'autre une variable de taille : la taille centroïde, définie comme la racine carrée de la somme des distances entre chaque *landmark* et le centroïde (le centroïde étant la moyenne arithmétique de tous les *landmarks*)(Bookstein, 1991).

1.2.6 Cartographie de l'épaisseur corticale

Pour décrire la topographie de l'épaisseur corticale des os longs, il faut mesurer en chaque point de la diaphyse la distance entre la surface interne et la surface externe pour élaborer une cartographie de l'épaisseur corticale. Le principe est assez simple, mais les protocoles existants présentent plusieurs problèmes qui les rendent inadaptés à notre application, il a donc été nécessaire d'élaborer un protocole *ad hoc*. (Figure 1.6 page 29)

Le premier problème est la définition des limites de la diaphyse. En effet, de la même manière qu'il est nécessaire pour la morphométrie géométrique que tous les *landmarks* soient homologues pour être comparés, les limites de la diaphyse doivent être homologues entre tous les spécimens si l'on veut que les mesures de l'épaisseur corticale soient comparables. Un des protocoles préexistants (Bondioli et al., 2010 ; Puymérail, 2013) définit les limites de la diaphyse par un pourcentage de l'os total, entre 20 et 80% de l'os, mais ce faisant, il rend les limites de la diaphyse dépendantes de la conformation des épiphyses : si sur un os les épiphyses sont particulièrement allongées, la longueur totale de l'os en sera augmentée, et puisque la diaphyse est définie en fonction de la longueur totale de l'os, sa longueur sera

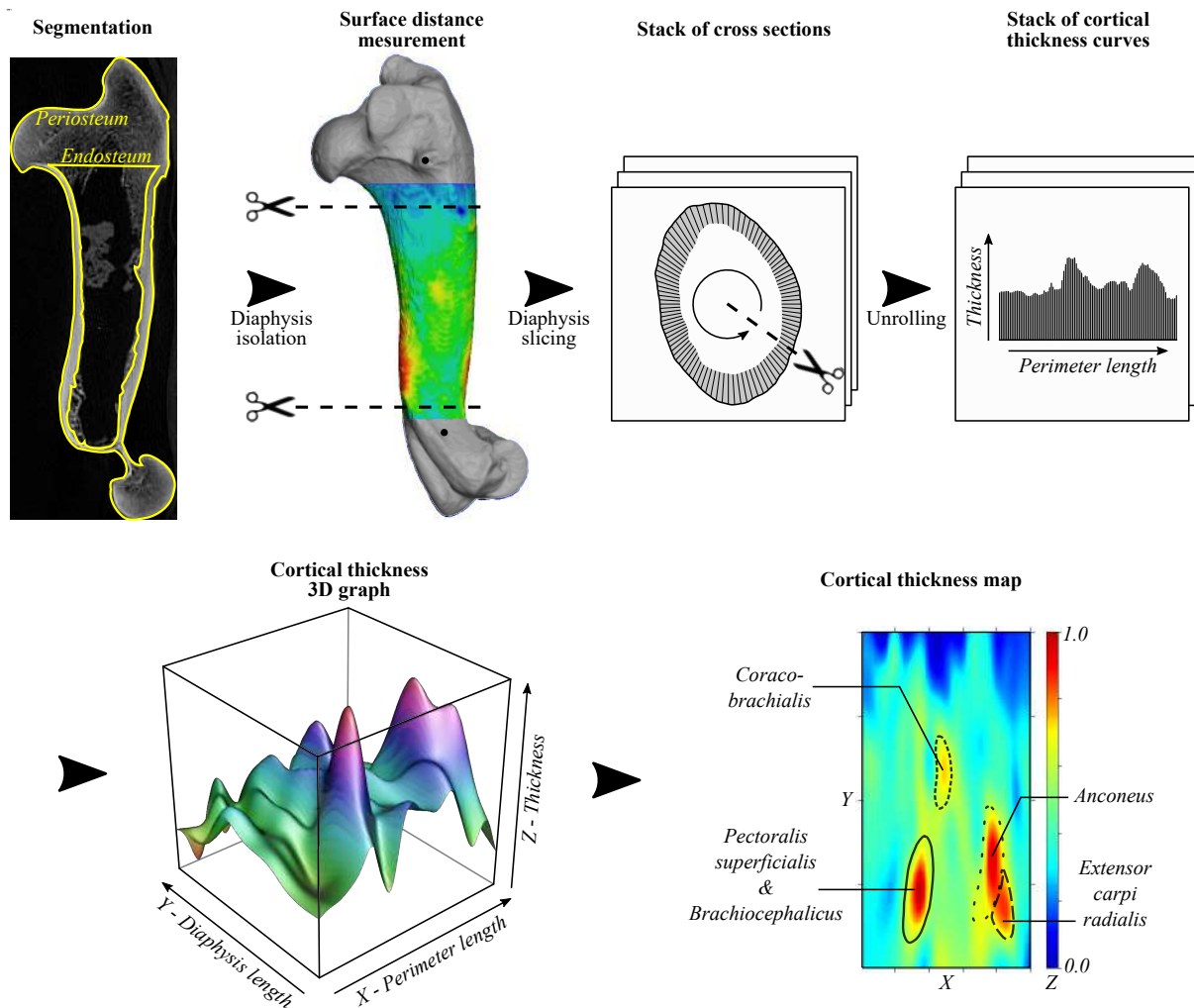


FIGURE 1.6 – Protocole d'analyse de la topographie de l'épaisseur corticale de l'humérus.

LM1 et *LM2* représentent les landmarks anatomiques qui permettent de définir les limites de la diaphyse. Le décalage entre les landmarks et la découpe finale s'explique par des marges qui ont été définies pour limiter les effets de bord. Les zones entourées sur la cartographie finale représentent les zones d'attaches musculaires.

surestimée. Cependant, ce protocole est destiné à être appliqué à un fémur humanoïde, qui a une conformation très longiligne, ce qui rend probablement les légères variations de la taille des épiphyses négligeables devant la longueur totale de l'os. En revanche, dans notre cas, le protocole doit être applicable à des humérus de sanglier et de cochon, dont la conformation est beaucoup plus trapue, mais surtout dont la variabilité au niveau des épiphyses est très importante, notamment entre sangliers et cochons, ce qui rend l'impact de la conformation des épiphyses beaucoup plus important sur la longueur totale de l'os. Un autre protocole déjà existant (Morimoto et al., 2011) utilise en revanche des *landmarks* anatomiques pour définir de façon homologue les limites de la diaphyse. C'est la solution que nous avons choisi d'adopter.

Le second problème est lié au premier, il s'agit de l'angle de la limite de la diaphyse. En effet, les limites sont tracées perpendiculairement à l'axe vertical, mais l'axe vertical dépend également de la conformation des épiphyses. Si un spécimen a une épiphyse légèrement courbée dans une direction, l'axe vertical va également être légèrement incliné dans cette direction, ce qui va conduire à des limites de la diaphyse légèrement inclinées, et donc non-homologues. Nous avons donc aligné l'axe vertical sur la longueur de la diaphyse, et non sur la longueur totale de l'os.

1.2.7 Mise à l'épreuve des nouvelles méthodes : Application archéologique

Une fois la preuve de concept réalisée sur chacun des deux os avec leur méthode respective, il sera nécessaire de la mettre à l'épreuve pour déterminer si nos méthodes peuvent réellement s'appliquer à du matériel archéologique et nous permettre de documenter des changements phénotypiques des populations de suinés du Néolithique en liaison avec des pressions environnementales d'origine anthropique. Pour cela, nous avons collecté une grande série archéologique de *Sus scrofa* à Chypre et en Europe occidentale, du Mésolithique au Néolithique final afin de couvrir toute la période d'arrivée du cochon en Europe et documenter l'impact de la néolithisation sur la diversité phénotypique de *Sus scrofa* en Europe. (Aparté historique 2)

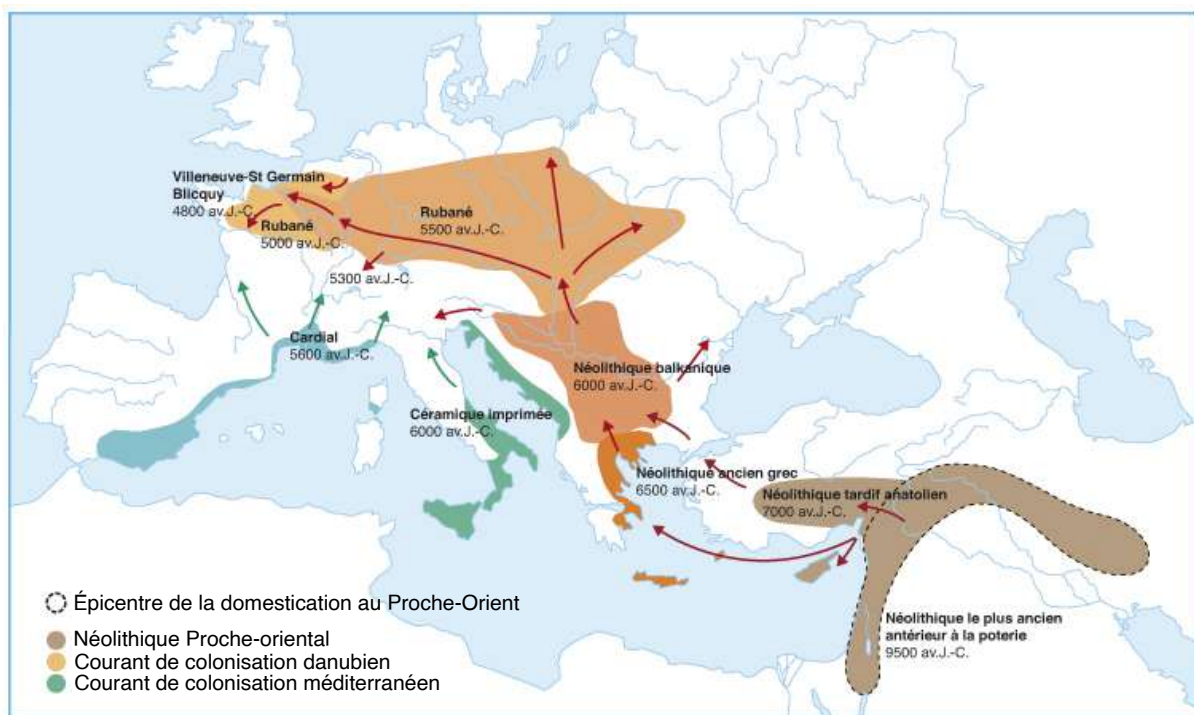


FIGURE 1.7 – Carte de la diffusion des populations Néolithiques en Europe à partir du Proche-Orient. (D'après Tresset et Vigne, 2011)

Aparté historique 2 Domestication du cochon et diffusion en Europe

Le cochon a été domestiqué indépendamment en deux endroits et à deux époques différentes : Une première fois au Proche-Orient vers 8 500 AEC (Conolly et al., 2011 ; Ervynck et al., 2001 ; Vigne et al., 2009), et une seconde fois en Chine vers 6 500 AEC (Cucchi et al., 2016, 2011 ; Groenen, 2016 ; Jing and Flad, 2002).

À noter que dès 11 400 AEC, donc bien avant la première domestication, le contrôle des populations de sangliers en Europe était déjà très important puisque des sangliers sauvages ont été transportés sur des embarcations et introduits sur l'île de Chypre, probablement pour pouvoir les chasser sur place (Vigne et al., 2009).

À partir de l'épicentre de domestication au Proche-Orient, les sociétés agricoles néolithiques ont migré vers l'Europe, transportant les cochons avec eux, en suivant deux itinéraires de dispersion.

1. La route maritime qui suit la côte de la mer Méditerranée par cabotage jusqu'à atteindre la péninsule italienne vers 6000 AEC et la côte française vers 5900 AEC (Manen et al., 2018).
2. La route continentale qui depuis les Balkans suit le cours du Danube et arrive en Europe vers 6000 AEC, et atteint le bassin parisien vers 5200 AEC (Guilaine, 2003 ; Ilett, 2010).

Dans la partie continentale, on retrouve des traces de cochon tout le long de l'itinéraire de dispersion jusqu'en France. Ainsi tous les porcs qui arrivent en Europe occidentale seraient d'origine proche-orientale (Larson et al., 2007), mais les études génétiques ont montré que tous les porcs domestiques actuels sont issus de sangliers européens (Larson et al., 2007 ; Ottoni et al., 2013), ce qui suggère une domestication locale en Europe qui serait en contradiction avec les études archéologiques (Rowley-Conwy, 2003).

Ce paradoxe a été en partie résolu grâce à de nouvelles études génétiques (Caliebe et al., 2017 ; Larson et al., 2007) qui ont montré que les porcs proches-orientaux ont été remplacés par les porcs européens au cours du 4e millénaire AEC. Ce remplacement pourrait être le résultat soit d'une domestication secondaire locale de sangliers européens, soit d'une hybridation de porcs du Proche-Orient avec des sangliers européens (Frantz et al., 2015).

En revanche la diffusion des cochons le long de la route méditerranéenne est moins bien documentée : des traces de cochons sont identifiées jusque dans la péninsule Italienne, en Corse et en Sardaigne, mais aucune trace formelle au-delà, ni en Ligurie ni en Provence jusqu'au 5e millénaire AEC. (Figure 1.7 page 31)

N.B. : Dans la mesure du possible, les dates présentées dans cette thèse sont exprimées "Avant l'Ère Commune" abrégé AEC, ou "Before Common Era" en anglais abrégé BCE. Cette locution a pour fonction de remplacer "Avant Jésus-Christ".

1.3 Structure de la thèse

Cette thèse se compose de trois chapitres qui suivent ce premier chapitre introductif, présentés soit sous forme d'article complet tel que publié dans la revue correspondante (chapitres 1 et 2), soit sous forme de manuscrit en préparation (chapitre 3), ainsi que d'un dernier chapitre permettant de synthétiser les conclusions des chapitres précédents, de les discuter et de présenter des perspectives de recherche.

- Chapitre 2 : The mark of captivity : plastic responses in the ankle bone of a wild ungulate (*Sus scrofa*).
Le second chapitre explore les réponses plastiques liées à la réduction de la mobilité dans la morphologie du calcaneus chez le sanglier, puis tente de quantifier à quel point ces modifications sont impactées par le lien fonctionnel entre os et muscles.
- Chapitre 3 : Investigating the impact of captivity and domestication on limb bone cortical morphology : an experimental approach using a wild boar model.
Le troisième chapitre vise à déterminer s'il est possible de détecter des modifications liées à la réduction de mobilité au niveau de la topographie de l'épaisseur corticale de l'humérus chez le sanglier, puis à quantifier à quel point ces modifications sont impactées par le lien fonctionnel entre os et muscles.
- Chapitre 4 : Pig domestication in Western Europe : assessing the impact of anthropogenic control over Early Neolithic *Sus scrofa* populations.
Le quatrième chapitre tente d'appliquer les marqueurs identifiés sur le calcaneus et l'humérus dans les chapitres précédents sur du matériel archéologique du Néolithique du Sud et du Nord de la France et de Chypre. L'objectif est de déterminer à quel point les populations de sangliers du Néolithique étaient sous contrôle des populations humaines afin d'apporter un nouvel éclairage sur la compréhension actuelle de la domestication précoce du porc en Europe occidentale.

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CHAPITRE

2

THE MARK OF CAPTIVITY : PLASTIC RESPONSES IN THE ANKLE BONE OF A WILD UNGULATE (*SUS SCROFA*)

N.B. : Dans ce chapitre, les ACSA (Anatomical Cross-Section Area) sont nommées par erreur PCSA (Physiological Cross-Section Area). L'article est paru avant que l'erreur n'ait été identifiée.

Research



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Author for correspondence:

Thomas Cucchi
e-mail: cucchi@mnhn.fr

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The mark of captivity: plastic responses in the ankle bone of a wild ungulate (*Sus scrofa*)

Hugo Harbers¹, Dimitri Neaux¹, Katia Ortiz², Barbara Blanc², Flavie Laurens³, Isabelle Baly³, Cécile Callou³, Renate Schafberg⁴, Ashleigh Haruda⁴, François Lecompte⁵, François Casabianca⁶, Jacqueline Studer⁷, Sabrina Renaud⁸, Raphael Cornette⁹, Yann Locatelli², Jean-Denis Vigne¹, Anthony Herrel¹⁰ and Thomas Cucchi¹

¹UMR 7209, Archéozoologie, Archéobotanique, Sociétés Pratiques et Environnements (AASPE), CNRS, Muséum national d'Histoire naturelle, Paris, France

²Réserve Zoologique de la Haute Touche, 36290 Oberterre, Muséum national d'Histoire naturelle, France

³Unité Bases de données sur la Biodiversité, Écologie, Environnement et Sociétés (BBEES), Muséum national d'Histoire naturelle, Paris, France

⁴Martin Luther University Halle-Wittenberg Central Natural Sciences Collections, Museum for domesticated animals

⁵CIRE, INRA, Nouzilly, France

⁶LRDE, INRA, Corté, France

⁷Natural History Museum of Geneva

⁸Laboratoire de Biométrie et Biologie Évolutive (LBBE), UMR 5558 CNRS, Université Lyon 1, Villeurbanne, France

⁹Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, France

¹⁰UMR 7179, Département Adaptations du Vivant, Bâtiment d'Anatomie Comparée, CNRS, Muséum national d'Histoire naturelle, Paris, France

DN, 0000-0001-9465-220X; IB, 0000-0002-9947-9378; RS, 0000-0003-4156-5414; SR, 0000-0002-8730-3113; AHe, 0000-0003-0991-4434; TC, 0000-0001-6021-5001

Deciphering the plastic (non-heritable) changes induced by human control over wild animals in the archaeological record is challenging. We hypothesized that changes in locomotor behaviour in a wild ungulate due to mobility control could be quantified in the bone anatomy. To test this, we experimented with the effect of mobility reduction on the skeleton of wild boar (*Sus scrofa*), using the calcaneus shape as a possible

phenotypic marker. We first assessed differences in shape variation and covariation in captive-reared and wild-caught wild boars, taking into account differences in sex, body mass, available space for movement and muscle force. This plastic signal was then contrasted with the phenotypic changes induced by selective breeding in domestic pigs. We found that mobility reduction induces a plastic response beyond the shape variation of wild boars in their natural habitat, associated with a reduction in the range of locomotor behaviours and muscle loads. This plastic signal of captivity in the calcaneus shape differs from the main changes induced by selective breeding for larger muscle and earlier development that impacted the pigs' calcaneus shape in a much greater extent than the mobility reduction during the domestication process of their wild ancestors.

1. Introduction

Documenting the domestication process of animals in archaeology provides insights into a major cultural and biological transition in human history and into the temporal depth of its impact over biodiversity and species evolution [1–6]. Yet, tracking the domestication process in the archaeological record is an extremely challenging task for bioarchaeologists, as it involves intertwined cultural, ecological and evolutionary components [7,8], and is entirely dependent on the species involved, its domestication pathway and the intensity of their relationship with humans [9–11]. To help identify this complex and elusive process in archaeology, the process of domestication and the concept of domestic animals should be separated. The former involves the control of wild animals and may provoke no visible bioarchaeological modification, especially in the initial stages. The latter is restricted to animal populations showing clear biological modifications due to domestication [12].

To document the biological process of animal domestication, bioarchaeologists have relied on genetic markers of reproductive isolation and trait selection, or genetically induced morphological markers [13]. These morphological markers, which are all parts of an integrated 'domestication syndrome' already mentioned by Darwin [14], are associated with an animal's response to new selective pressures within a human environment [15,16], long before the selection of specific traits useful to humans [17] and are only visible after several generations [18,19]. They can be traced in the archaeological record through bone and tooth size reduction, the reduction of the volume of the brain cavity or the jaw's shortening [20]. These morphological markers have been considered as a universal trait package of animal domestication syndrome since the Russian fox farm experiment initiated by Dr Dmitri Belyaev, which demonstrated the link between the selection for tameness and the domestication syndromes. However, recent historical review called into question the ubiquity and indeed the utility of the domestication syndrome trait package [21]. Furthermore, it remains questionable for tracking early domestication processes in the archaeological record [10,22], especially when gene flow between wild and domestic populations was common [23–26], thus delaying the expression of these syndromes. So how early can bioarchaeologists document the domestication process? Can they access the plastic (non-heritable) changes immediately induced by human control over wild animal behaviour over the course of its lifetime? If such signatures of human control could be deciphered from the archaeological record, an entire new range of incipient domestication and human–animal interactions could be accessed, several millennia before the earliest visible genetically induced morphological change.

Independent of any genetic change, modifications in the use of a skeletal trait may trigger adjustments of the musculature, which can subsequently induce morphological variation through skeletal plasticity: muscle stimulation influences bone growth, development and remodelling [27,28]. To date, the 'environmental' or 'plastic' morphological responses to conditions experienced by animals under human control have received scant attention [29] despite their potential to generate fast responses in the context of domestication. Such processes could have potentially triggered a phenotypic response as early as the first generation of wild-caught animals bred or maintained in captivity. In this paper, we explore if bone plasticity can trace human-induced changes in locomotor behaviour generated by imposed restrictions on an animal's movements through captivity. The effect of several generations of captivity on the morphology of the skeleton of wild mammals (mainly felines and primates) has already been described [30–32], but many of these studies relate to the process of selection in captive populations similar to the domestication syndrome [30,33–35]. The plastic responses in the skeleton over the lifespan of a wild-caught mammal induced by captivity have been explored only in the house mouse [36]. Therefore, whether change in locomotor behaviour of a wild mammal taken out of its ecological context can have a significant impact on its bone

anatomy and how much this plastic signal can be separated from the selection on behaviour remains unknown.

To test this hypothesis, we used an experimental approach on the wild boar (*Sus scrofa*), since ungulates played a major role as food in the Neolithic transition and because few studies have used ungulates to explore the effects of captivity [30]. To control for genetic and environmental factors of skeleton variation, we captured weaned piglets from a genetically homogeneous wild boar population, few kilometres away from the experimental farm where they were reared according to two regimes of mobility reduction. The initial objectives were to explore whether captive locomotor behaviour could lead to bone shape modifications beyond the reaction norm observed in wild-caught wild boar and to quantify how much these plastic modifications are impacted by the functional link between bone and muscles. The second objective was to compare this experimental plastic response to captivity with the phenotypic changes induced by selective breeding (artificial selection) in pigs over the last 200 years. In order to compare current and past phenotypic variation and to track these markers of plasticity in the archaeological record, we chose the ankle bone (the calcaneus) as a phenotypic marker. This bone is key in terrestrial mammal locomotor behaviour, acting as a lever arm for the ankle extensors, and is subjected to high tensile, bending and compressive forces [37,38]. Furthermore, even though its proximal epiphyses fuse rather late, this bone is well preserved in archaeological contexts thanks to its compacity. Finally, it was not purposely broken to access the bone marrow, as is the case for long bones and is thus often retrieved intact [39].

2. Material and methods

2.1. Experimental design

To experimentally test the plastic response of mobility reduction on the shape of the calcaneus in a wild ungulate, we rely on a control population of wild boar living in a 100 000 m² (10 ha) fenced forest in Urciers (Indre, France), where human interaction is intentionally kept to a minimum in order to ensure that the boars' behaviour remains as natural as possible. Consequently, the mobility of this control population is not very different from the pre-Neolithic situation in the Near East where wild boar were probably partly commensal before being fully domesticated [40,41]. From this genetically homogeneous control population, we captured 24 6-month-old piglets that we divided into two groups of equal sample size and sex ratio. Both groups were raised in a zoological reserve 100 km away from the control population until the age of 24 months, in two different contexts of mobility: a 3000 m² (0.3 ha) wooded pen and an indoor stall of 100 m², where males and females were separated. To better control the effect of diet on the growth of the two groups, they were both supplied with standardized food pellets in order to maintain a healthy weight, according to the standard nutritional requirements of European wild boar populations [42]. Water was available ad libitum.

This experiment received full ethical agreement (APAFIS#5353-201605111133847).

2.2. Comparative collection

The captive signal at adulthood in wild boars reared in stalls and pens was contrasted with 28 adult wild-caught wild boars from the control population in Urciers, three other populations in France and two in Switzerland (table 1). All these specimens were wild caught between 1 and 18 years of age. We also included two captive wild boars from the museum for domesticated animals in Halle (Museum für Haustierrkunde 'Julius Kühn', MHK). These specimens were captured around 1900 at an unknown age from a population of German wild boars, but we know their mobility was significantly reduced for between 10 and 15 years before their death.

To compare the plastic response of captivity with the phenotypic change driven by the last 200 years of artificial selection, we collected 19 domestic pigs, including 11 specimens from traditional landraces, which were part of a conservation programme, and eight from an intense breeding programme dedicated to industrial meat production (table 1). All these domestic specimens are part of the historical collections of the MHK. They were reared in stalls and were aged between 1 and 9 years. We also included five free-range Corsican landrace pigs (*U nustrale*) 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 to access natural resources for their diet [43].

Table 1. Sample size and origin of the samples. MNHN: Muséum national d'Histoire naturelle in Paris, MHK: Museum für Haustierkunde Julius Kühn in Halle, MHNG: Muséum d'Histoire Naturelle in Geneva. For information regarding body mass, age, sex, muscles and status of the individuals included, please see electronic supplementary material, SI 1.

status	category	population/Breed	mobility	curation	N GMM	N muscle data	N body mass	grouping factor
wild boar	control (France)	Urciers	wild caught	MNHN	5	3	5	WB_ctrl
wild boar	experiment (France)	Urciers	captive reared (stall)	MNHN	12	10	12	WB_stall
wild boar	experiment (France)	Urciers	captive reared (pen)	MNHN	12	12	12	WB_pen
wild boar	Switzerland	Bois de la Batie	wild caught	MHNG	5	0	5	WB_wc
wild boar	Switzerland	Dardagny	wild caught	MHNG	2	0	2	WB_wc
wild boar	France	Saint-Jean-D'Aulps	wild caught	MHNG	6	0	6	WB_wc
wild boar	France	Compiègne	wild caught	MNHN	4	0	4	WB_wc
wild boar	France	Chambord	wild caught	MNHN	6	1	6	WB_wc
wild boar	Germany	Germany	captive reared (stall)	MHK	2	0	2	WB_MHK
pigs	landraces	Bayerisches Landschwein	captive reared (stall)	MHK	5	0	0	DP_Land
pigs	landraces	Hannover-Braunschweig Landschwein	captive reared (stall)	MHK	3	0	0	DP_Land
pigs	landraces	Lincolnshire	captive reared (stall)	MHK	1	0	0	DP_Land
pigs	landraces	Tamworth	captive reared (stall)	MHK	2	0	0	DP_Land
pigs	landraces	Corsican breed	free range	MNHN	5	0	0	DP_Cor
pigs	improved breeds	Berkshire	captive reared (stall)	MHK	4	0	0	DP_Improv
pigs	improved breeds	Deutsches edelschwein	captive reared (stall)	MHK	2	0	0	DP_Improv
pigs	improved breeds	Veredeltes Landschwein	captive reared (stall)	MHK	2	0	0	DP_Improv

2.3. Calcaneus three-dimensional models

To compare the specimens from the different institutions, we combined three-dimensional images acquired from medical CT scan and photogrammetry. Previous studies have shown that the results from these methods are comparable [44,45]. Seventy specimens were CT scanned on a Siemens Somatom® medical CT scanner with a spatial resolution of 100 to 500 micrometres at the CIRE imaging service of the INRA in Nouzilly. Sixteen specimens from Germany were scanned using the medical CT scanner of the Halle hospital with the same parameters. For each calcaneus, three-dimensional surfaces were obtained from the DICOM images stacks using Avizo v. 8.0.

The three-dimensional models of 13 specimens from Switzerland and MHK were obtained using photogrammetry. We used a Sony DSLR-A350 camera with a 50 mm lens. Each calcaneus was placed on a rigid, planar cardboard sheet with a calibrated reference pattern. The photographs were shot at regular intervals of approximately 22° near the proximal and distal extremities and 45° near the lateral and medial sides as the operator rotated the cardboard sheet. Sets of 12 pictures were acquired from three different vertical angles (approximately 10°, 40° and 70°) for both dorsal and plantar sides. Some additional pictures were shot to ensure every detail was captured. In total, more than 72 (12 × 3 × 2) pictures were used to reconstruct each model. Sets of images were processed with Agisoft PhotoScan to obtain three-dimensional surface files of each calcaneus and scaled using the 'Transform: Scale' tool in MeshLab.

2.4. three-dimensional shape and centroid size variables

To capture the complexity of the calcaneus form, encompassing the articulation and muscle insertion areas, we used a three-dimensional sliding semi-landmark procedure [46] (figure 1 and table 2). This included 14 anatomical type III landmarks on the maxima of curvature due to the lack of structures for placing type I or type II landmarks. A total of 181 sliding semi-landmarks on seven curves constrained by anatomical landmarks and corresponding to joint surfaces, muscle attachment surfaces and the junction with the epiphysis were also taken. Finally, 763 surface sliding semi-landmarks uniformly distributed over the surface were taken. Anatomical landmarks and sliding semi-landmarks were obtained from the three-dimensional polygonal surfaces using IDAV Landmark v. 3.0 [47]. Semi-landmarks were slid while minimizing the bending energy using the R package 'Morpho' [48]. We used a generalized Procrustes analysis [49] to rotate, translate and scale the landmark configurations to obtain a new set of shape variables (Procrustes coordinates) and the centroid size (CS) of the calcaneus using 'Morpho'. CS is the square root of the sum of squared distances of the landmarks from their centroid.

2.5. Life-history dataset

To analyse the covariation between life-history traits and the calcaneus form in wild boar, we collected body mass, sex and age for the wild boar specimens (electronic supplementary material, SI 1). Captive-raised wild boars have a known age at death, but wild-caught wild boars had to be aged according to their dental eruption and occlusal attrition stages [50,51].

2.6. Muscle force estimates

To measure the covariation between calcaneus shape and the functional properties of the muscles attached to the calcaneus, we dissected the lateral gastrocnemius (LG), the medial gastrocnemius (MG) and the soleus (S) of 22 experimental captive-reared wild boars, four specimens from the control population, and eight wild boars from French populations (table 1, electronic supplementary material, SI 1). Muscle data were not available for other specimens. The muscles were weighed to the nearest gram and muscle fascicle length was measured with calipers. Based on the known density of mammalian muscle (1.06 g cm⁻³) [52], we calculated the physiological cross-sectional area (PCSA) as a proxy for muscle force by dividing the muscle volume by the fibre length [53].

2.7. Available area for locomotion

In order to measure the influence of mobility restriction on calcaneus shape variation in wild boars, we collected information on the available area for each of the experimental groups and the wild populations

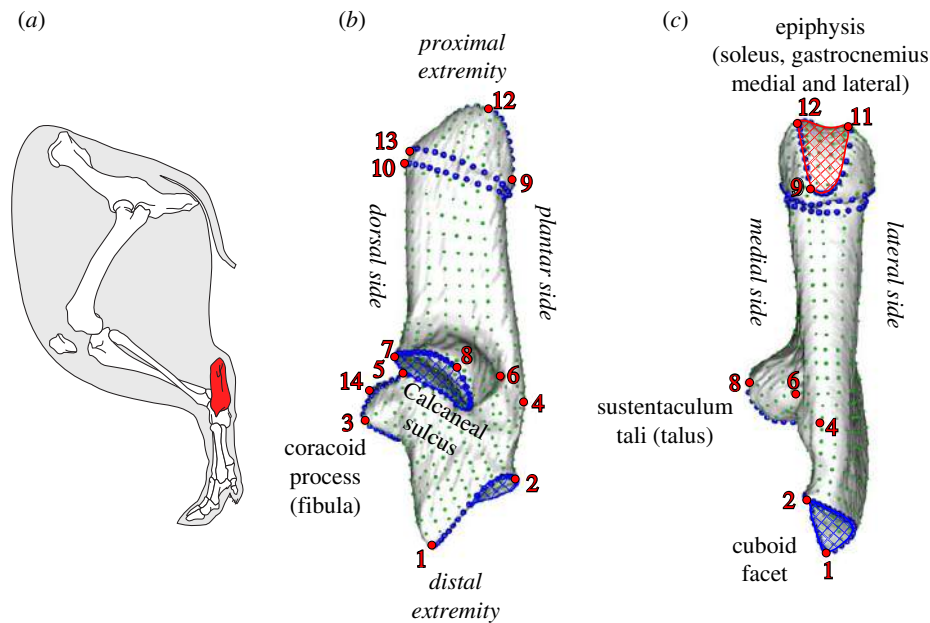


Figure 1. (a) The wild boar calcaneus in lateral view in relation to the other bones and muscles of the leg. (b) and (c) Medial and plantar views with landmarks (red dots), semi-landmarks on curves (blue dots) and semi-landmarks on surfaces (green dots). Blue shaded areas represent articular surfaces and the red shaded area represents the muscle attachment surface.

Table 2. Anatomical definition of the 14 landmarks (LM) and 7 curves (C).

LM1	distal end of the cuboid facet
LM2	proximo-plantar end of the cuboid facet
LM3	end of the beak of the coracoid process
LM4	maximum of curvature of the plantar bulge on the plantar margin
LM5	dorso-proximal end of the calcaneal sulcus
LM6	planto-lateral end of sustentaculum tali
LM7	dorsal end of the sustentaculum tali
LM8	medial end of sustentaculum tali
LM9	plantar end of the epiphysis
LM10	dorso-proximal end of the bulge of the proximal part (not on the epiphysis)
LM11	proximal end of the lateral lobe of the epiphysis (secondary lobe)
LM12	proximal end of the medial lobe of the epiphysis (main lobe)
LM13	dorsal end of the epiphysis
LM14	dorso-proximal end of the lateral part of the coracoid process
C1	edge of the articular surface of the cuboid facet
C2	medial edge of the coracoid process
C3	edge of the articular surface of the sustentaculum tali
C4	lateral edge of the coracoid process
C5	edge of the attachment surface of the tendon on the epiphysis
C6	distal delineation of the junction zone between the epiphysis and the rest of the calcaneus
C7	proximal delineation of the junction zone between the epiphysis and the rest of the calcaneus

(electronic supplementary material, SI 1). The areas available for the experimental contexts (pens and stalls) were known; however, the size of enclosures for the MHK wild boars had to be estimated from archive photos. The available areas for free wild boar populations from France and Switzerland were measured using Google maps, based on the measured area of the forest in which the specimens were caught.

2.8. Statistical analyses

2.8.1. Size, shape and life traits covariation in captive and wild-caught wild boars

The difference in calcaneus size and body mass variation among captive-reared and wild-caught wild boars, taking into account their sex, was visualized with a box plot and tested with factorial analysis of variance (ANOVA) and pairwise test. The correlation between calcaneus size and body mass was tested using the Pearson test.

We tested whether the calcaneus shape differed among wild-caught and captive-reared wild boars using their status (GP1) as grouping factor while accounting for shape covarying with age, body mass and bone centroid size (allometry) using a factorial MANCOVA with 1000 permutations.

We visualized and tested the PCSA differences among wild-caught and captive-reared wild boars using a box plot and ANOVA. The correlations between PCSA and calcaneus centroid size and body mass were tested with a regression and the Pearson test. For the visualization of shape deformation associated with body mass, calcaneus centroid size, available area for locomotion (in m²) and intrinsic muscle force (PCSA), we used partial least squares (PLS) analyses [54,55]. For the available area of mobility, as every specimen from each group had the same available area, we used group means for the PLS analysis.

2.8.2. Comparing plastic size and shape response to captivity with changes induced by artificial selection

Size differences between wild boars and domestic pig groups were tested using an ANOVA with the pairwise comparison tests (Bonferroni correction) and visualized with a box plot. The shape differences were tested with a Procrustes ANOVA and visualized using a Canonical Variate Analysis (CVA); both were performed on a shape-reduced dataset after a principal component analysis (PCA) performed on the Procrustes coordinates to keep 95% of the variance [56]. To visualize shape deformations along the canonical axes, we calculated the theoretical minimum and maximum shapes for each axis, associated with a heatmap on landmarks corresponding to the distance between the minimum and maximum of the axis. We also visualized the deformation along two vectors using the mean shape of wild-caught wild boars as a reference, towards the mean shape of captive-reared wild boars as the first vector and the mean shape of domestic pigs as the second vector.

To test the shape difference depending on the main categories (GP2: wild boars/traditional pig breeds/improved pig breeds) and their sex, including the interaction of these two factors, we used a factorial MANOVA with a 1000 permutations procedure.

All the statistics were performed using R [57]. Factorial MANOVA, Procrustes ANOVA and PLS were performed using the R package 'geomorph' [58]. ANOVA, PCA were performed using the package 'stats' [57], CVA using the package 'Morpho' [48] and visualizations were performed by using 'Morpho', 'stat' and 'plotrix' [59].

3. Results

3.1. Plastic responses to captivity in wild boars

We found no significant differences in body mass (ANOVA: $F = 1.171$, $p = 0.33$) and calcaneum centroid size (ANOVA: $F = 0.673$, $p = 0.57$) between the wild-caught and captive-reared wild boars. A slight trend towards greater bone size and body mass in captive-reared specimens compared to wild boars can be observed. Yet, no difference exists among the two captive-reared groups (figure 2). Sexual dimorphism is significant in calcaneus size (ANOVA: $F = 14.385$, $p = 0.0004$) but not in body mass (ANOVA: $F = 3.2$, $p = 0.08$). This absence of sexual dimorphism in body mass was mainly true for captive-reared specimens in stalls (figure 2b). The correlation between calcaneus centroid size and body mass was overall very strong (Pearson correlation coefficient: 0.82, $p < 0.0001$). Yet, stall-reared specimens display weaker correlation than wild-caught and pen-reared specimens (figure 2c).

Shape differences were significant between wild-caught and captive-reared wild boars ($F = 2.1902$, $p = 0.015$) as well as age effect over shape ($F = 2.1597$, $p = 0.012$), body mass ($F = 2.8195$, $p = 0.003$) and CS ($F = 3.5100$, $p = 0.001$). The three groups of wild-caught and captive-reared wild boars show a common shape covariation with age (GP1 \times age: $F = 0.0332$, $p = 0.476$) and centroid size (GP1 \times size: $F = 1.0442$, $p = 0.163$), but differed in the way body mass impact the calcaneus shape (GP1 \times mass: $F = 2.7302$, $p = 0.001$).

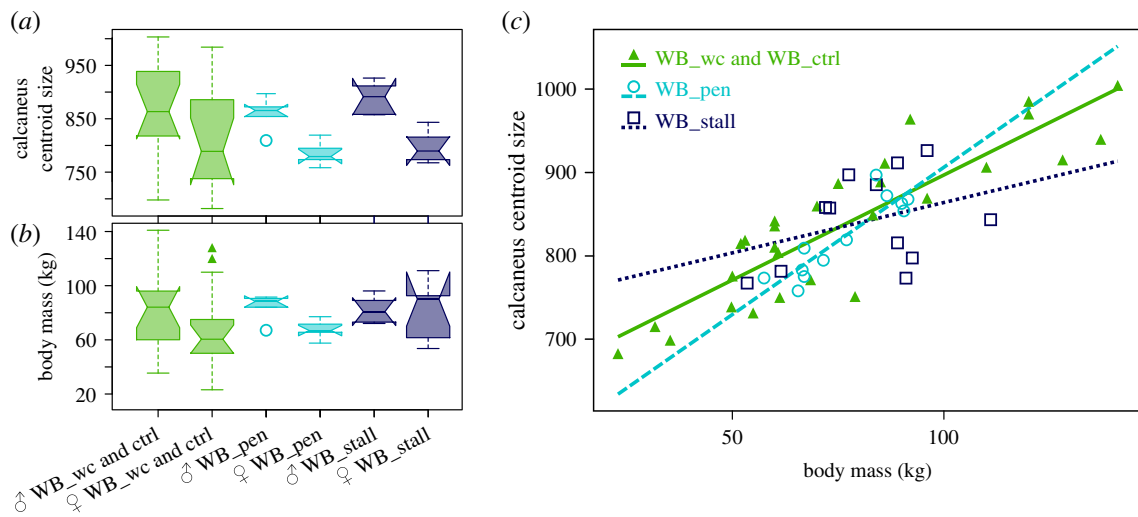


Figure 2. Differences among captive-reared and wild-caught wild boars in (a) calcaneus centroid size and (b) body mass. (c) Regression between calcaneus centroid size and body mass among wild-caught and captive-reared wild boars.

Compared to the wild-caught wild boars, the captive-reared wild boars had significantly greater muscle PCSA for the lateral (figure 3a, ANOVA: mean square=19.732, $F=8.63$, $p=0.0015$) and medial (figure 3b, ANOVA: mean square=18.716, $F=12.754$, $p=0.0001$) gastrocnemius, but not for the soleus (figure 3c, ANOVA: mean square=2.807, $F=2.866$, $p=0.075$). Sexual dimorphism in muscle PCSA among wild-caught and captive-reared wild boars was significant only for the lateral gastrocnemius (figure 3c, ANOVA: $F=6.518$, $p=0.0169$).

Similar calcaneus shape changes were found in association with body mass and calcaneus centroid size increase (figure 4a,c). Changes are localized in the distal part of the calcaneus with a more dorso-plantarily curved calcaneus and a shift of sustentaculum tali towards the distal extremity. The mobility reduction (figure 4b) and a greater force generation potential of the lateral and medial gastrocnemius muscles (figure 4d) is associated with a more elongated epiphysis that is curved towards the dorsal side and a more distally shifted sustentaculum tali.

3.2. Comparing plastic response to captivity in wild boars to artificial selection signal in domestic pigs

The calcaneus CS (figure 5) differed significantly among the groups (ANOVA: $F=5.75$, $p<0.001$). All the domestic pigs from the traditional and improved breeds had a larger calcaneus than wild-caught and captive-reared wild boars, except for the Corsican free-ranging pigs which were intermediate and showed no significant differences with the landraces, improved breeds or the wild-caught and captive-reared wild boars. The German captive-reared wild boars were in the upper range of wild-caught wild boars, probably because they are old specimens and their different genetic pool. These results suggest that calcaneus size increase is not affected by a change in locomotor behaviour but rather by artificial selection.

The calcaneus shape differed significantly among the eight groups of wild boars and domestic pigs (MANOVA: $F=3.0564$; $p<0.0001$). The main shape differentiation shown on the first canonical axis (figure 6a) was driven by the divergence between wild boars and pig breeds, with modern breeds being the most divergent in shape. Factorial MANOVA showed that difference between wild boars/traditional pig breeds/modern breeds accounted for 19% of the total variance of calcaneus shape in adults ($p<0.01$), while sexual dimorphism had almost no effect on shape variation and was similar in both wild boars and domestic breeds (electronic supplementary material, SI 2). The shape deformation associated with the divergence between wild-caught wild boars and domestic pigs (figure 6b,d) is marked by an increase in calcaneus robustness and thickness with a medio-laterally wider calcaneus, particularly on the medial side at the junction with the epiphysis where we can see a bulge. The coracoid process and the cuboid facet are also more robust and the epiphysis is longer in domestic pigs than in wild boars.

The second canonical axis is related to the difference in mobility, expressed both in wild boars and pigs (figure 6a). The captive-reared wild boars were strongly divergent from their wild-caught

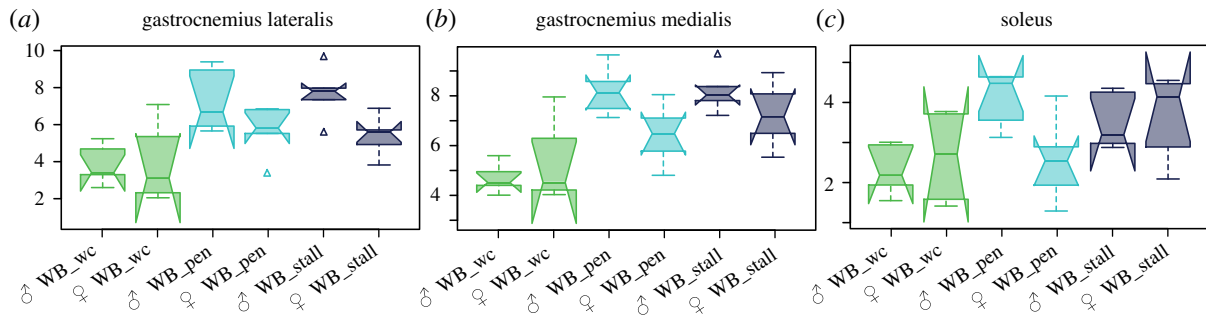


Figure 3. Difference in muscle PCSA among wild-caught and captive-reared wild boars taking into account their sex for (a) the lateral gastrocnemius, (b) the medial gastrocnemius and (c) the soleus.

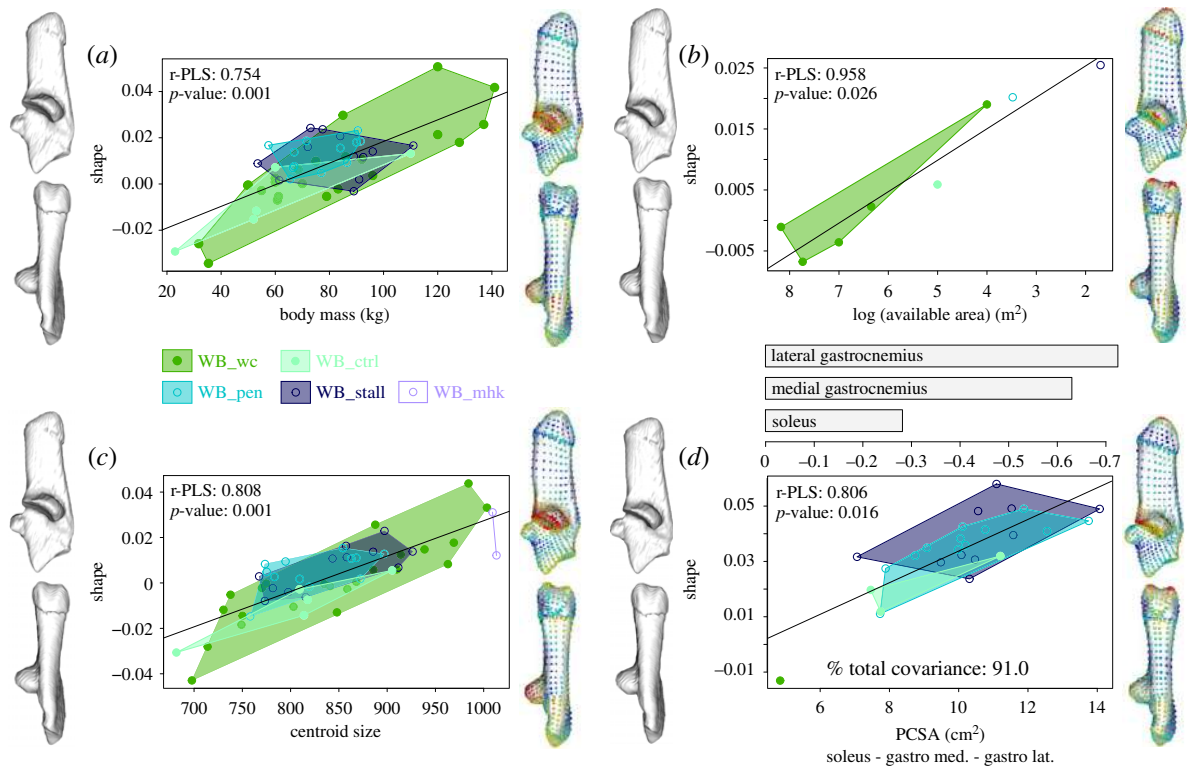


Figure 4. Relationships between the calcaneus shape and four continuous variables: (a) body mass (kg), (b) log (available area for mobility) (m^2), (c) calcaneus centroid size and (d) muscle PCSA (cm^2). Wild-caught wild boars are visualized in green and captive-reared wild boars in blue. Black lines represent the PLS regression line. Shape deformations are visualized with negative extreme shapes on the left of the scatterplot and positive extreme shapes are on the right. The heatmap on landmarks for positive extreme shapes represents the distance of each landmark from the negative extreme shape—the greater the distance the hotter the colour.

relatives along this axis, whereas the difference between the stall- and pen-reared wild boars was not significant (MANOVA, $F=5.1959$; $p=0.1736$). In pigs, the free-roaming Corsican pigs are the most divergent from the captive, modern breeds. The shape divergence on CV2 (figure 6c) and along the vector between wild-caught and captive-reared boars mean shapes (figure 6d) was localized on the proximal epiphysis, which was longer and curved towards the dorsal side in captive specimens. The sustentaculum tali was also slightly shifted towards the distal end compared to wild-caught wild boars.

4. Discussion

4.1. Plastic response to captivity

Previous studies have shown that several generations of captivity-induced changes in diet, exercise and stress could impact the morphology and physiology of captive populations [30]. However, most of these studies have investigated the phenotypic effect as an equivalent of the domestication syndrome, combining relaxed natural selection and unconscious selection for tameness [30,34,60]. Our

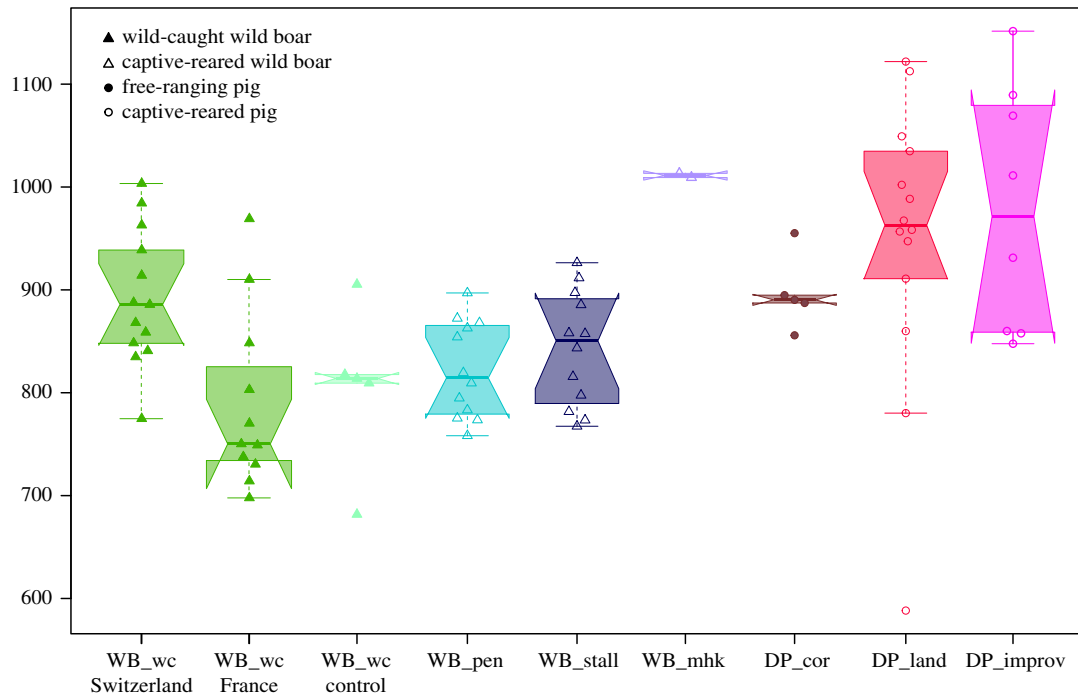


Figure 5. Box plot representation of the calcaneus centroid size variation in wild boars and pigs from free-ranging or captive environments.

experimental results provide the first evidence that the growth of a wild ungulate in a captive environment, where its locomotor behaviour is altered, impacts the shape of its calcaneus beyond the reaction norm of wild-caught populations. This evidence shows that morphological change in captivity can be driven by phenotypic plasticity and is probably a reflection of changes in the biomechanical environment of an animal during the course of its lifetime. These results contradict the only other study on the impact of captivity on the scapula of chimpanzees, which found no scapula shape differences among wild and captive extant populations of great apes [32], but they are in agreement with the study evidencing no foot size reduction between wild-caught and captive-reared house mice (*Mus musculus*) [36].

Indeed, we found no bone size reduction in captive-reared wild boars, suggesting that ankle bone shape has greater plasticity than overall bone size when a wild animal is facing modifications of its locomotor environment during its growth. Skeleton size reduction has been evidenced in captive black-footed ferrets (*Mustela nigripes*) after 10 years of captivity with increased mobility reduction over time [33]. This suggests that skeleton size reduction would only occur after several generations of selection for phenotypes that maximize fitness in captivity. Plastic bone size reduction in captivity is probably more a consequence of food shortages and overcrowding [61,62]. On the other hand, a plastic size increase is more likely to happen in captivity due to unrestricted access to food, driving faster growth as shown in captive chimpanzees [63].

4.2. Captivity and change in muscular function

The plastic imprint of captivity on the wild boar calcaneus, associated with changes of mobility reduction and an increase in intrinsic muscle force, clearly suggests that it is driven by an increase in the force exerted by the muscles on the bone when mobility reduction prevents the expression of full locomotor behaviour. The association between reduced mobility and increased muscle forces could seem counterintuitive at first. Indeed, in the wild, wild boar locomotor behaviour includes different types of movements (feeding, fleeing and dispersal) [64,65], which involve running fast up to 40 km h^{-1} , jumping high up to 150 cm [66] and daily travel, typically under 10 km but which can reach up to 80 km in one night [67]. Compared to the locomotor behaviour in captivity, where the need to search for food, flee predators, disperse or compete is suppressed, one would expect that the greater range of movements of free-ranging wild boars would have produced stronger gastrocnemius and soleus muscles. The answer possibly lies in the stereotyped locomotor behaviour induced by captivity, which may involve a reorientation of the calcaneus position due to more upright standing and thus more activity in the ankle extensors inducing greater stress on the

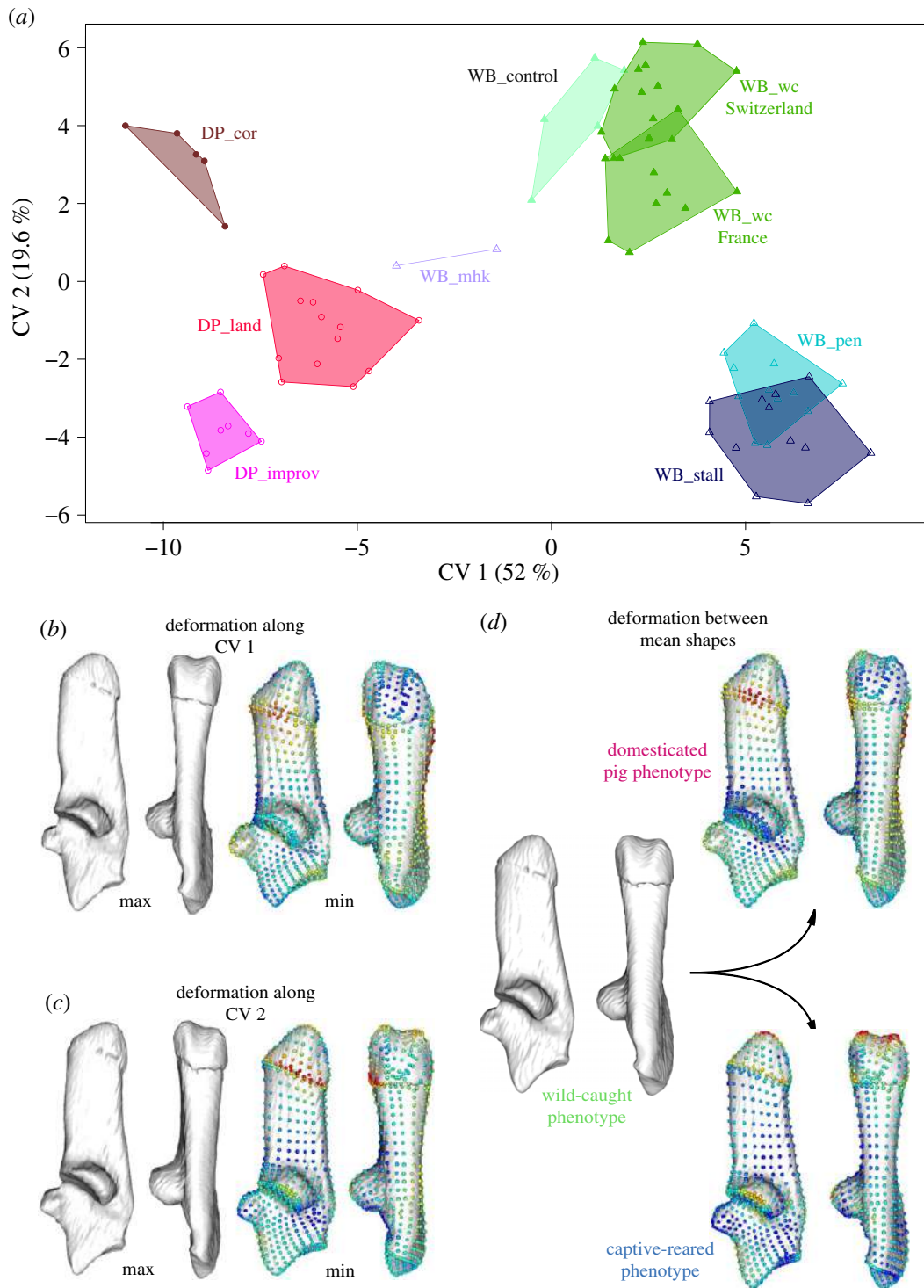


Figure 6. Morphospace based on a CVA representing the pattern of shape divergence among adult wild boars and pigs living in free-ranging or captive environments (a). Shape deformations correspond to the difference between the theoretical maximum and minimum shapes for axis 1 (b) and 2 (c). For better visibility, the extreme shapes were amplified by a factor of two and visualized from the maximum to the minimum. Calcaneus shapes are represented in medial and plantar views. The heatmap superimposed on landmarks for the minimum shape represents the distance of each landmark from the maximal shape: blue indicates a shorter distance and red indicates a greater distance. Shape deformations are also visualized between three mean shapes (d): wild-caught, captive-reared and pigs.

calcaneus [68]. Reorientation of the calcaneus shape has been observed in cervids living in closed environments that used fast-twitch muscles for more saltatorial locomotion compared to those living in open environments which use slow-twitch muscles for more cursorial locomotion [69]. Additionally, changes in the type of movement from long distance to slower movements requiring slower oxidative muscles—characterized by a lower cross-sectional fibre area versus more burst-type short distance locomotion in captivity associated with fast-contracting muscles involving a greater muscle fibre cross-sectional area—may drive this pattern.

4.3. Plastic versus selective changes

These plastic shape differences in captive-reared wild boars follow a different phenotypic trajectory compared to the shape divergence between wild-caught and domestic phenotypes induced by the last 200 years of selective pig breeding. However, this signal is also expressed in pigs, since we found a divergence between captive-reared and free-ranging pig breeds, suggesting that this plastic signal is of a more general nature. The patterns of covariation we observed between calcaneus shape and body mass, bone centroid size, available space for movements and muscle force suggest that shape divergence between domestic breeds and wild boar phenotypes may have been driven by increases in overall body mass and associated bone size (figure 4). Selection in breeding programmes for larger and heavier individuals [70–72] through growth rate, carcass length and muscle production [68] has produced a very different set of external loads on the bones [71], probably mediated by a different locomotion posture [73] compared to wild boars. Both the increased loads from the increased body mass and the muscle forces generated during locomotion inducing greater bone mass and strength [74] could explain the change in calcaneus shape towards greater shape robusticity observed in pigs.

5. Conclusion

Our results provide strong evidence that changes in locomotor behaviour induced by captivity can impact the bone anatomy of a wild ungulate over the course of its lifetime. This plastic imprint of captivity in wild boar calcaneus produces a phenotype beyond the usual reaction norm in natural environments but along a different trajectory than the divergence driven by selective breeding. If we consider that human control and modification of a wild animal's movements is one of the first steps towards domestication, our results provide new methodological perspectives for bioarchaeological approaches linking plastic responses to the domestication process involving cultural control of wild animal movements. Further studies now need to explore when these changes are implemented during the growth to understand the developmental processes behind these plastic changes.

Data accessibility. Code, data and metadata to perform statistical analyses on the calcaneus form and muscle PCSA are archived in the Dryad Digital Repository (<http://datadryad.org/>) and are currently accessible at the following location: <https://doi.org/10.5061/dryad.1zcrjdfnr>.

Authors' contributions. T.C. designed the research with A.He. and J.-D.V.; Y.L., K.O., B.B. and T.C. conducted the experimental fieldwork; T.C. collected the CT data with F.Le.; H.H. collected the photogrammetry data and A.He. collected the muscular data; F.La., I.B., C.C. and T.C. created the database of the project; H.H. carried out the GMM analyses and interpreted the data with T.C., A.He., R.C., D.N. and S.R.; T.C. and H.H. led the manuscript with scientific and editorial input from A.He., S.R., J.-D.V., D.N., R.S., A.Ha., F.C. and J.S. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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CHAPITRE

3

INVESTIGATING THE IMPACT OF
CAPTIVITY AND DOMESTICATION ON
LIMB BONE CORTICAL
MORPHOLOGY :
AN EXPERIMENTAL APPROACH USING
A WILD BOAR MODEL (*SUS SCROFA*)



OPEN

Investigating the impact of captivity and domestication on limb bone cortical morphology: an experimental approach using a wild boar model

Hugo Harbers^{1✉}, Clement Zanolli², Marine Cazenave^{3,4}, Jean-Christophe Theil⁵, Katia Ortiz⁶, Barbara Blanc⁶, Yann Locatelli^{6,7}, Renate Schafberg⁸, Francois Lecompte⁹, Isabelle Baly¹⁰, Flavie Laurens¹⁰, Cécile Callou¹⁰, Anthony Herrel⁵, Laurent Puymeraill^{1,11,12} & Thomas Cucchi^{1✉}

The lack of bone morphological markers associated with the human control of wild animals has prevented the documentation of incipient animal domestication in archaeology. Here, we assess whether direct environmental changes (i.e. mobility reduction) could immediately affect ontogenetic changes in long bone structure, providing a skeletal marker of early domestication. We relied on a wild boar experimental model, analysing 24 wild-born specimens raised in captivity from 6 months to 2 years old. The shaft cortical thickness of their humerus was measured using a 3D morphometric mapping approach and compared with 23 free-ranging wild boars and 22 pigs from different breeds, taking into account sex, mass and muscle force differences. In wild boars we found that captivity induced an increase in cortical bone volume and muscle force, and a topographic change of cortical thickness associated with muscular expression along a phenotypic trajectory that differed from the divergence induced by selective breeding. These results provide an experimental proof of concept that changes in locomotor behaviour and selective breeding might be inferred from long bones morphology in the fossil and archaeological record. These trends need to be explored in the archaeological record and further studies are required to explore the developmental changes behind these plastic responses.

Exploring the process of domestication as an integration of animals into human society provides a unique insight into one of the key steps in *Homo sapiens* evolution, at the root of its global impact over the biosphere¹ and species evolution². However, documenting this process, as an intensification of the relationship between humans and animals in archaeology³, is challenging^{4,5}. One of the main issues is that no relevant methodological approach has been able to capture this elusive process. Bioarchaeologists have relied on a morphological ‘syndrome of

¹Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, UMR 7209, Muséum national d’Histoire naturelle, CNRS, Paris, France. ²Laboratoire PACEA, UMR 5199, Université de Bordeaux, Bordeaux, France. ³School of Anthropology and Conservation, Skeletal Biology Research Centre, University of Kent, Marlowe Building, Canterbury, Kent CT2 7NR, UK. ⁴Department of Anatomy and Histology, School of Medicine, Sefako Makgatho Health Sciences University, Pretoria, South Africa. ⁵Mécanismes Adaptatifs et Evolution, UMR 7109, Muséum national d’Histoire naturelle CNRS, Paris, France. ⁶Réserve Zoologique de la Haute Touche, Muséum national d’Histoire naturelle, Obterre, France. ⁷Physiologie de la Reproduction et des Comportements, UMR 7247, National Research Institute for Agriculture, Food and Environment (INRAE), CNRS Université de Tours IFCE, Nouzilly, France. ⁸Central Natural Science Collections, Martin Luther University Halle-Wittenberg, Halle, Germany. ⁹Plateforme CIRE, National Research Institute for Agriculture, Food and Environment (INRAE), Nouzilly, France. ¹⁰Unité Bases de Données sur la Biodiversité, Écologie, Environnement et Sociétés, UMS 3468, Muséum national d’Histoire naturelle, Paris, France. ¹¹Anthropologie bio-culturelle, droit, éthique et santé (ADES), UMR 7268, Faculté de Médecine Site Nord, Marseille, France. ¹²Laurent Puymeraill is deceased. ✉email: hugo.harbers@edu.mnhn.fr; cucchi@mnhn.fr

domestication' of the skeleton first proposed by Darwin⁶ and later tested experimentally by Belyaev in his famous fox farm experiment^{7–9}. These morphological syndromes, including bone size reduction and changes in craniofacial morphology, have often been considered as a pleiotropic consequence of tameness selection¹⁰ through the perturbation of the neural crest cells involved in bone and chondral development¹¹. However, these syndromes imply complete genetic isolation and strong artificial selection, which are not transferable to the early process of domestication by the first farming communities^{12,13}. Furthermore, syndromes are not shared across species and mainly relate to breeding rather than behavioural selection¹⁴. For all these reasons, new morphological markers are required to further document the early interaction between the ecological dynamics of humans and animals based on archaeological remains.

Here, we provide an experimental proof of concept that direct environmental changes (i.e. mobility reduction) could immediately affect ontogenetic changes in long bone structure, providing a skeletal marker of early domestication. One of the least understood aspects when documenting animal domestication in archaeology is the morphological response to environmental conditions experienced by animals under human control⁵. To date, it has been generally considered that morphological changes such as bone size reduction or craniofacial modifications are subsequent to the integration of animals into human society^{15,16}. Therefore, morphological markers have been deemed irrelevant to document the initial domestication process as they would only be detectable in an already domesticated animal; i.e. once genetic isolation and breeding selection were already in place³. However, the ecological responses to the environmental stress of human control at an individual scale may induce phenotypic plasticity that can be quantified by its reaction norm¹⁷. Phenotypic plasticity is the outcome of the interaction between the genotype and the environment through development without any genetic mutations¹⁸. The growth of bones is directly affected by their habitual loading environment¹⁹. Activity and motion will produce muscular strains and loading that bones will have to resist. The bone resistance to these stresses can be achieved through bone mass, bone geometry and reorganization of bone microstructure with modelling activity²⁰. The bone adaptation to mechanical stimuli during growth is immediate and can last into adulthood. So far, the plastic response of animal's bone morphology under human control has been investigated in archaeology through bone pathologies²¹ and discrete morphological differences (see refs. in⁵). Histological differences have been used to document variations between wild specimens and domestic breeds^{22,23}. Despite the well-known plasticity of limb bones to changes in the biomechanical stimuli of their environment through bone growth (modelling) and turnover (Haversian remodelling) of their shaft²⁰, no studies have used this framework to explore how human control of the natural behaviour of a wild animal impacts its limb bone structure and how these changes might inform the early process of animal domestication.

The ability of the limb bone to adapt its mass, shape and architecture to fit the biomechanical demands that prevail in its environment has been recently investigated in rodents²⁴ and mustelid^{25–27} mammals. Since cortical bone is well preserved in fossil and archaeological deposits, researchers in physical anthropology have investigated structural variation in limb bones in relation to environmental variation to infer locomotor adaptations and behaviour in past hominins. These approaches include the study of the diaphyseal cross-sectional geometry^{20,28} or markers of muscle insertions visible on the periosteal surface, also known as enthesal changes^{29–32}. More recently, virtual imaging has allowed the development of a comprehensive approach to study variation in cortical thickness in limb bones using 3D morphometric mapping^{33–39}. However, Pearson and Lieberman²⁰ argued for caution in the interpretation of these markers to reconstruct past human behaviour without further experimental approaches. Subsequent studies explored the relevance of functional inferences from bone morphology using experimental studies on domestic vertebrates^{40–42} or cross-sectional studies on primates³⁷. These studies supported the validity of the reconstruction of locomotor behaviour based on changes in the cortical structure of limb bones. Yet, no support was found for a relation between enthesal changes and variation in locomotor behaviour. Experiments using electrical muscle stimulation in mice, however, show that enthesal changes can reflect the repetitive use of muscles⁴³.

This study tested experimentally the hypothesis that reduced mobility during growth in a wild ungulate, induced by captivity, results in measurable structural variation in limb bone morphology. Considering that physical activity stimulates bone remodelling, we expected that a free-ranging wild ungulate, having space to fully express their locomotor behaviour, to have a thicker cortical bone in the humerus than a wild ungulate which had grown in captivity. If such plastic responses could be quantitatively differentiated from the reaction norm in extant wild ungulates exhibiting natural behaviour, it would represent a marker of human control over wild animal movements, transferable to the archaeological record in order to reconstruct the early process of human control of wild animal populations⁴⁴. This study relied on a large-scale experiment controlling genetic and environmental factors while imposing changes in locomotor behaviour during growth in a population of captive wild boar (*Sus scrofa*). The structural changes in the limb bones were quantified using 3D morphometric mapping of cortical thickness. We evaluated the effects of age, body mass, sex, and muscle cross-sectional area. The captivity signal in the bone morphology of the experimental wild boars was contrasted with the cortical signal from free-ranging wild boar populations, to explore how much the response to captivity can be differentiated from the reaction norm of bones of animals in their natural habitat. Finally, we contrasted the captivity signature with the impact of selective breeding on bone cortical morphology using pigs from traditional and industrial breeds to assess whether breeding selection and mobility control can be distinguished from one another.

Material and methods

Experimental design. To test how a change in locomotor behaviour through mobility reduction affects the topographic variation of the cortical thickness of the humerus shaft in a wild ungulate, we relied on a genetically homogenous population of wild boar living in a 100,000 m² (10 ha) fenced forest in Urciers (Indre, France) thus controlling for variation in genetic diversity and environment. Human interaction with this population was

Status	Category	Population/breed	Mobility	Curation	N cartography	N muscle data	N body mass	Grouping factor
Wild boar	Control (France)	Urciers	Wild caught	MNHN	5	1	5	WB_ctrl
Wild boar	Experiment (France)	Urciers	Captive reared (stall)	MNHN	12	10	12	WB_stall
Wild boar	Experiment (France)	Urciers	Captive reared (pen)	MNHN	12	12	12	WB_pen
Wild boar	France	Compiègne	Wild caught	MNHN	4	0	4	WB_wc
Wild boar	France	Chambord	Wild caught	MNHN	14	6	11	WB_wc
Pigs	Landraces	Bayerisches Landschwein	Captive reared (stall)	MHK	5	0	0	PIG_Land
Pigs	Landraces	Hannover-Braunschweig Landschwein	Captive reared (stall)	MHK	5	0	0	PIG_Land
Pigs	Landraces	Mangalitza	Captive reared (stall)	MHK	1	0	0	PIG_Land
Pigs	Landraces	Polnisches Landschwein	Captive reared (stall)	MHK	1	0	0	PIG_Land
Pigs	Landraces	Corsican Breed	Free range	MNHN	5	0	0	PIG_Cor
Pigs	Improved breeds	Berkshire	Captive reared (stall)	MHK	4	0	0	PIG_Improv
Pigs	Improved breeds	Unknown	Captive reared (stall)	MNHN	1	0	0	PIG_Improv

Table 1. Sample origin and number of available specimens for the different parameters analysed in this study. *MNHN* Muséum national d'Histoire naturelle in Paris, *MHK* Museum für Haustierkunde Julius Kühn in Halle, *MHNG* Muséum d'Histoire Naturelle in Geneva. For information regarding body mass, age, sex, muscles and status of the individuals included, please see data availability.

intentionally kept to a minimum, ensuring that the behaviour of the boars remained as natural as possible. From this controlled population we captured 24 6-month-old piglets that we divided into two groups of equal sample size and sex ratio. Both groups were raised until the age of 24 months under two different contexts of mobility: a 3000 m² (0.3 ha) wooded pen and an indoor stall of 100 m², where males and females were separated. We created two captive settings, expecting that they would induce a difference in the amount of movement, sufficient to produce observable changes in humerus cortical bone. Both groups were supplied with standardized food pellets in order to maintain a healthy weight, according to the standard nutritional requirements of European wild boar populations (Étienne 2003). Water was available ad libitum.

This experiment was undertaken in the zoological reserve of La Haute Touche, Obterre (France) and received full ethical agreement from the Ethical Committee for animal experimentation of the Natural History Museum of Paris (Comité Cuvier) and the French Ministry of higher education and research (APAFIS#5353-201605111133847). This experiment was performed in accordance with relevant guidelines and regulations.

Comparative collection. The captivity signal in the experimental wild boars at adulthood was contrasted with the variation in morphology observed across 23 wild-caught adult wild boars from the control population in Urciers (Indre, France) and three other populations in France (Table 1). All these specimens were wild caught between 1 and 3 years of age.

To compare the plastic response of captivity with the phenotypic change induced by the last 200 years of artificial selection, we collected data on 17 domestic pigs, including 12 specimens from traditional landraces, which were part of a conservation programme, and five from an intensive breeding programme dedicated to industrial meat production (Table 1). All the domestic specimens are part of the historical collections of the *MHK* (*Museum für Haustierkunde Julius Kühn*, Halle). They were reared in stalls and were aged between 1 and 5 years of age. We also included five free-range Corsican landrace pigs (*U nustrale*) aged between 14 and 18 months. These pigs were bred according to traditional and extensive herding practices in Corsica where pigs roam freely in large areas of maquis shrub land to access natural resources for their diet (Molenat and Casabianca, 1979).

Humerus 3D models. In this study, we focused on the humerus as this bone is better preserved than other limb bones in archaeological deposits, mainly thanks to their early distal epiphyseal fusion and greater distal density⁴⁵. To compare specimens from the different institutions we used images acquired from medical CT scanners. Specimens from France were CT scanned on a Siemens SOMATOM medical CT scanner with an isotropic spatial resolution ranging from 100 to 500 microns. Specimens from Germany were scanned using the medical CT scanner of the Halle/Saale hospital with the same parameters. For each humerus, 3D surfaces were obtained from the DICOM images stacks Automatic segmentation using the Avizo v 8.0 software (Visualization Sciences Group Inc., Bordeaux). This was carried out using the average value between the maximum density of the bone and the minimum density of the air as a threshold, in order to generate two surfaces corresponding to the external (periosteum) and the internal (endosteum) surfaces of the bone.

Bone volume. For each specimen, the bone volume of the shaft was defined as the total volume included within the external surface of the bone diaphysis, including the volume of the medulla. Here we have chosen the shaft bone volume instead of the bone length for two reasons. First this approach is meant to be applied to the archaeological record where complete long bones are rare, thus preventing the acquisition of the maximum length. Secondly, bone volume has been proven relevant to discriminate long bones of wild and farmed mustelids⁴⁶. The bone volume was calculated using the 'Surface Area Volume' function of the Avizo v 8.0 soft-

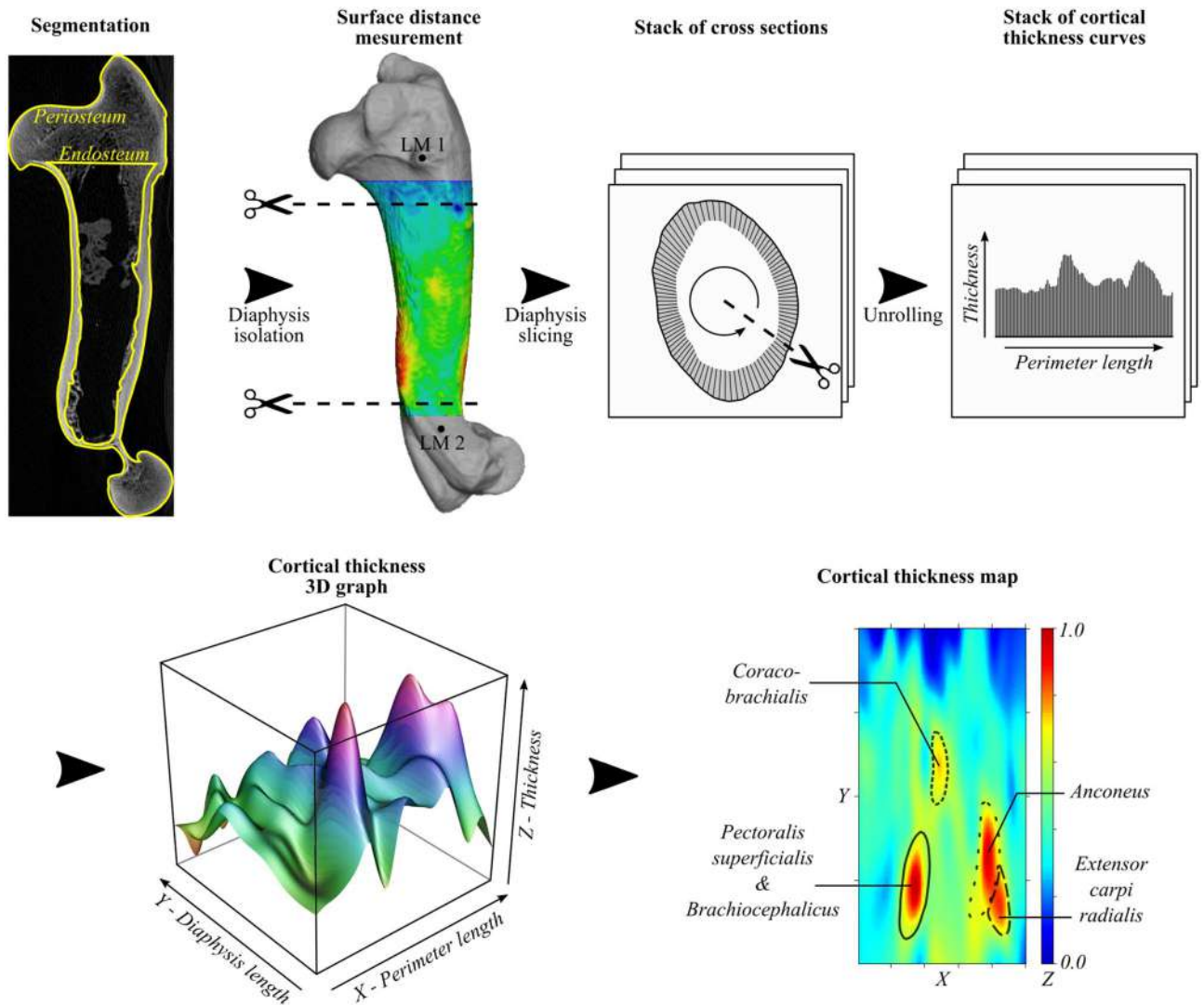


Figure 1. Diagram of the different stages of the Morphometric mapping protocol. The heatmap in the last stage represents the cortical thickness: the minimal distance between the periosteum and endosteum. The greater the thickness the hotter the colour. The circled areas are hand drawn as visual cues and correspond to the attachment sites of muscles according to Barone⁴⁷.

ware. This function calculates the values for the area and volume of the individual patches of a surface (here the diaphysis surface).

Morphometric mapping of the humeral cortical thickness. Cortical thickness is defined here as the distance between each point of the periosteum and the closest point of the endosteum³⁵. The limits of the analysed portion (i.e., the diaphysis) were defined in two steps (Fig. 1). The first step involved the definition of a controlled cylinder using two planes orthogonal to the longitudinal axis of the diaphysis fixed by two anatomical landmarks near the metaphyses: the extremity of the *teres minor* tuberosity (LM1) for the proximal limit, and the distal fork of the medullary cavity (LM2, internal landmark, visible only in cross section) for the distal limit. The cylinder obtained therefore still had the metaphyses at the end parts due to the position of the landmarks. The second step consisted of removing a margin of 10% on the proximal side and 5% on the distal side to obtain a cylinder corresponding only to the diaphysis.

Given the almost cylindrical shape of the shaft, we used the method A described in³⁵ (Fig. 1): the original shape of the shaft periosteum was projected onto a cylinder whose diameter corresponds to the maximum width of the original surface. The cylinder was then cut longitudinally along the cutting line, parallel to the longitudinal axis of the diaphysis which passes through LM1 and is unrolled on a plane. The direction of the unrolling is processed according to the laterality of the bone, ensuring completely comparable maps irrespective of the laterality³⁵. The unrolling method slightly adjust the shape of the diaphysis (that is not a perfect cylinder) to make it fit into a rectangle during the unrolling process. With the standardization, the absolute height and circumference of the diaphysis cannot be directly represented by the height and width of the maps. The maps approximate the unrolled diaphysis shape, but they are not directly equivalent.

Standardization. To statistically compare the topographic variation in cortical thickness, it was necessary to standardize the measurements and to map the cortical thickness of the shaft. This second aspect is critical, since any comparison should ideally be based on homologous landmarks of the original 3D object. Because there were few or no truly homologous landmarks on these cylindrical regions, the solution adopted was to map the original surface by means of a regular mesh of K rows and M columns. Here, $M = 100$ and $K = 200$ in order to maximize the spatial resolution of the grid without unduly increasing the computation time and to maintain a square cell shape. Using this method, the values of cortical thickness at the grid intersections were evaluated by thin plate spline regression of the original data⁴⁸. Before the thin plate spline regression, the thickness values were standardized between 0 and 1. The resulting mapping represents the standardized thickness estimated at the intersection of the same number of grid lines projected on the exterior surface of each original shape. The use of a flat thin plate spline regression, which is part of a statistical approach based on generalized additive modelling (GAM)⁴⁹, facilitates statistical comparisons. After the GAM, we obtained a table of $M = 100$ columns and $K = 200$ rows containing the cortical thickness values ranging between 0 and 1. For each cell the column number was given the value of x (diaphysis length), the row number the value of y (diaphyseal circumference), and the cortical thickness the value of z , we therefore obtained a new table of 20,000 rows and 3 columns (x , y and z) which can be analysed statistically (Fig. 1). Another property of the GAM-based approach was the ability to construct consensus maps using many specimens from a sample by merging all of the individual information into a single dataset and evaluating the effectiveness of consensus using generalized cross-validation (GCV)⁴⁹.

Life history dataset. To test potential covariations between life-history traits and humeral cortical thickness in wild boar we collected body mass, sex, and age for the specimens (See data availability). Captive-raised wild boars have a known age of death but wild-caught wild boars had to be aged according to their dental eruption and occlusal attrition stages^{50,51}.

Muscle force estimates. To measure the covariation between the humerus cortical thickness and the functional properties of the muscles attached to the humerus we dissected the *anconeus* (ANC), which abducts on the ulna and allows an extension of the elbow; the *brachiocephalicus* (BRA), which originates at the neck and the back of the head and allows the protraction of the humerus; the *coracobrachialis* (COR), which originates on the coracoid process of the scapula and allows retraction of the humerus and adduction of the arm; the *extensor carpi radialis* (ECR), which inserts on the metacarpal tuberosity and allows an extension of the carpal joint and flexion the elbow joint; and the *pectoralis superficialis* (PEC), which originates on the sternum and allows the adduction and retraction of the limb⁴⁷, of 22 experimental captive-reared wild boars, one specimen from the control population and five wild boars from French populations (Table 1, See data availability). Muscle data were not available for other specimens. The muscles were weighed to the nearest gram and we measured muscle fascicle length with callipers. Based on the known density of mammalian muscle (1.06 g/cm^3) (Mendez et al., 1960) we calculated the anatomical cross-sectional area (ACSA) as a proxy for muscle force⁵².

Statistical analyses. *Size, shape and life trait covariations in wild-caught and captive wild boars.* The difference in humerus volume and body mass variation among captive-reared and wild-caught wild boars, taking into account their sex, was visualized with a box plot and tested with factorial analysis of variance (ANOVA). The correlation between humerus volume and body mass and between humerus volume and age, taking into account sex, was tested using the Pearson correlation test. The cortical thickness difference among wild-caught and captive-reared wild boars while accounting for age, body mass, and bone volume was explored using a factorial MANCOVA with 1000 permutations.

We tested and visualized the ACSA differences among wild-caught and captive-reared wild boars using ANOVA and a box plot. To visualize and test the covariation between body mass, bone volume, age, and intrinsic muscle force with topographic bone variation of the cortical across the shaft in wild-caught and captive wild boars, we used a two-block partial least squares (2B-PLS) analyses^{53,54} using the standardized morphometric maps as variables.

Comparing plastic size and shape response to captivity with changes induced by artificial selection. Bone volume differences between wild boars and domestic pig groups were tested using an ANOVA with the pairwise comparison tests (Bonferroni correction) and visualized with a box plot. The cortical thickness differences were tested with a Procrustes ANOVA and visualized using a Canonical Variate Analysis (CVA); both were performed on a cortical thickness reduced dataset after a Principal Component Analysis (PCA) performed on the Procrustes coordinates to keep 95% of the variance⁵⁵. To visualize cortical thickness variations along the canonical axes we calculated the theoretical minimum and maximum morphometric map for each axis. On each cartography, attachment sites of the four muscles are displayed as visual cues. We also visualized the consensus map of wild-caught wild boars, captive-reared wild boars, captive-domestic pigs and free-ranging domestic pigs to facilitate the interpretations. Deformation maps between two consensus maps were calculated by subtracting the values of the consensus map. To differentiate the topographic variation of the cortical thickness between wild boars, traditional pig breeds and improved pig breeds, taking into account their genetic history and their sex, we performed a factorial MANOVA with a 1000 permutations procedure.

All the statistics were performed using R (R Core Team. 2017). Factorial MANOVA, Procrustes ANOVA and PLS were performed using the R package "geomorph"⁵⁶. ANOVA, PCA were performed using the package "stats" (R Core Team. 2017), CVA using the package "Morpho"⁵⁷ and visualizations were performed by using "geomorph".

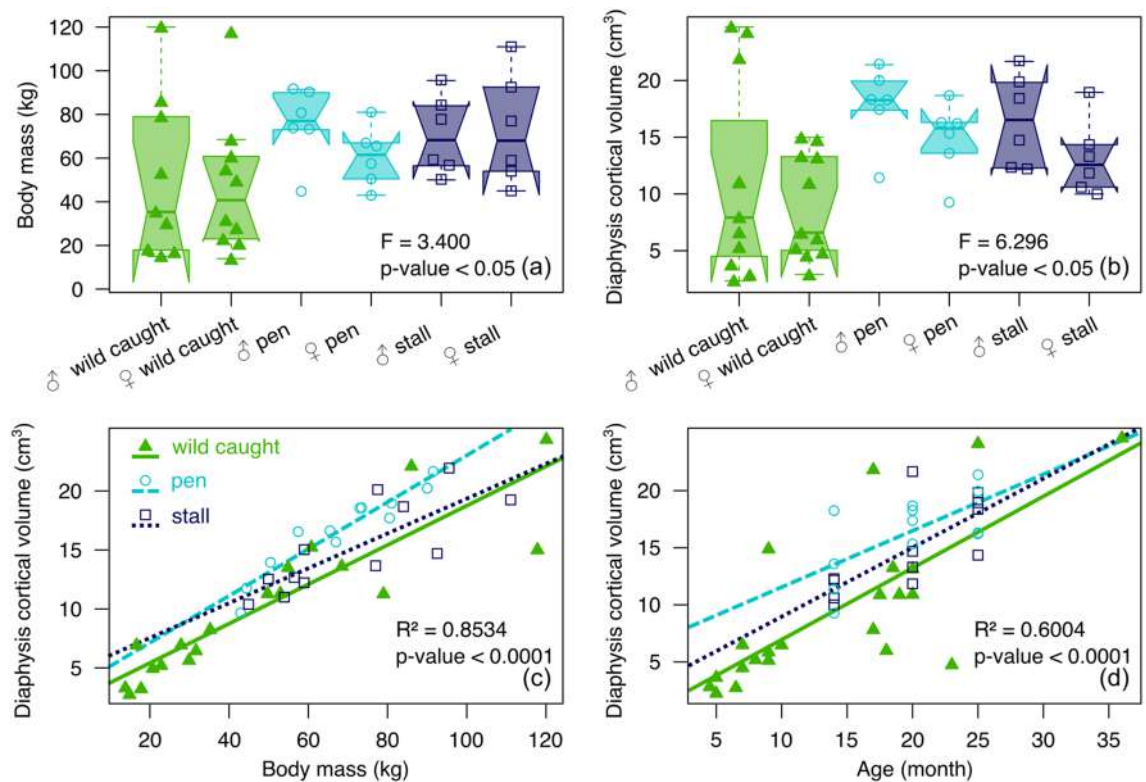


Figure 2. Box plots displaying differences among captive-reared and wild-caught wild boars in (a) body mass and (b) bone volume. The box represents 50 percent of data (interquartile) and the horizontal bar inside is the Median. The “notch” represents 95% confidence interval of the Median. The lower and upper whiskers represent respectively the minimum and maximum values. Regressions between (c) bone volume and body mass, and (d) bone volume and age, among wild-caught and captive-reared wild boars.

Results

Lifetime changes in humerus cortical thickness in wild boars associated with mobility reduction.

Free-ranging wild boars did not differ in body mass compared to pen ($P=0.149$) and stall ($P=0.064$) boars (Fig. 2 a) even when we comparing wild-caught and captive wild boars using the same age range (pen: $P=0.18$; stall: $P=0.71$). We also found that compared to wild caught wild boars, captive specimens have greater bone volume either in pen ($P<0.01$) or in stall ($P<0.01$) (Fig. 2b). In addition, males wild boars had a higher bone volume than females ($P<0.05$) (Fig. 2b). The correlation between bone volume and body mass is strong for free-ranging boars (slope: 0.20, $P<0.0001$, $R^2=0.89$) and those raised in the pen (slope: 0.20, $P<0.0001$, $R^2=0.89$), but weaker for wild boars raised in a stall (slope: 0.15, $P<0.01$, $R^2=0.61$) (Fig. 2c). The correlation between bone volume and age is strong for free-ranging wild boars (slope: 0.63, $P<0.0001$, $R^2=0.54$), but weaker for pen boars (slope: 0.60, $P<0.01$, $R^2=0.48$) and stall boars (slope: 0.49, $P<0.05$, $R^2=0.38$) (Fig. 2d).

Captive boars generally have higher ACSA values (Fig. 3a–e) than free-ranging boars, especially for the extensor *carpi radialis* (Fig. 3d, $F=32.79$, $P<0.0001$), the *coracobrachialis* (Fig. 3c, $F=13.52$, $P<0.001$), and the *pectoralis* (Fig. 3e, $F=4.51$, $P<0.05$). Moreover, males have higher ACSA values than females, especially for the extensor *carpi radialis* (Fig. 3d, $F=17.04$, $P<0.001$), the *coracobrachialis* (Fig. 3c, $F=6.61$, $P<0.05$), and the *pectoralis* (Fig. 3e, $F=5.14$, $P<0.05$).

The covariation between the cortical topography of the humerus in free-ranging wild boars and body mass, age and bone volume (Fig. 4a) is highly significant. We can see on the visualizations that an increase in body mass, age, and bone volume induce the shift of muscular attachment towards the distal part of the bone. The contrast in thickness between the different zones also increases. In addition, the relative thickness of the muscle attachment area of the ECR (bottom right) increases sharply with this increase in body mass, age, and bone volume. The three parameters, mass, age and volume have a comparable impact on the variations in cortical thickness (Fig. 4a), even if the effect of age is slightly less important.

On the other hand, there is no significant covariation between the cortical topography of the captive boars and the ACSA of the limb muscles (Fig. 4b).

Relative impacts of locomotor behaviour and selection in humerus cortical thickness. Bone volume varied significantly among wild boars (wild caught and captive) and pigs (ANOVA: $F=9.115$, $P<0.001$). Pigs have significantly higher bone volume than wild boars but captive boars have an intermediated range of humerus bone volume, greater than wild-caught wild boars but lower than free-ranging and improved pig breeds (Fig. 5).

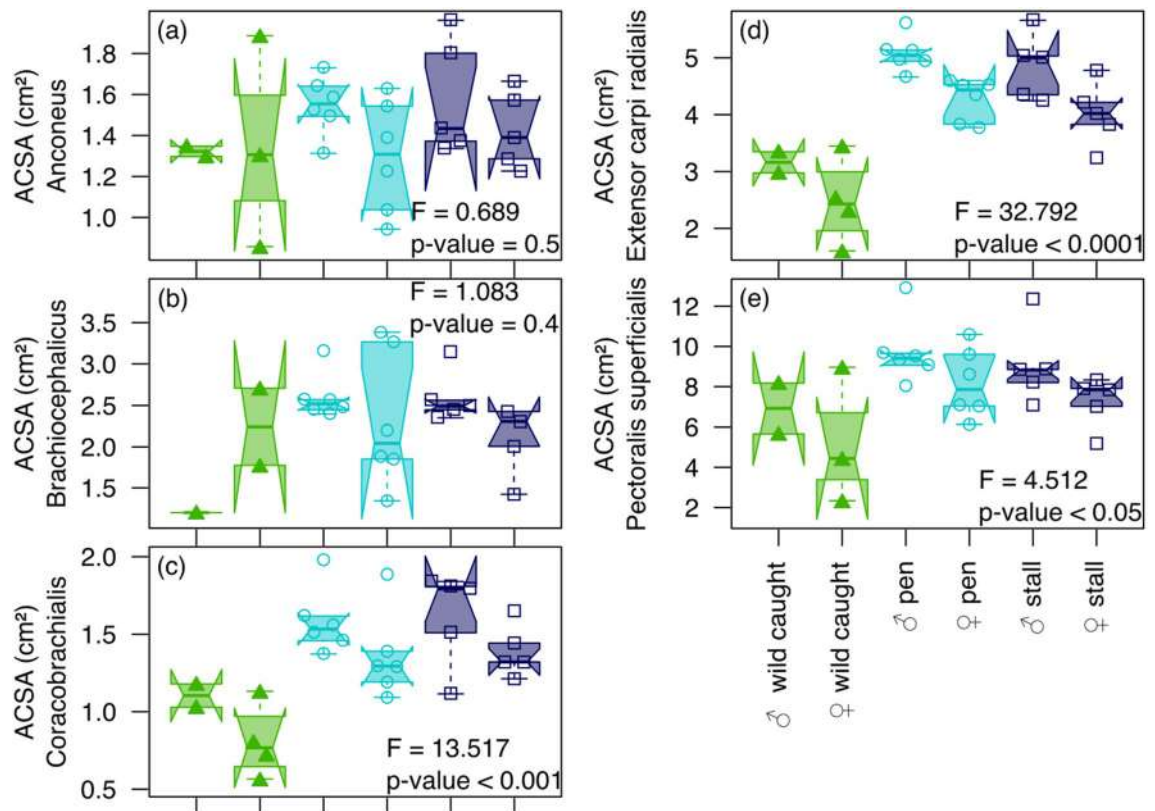


Figure 3. Box plots displaying differences in muscle ACSA among wild-caught and captive-reared wild boars taking into account their sex for (a) the anconeus, (b) the brachiocephalicus, (c) the coracobrachialis, (d) the extensor carpi radialis, and (e) the pectoralis superficialis. The box represents the 50 percent of data (interquartile) and the horizontal bar inside is the Median. The “notch” represents the 95% confidence interval of the Median. The lower and upper whiskers represent respectively the minimum and maximum values.

Cortical thickness topography varies significantly among wild boars (wild caught and captive) and pigs of our dataset (MANOVA: $F = 2.6156$; $P < 0.0001$). The factorial MANOVA shows that significant differences can be observed between wild boar populations and pig breeds (traditional, industrial) ($R^2 = 0.048$, $P < 0.05$) and between sexes ($R^2 = 0.016$, $P = 0.345$). The interaction denotes that sexual dimorphism differs among the wild and domestic populations ($R^2 = 0.011$, $P = 0.512$) but with almost no influence on the total variance. The first axis 1 of the CVA displays the divergence between the captive boars and the pigs respectively in the negative and the positive side of the shape space (Fig. 6a). The difference in cortical thickness topography between captive boars and pigs corresponds to a relative change in the muscle topography between the area of the PEC and BRA entheses on the one hand and the area of ECR entheses on the other. The two areas of muscular insertion are relatively thick in captive boars while in pigs, only the PEC and BRA area show a relative increase in thickness. The CV2 distinguishes free-ranging boars in the negative part from captive boars and pigs in the positive part. Captive boars are also distinguished from their free-ranging counterparts on this axis, but animals raised under the two contexts of captivity (enclosure and stable) have a very similar cortical thickness. For pigs, free-ranging Corsican pigs seem to have a cortical thickness that is intermediate between captive pigs and free-ranging boars.

The comparison of the consensus cortical topography of the four main morphological groups (Fig. 6b) shows that the difference between free-ranging and captive boars mainly corresponds to a sharp relative decrease in cortical thickness at the attachment site of PEC and BRA, as well as a relative increase in cortical thickness at the ECR attachment site. The difference between free-ranging boars and free-ranging pigs corresponds to a relative increase in cortical thickness at the attachment sites of ANC, ECR, PEC and BRA and a decrease in two zones in the proximal part of the shaft. At these muscle attachment sites, the difference between free-ranging boars and captive pigs is moderate, resulting in a slight overall increase in thickness associated with a slight thickness decrease at in the proximal part of the diaphysis.

Discussion

In this paper we tested whether the cortical structure of the humerus could record changes in the locomotor behaviour of a wild ungulate during growth due to captivity. Understanding these effects is key to documenting the early process of animal domestication in archaeology prior to genetic isolation and breeding selection. However, quantifying a functional signal in long bone diaphyses allowing for the reconstruction of past behaviour from long bone morphology has so far been challenging^{37,38,58}. Our project has exploited the results of a unique experiment where locomotor effects can be explored at the scale of wild ungulate populations while controlling

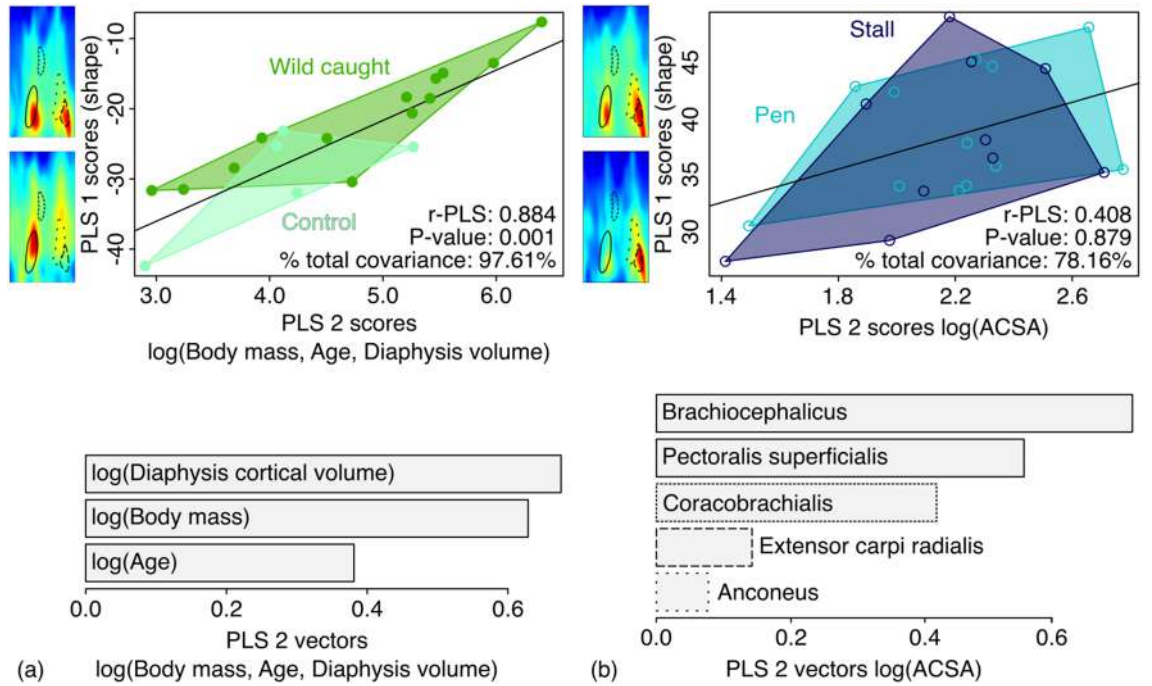


Figure 4. PLS regression between the humerus shaft cortical topography block and (a) life history traits (body mass, age, bone volume) and (b) muscle ACSA blocks. Wild-caught wild boars are visualized in the filled green circles and captive-reared wild boars in the open blue circles. Black lines represent the PLS regression line. Shaft cortical topography deformations are visualized with two extreme cortical thickness maps where muscle attachment sites are encircled as visual cues. Singular vectors are shown using a barplot for life history (a) muscle ACSA and (b) blocks.

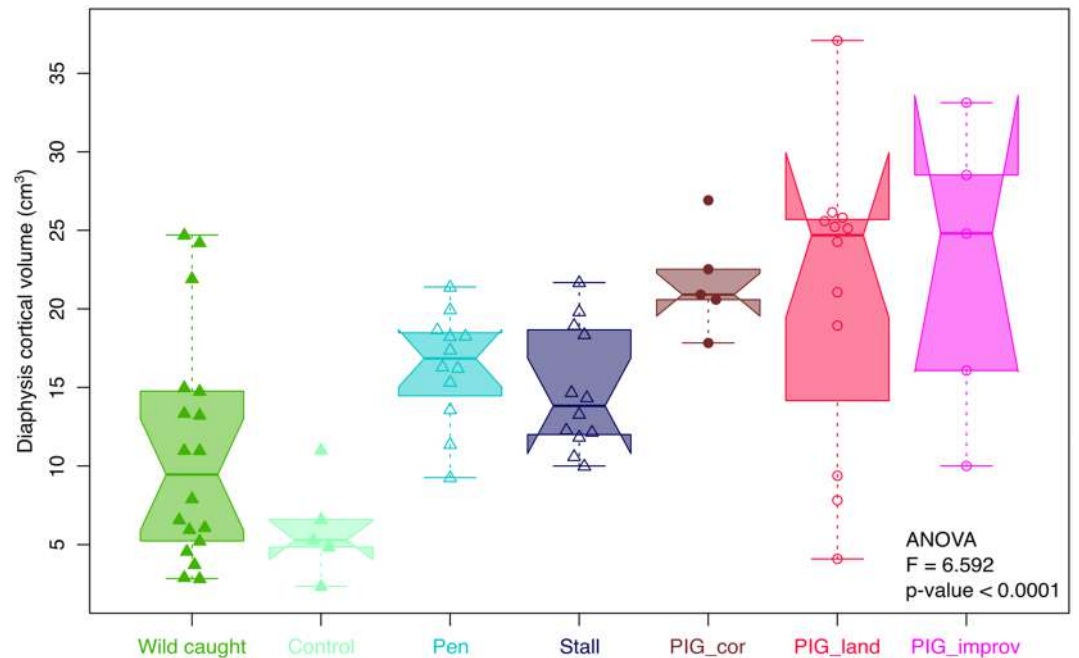


Figure 5. Box plots displaying humerus bone volume variation in wild boars (triangles) and pigs (circles). Free ranging (filled) or captive environments (open) are also indicated. The box represents the 50 percent of data (interquartile) and the horizontal bar inside is the Median. The “notch” represents the 95% confidence interval of the Median. The lower and upper whiskers represent respectively the minimum and maximum values.

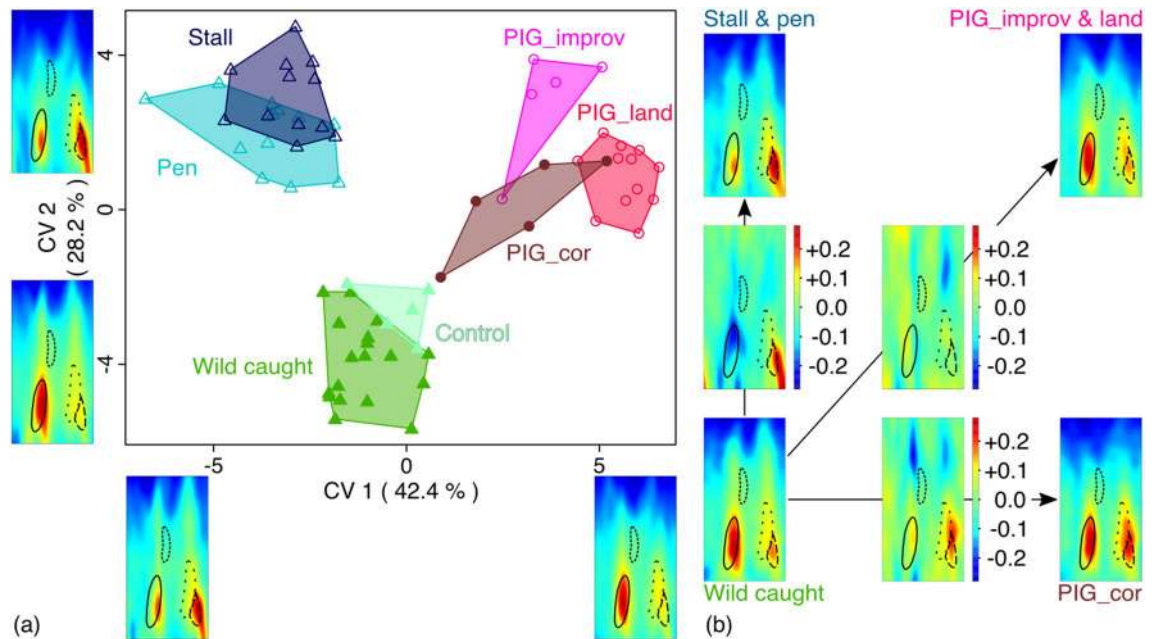


Figure 6. (a) Morphospace based on a CVA representing the pattern of humerus shaft cortical topography divergence among wild boars and pigs living in free-ranging or captive environments. Minimum and maximum shaft cortical topography are shown for each axis. See Fig. 1 for the identification of each muscle attachment in the consensus map. (b) Consensus maps are shown for four groups: wild-caught wild boars (WB_wc & ctrl; GCV = 0.009016), captive-reared wild boars (WB_stall & pen; GCV = 0.006548), captive pigs (DP_improv & land; GCV = 0.011224), and free-ranging pigs (DP_cor; GCV = 0.003657). Each consensus map is compared with the wild-caught wild boars map, and the deformation map is displayed between them. On each map, attachment sites of the four muscles are displayed as visual cues.

for genetic and environmental factors. In association with a comprehensive morphometric mapping of the humerus shaft, this study provides evidence that the functional changes associated with captivity are recorded in the internal structure of limb bones, thus offering a new methodological perspective to understand the early stages of animal domestication.

This experiment confirms that the cortical bone volume of the humeral shaft in free-ranging populations of wild boars is strongly influenced by the interrelated effects of body weight increase, growth and sexual dimorphism^{37,59,60}. This experiment shows that mobility reduction increases the bone volume of the shaft in captive wild boars compared to their wild counterparts when sex differences are taken into account, supporting previous studies showing that captivity increase the body weight and accelerates growth in many mammalian taxa when the diet is nutritiously balanced^{46,61,62}. However, exercise during growth is known to stimulate bone modelling²⁰ and a reduction of cortical thickness has been observed in the jaw bones of captive weeper capuchin⁶³. Therefore we expected that captive wild boars, with less frequent activities and a lower motion intensity, would have displayed less cortical volume than free-ranging individuals. However, we observed that mobility reduction increased the weight and age-related bone volume. This suggests that developmental disruptions through the body mass increase in captivity could have changed the biomechanical loads during puberty. Despite a reduction of mobility, body mass increase in captivity could have driven bone growth, providing some resolution to this paradox. This bone robusticity associated with a body mass increase has a correlate in humans. Indeed, obesity has been shown to increase the bone density in men and women through the stimulation of bone formation induced by the mechanical loading conferred by weight^{64,65}.

This experiment provides further evidence that growth in captivity impacts the muscular system of wild boars, with captive specimens displaying greater muscle cross-sectional areas. Although presumably less physically active than their wild counterparts, captive wild boars did not display a localized increased of the scapular bracing muscular apparatus shown in the enthesal change of captive reindeer⁶⁶. Here, we found an overall increase in the cross-sectional area of the humerus muscles which was previously also demonstrated for muscles attached to the calcaneum⁶⁷ and described for other mammals bred in captivity⁶¹. Until further ethological and physiological studies in captivity have been performed, we can only hypothesize that this increase in the muscular system of captive specimens is the cumulative and interrelated consequences of (1) increased body mass, (2) protein rich diet, and (3) stereotypical behaviour increasing the frequency of muscular use. All these factors are likely to be responsible for reinforced muscle attachments. Our experimental specimens were fed nutritiously balanced pellets (15% protein) dedicated to pig farming to ensure steady growth and bone formation⁵⁹, which may have provided the opportunity for muscle growth beyond what is possible under natural conditions.

Our experimental study showed that the topographic variation in cortical thickness of the humeral shaft is multifactorial and strongly influenced by age and body mass. Our results further show that body mass and its associated bone volume increase are key to predicting cortical thickness variation, in contrast to previous studies

on primates^{37,59,68–70}; although differences in the functional use of the forelimb between wild boars and primates could explain this inconsistency. We did not detect significant covariation between the muscular cross sectional-areas and the relative topography of the cortical thickness of the humerus in wild boars. These results are congruent with the hypothesis that in vivo muscular load does not affect entheses unless they are pathological⁴². We strongly suspect, however, that covariations were simply not detected, as the impact of the muscle-cross sectional area on the cortical thickness topography is likely reflected in absolute rather than relative thickness differences. As thickness values were normalized on a 0–1 scale before the GAM standardization, this only allowed the detection of relative thickness differences along the shaft.

We found that mobility reduction significantly impacted cortical thickness topography, supporting the hypothesis that captivity can be inferred from bone structure, a signal already acknowledged in studies on primates³⁷ and reindeers⁶⁶. Captive and free-ranging wild boars from the same population and of the same age showed distinct patterns of cortical thickness at the distal part of diaphysis. Compared to the free-ranging wild boars, captive individuals showed a distinct relative reduction of the cortical thickness located at the *brachiocephalicus* and *pectoralis superficialis* entheses and a relative increase of the *extensor carpi radialis*, suggesting decreased use of the extensors of the forelimb in captive specimens. Changes in cumulative use instead of load can probably better explain how muscular activity might impact the diaphyseal cortical thickness.

Selection due to domestication has also left a clear signal on the volume and topography of the cortical bone of the humerus. The selective breeding of the last 200 years drastically increased the humerus cortical volume, with current pig breeds showing an almost two-fold increase of the cortical bone volume compared to extant wild boars from France. The selective breeding of pigs has also impacted the humerus cortical thickness topography along a very different functional trajectory than what is observed due to mobility reduction. Compared to free-ranging and captive wild boars, pig breeds display an increase of the *anconeus*, an extensor of the forelimb. This phenotypic divergence could be related to breeding selection⁷¹ inducing multifactorial and interrelated influences. Selection on early growth probably had a drastic impact on the developmental programming of the diaphysis bone morphology. Moreover, selection for large muscles and quick gain of body weight potentially impacted the gait of the animal and may have affected cortical bone volume and its topography. This divergent trajectory in cortical topography between wild boars which cannot fully express their locomotor behaviour and pigs from traditional or industrial breeds selected for meat production, suggests that the anthropogenic control of a movement in a wild ungulate and the selective breeding for body growth induce different responses in the cortical morphology. Therefore, both anthropogenic influences over ontogeny of an ungulate should be possible to discriminate in the archaeological record.

Conclusion

We demonstrated that despite the multifactorial influences of ontogeny, sex, and body mass on the humerus cortical shaft volume and topography, changes in locomotor behaviour induced by captivity produced changes in the cortical topography beyond what is observed in the natural habitat and along a different phenotypic trajectory than changes induced by recent selective breeding. These results provide an experimental proof of concept that changes in locomotor behaviour and selective breeding might be inferred from long bones in the archaeological record. However, this proof of concept now needs to be confronted to the archaeological records of *Sus scrofa* since the early Holocene to assess whether the trends in the cortical thickness observed under experimental constraints and with modern populations could prove relevant to explore the process of domestication and the role of anthropogenic forces in the evolutionary changes of wild species⁷². This survey should include contexts of hunter-gatherers societies before the Neolithisation and performed across the contexts of emergence of animal domestication until at least periods when the domestication syndrome is clearly observable in the archaeological record.

Further studies are now required to explore the impact of mobility reduction in the trabecular architecture of the humerus and the developmental changes behind these plastic responses. Large scale muscular measurements from wild populations are also required to build biomechanical models⁷³ needed to fully infer the functional changes induced by captivity on limb bone morphology.

Data availability

Code, data and metadata to perform statistical analyses are archived in the Dryad Digital Repository (<https://datadryad.org/>) and are currently accessible at the following location: https://datadryad.org/stash/share/q04zdMbnHjwY0EciL_DqDwKtFvafkAOTvFvbLu5SG7g.

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Author contributions

T.C. designed the research with L.P. and A.H.; Y.L., K.O., B.B. and T.C. conducted the experimental fieldwork; T.C. collected the CT data with F.Le.; H.H. collected the morphometric data. A.H. and J.-C.T. collected the muscular data; F.La., I.B., C.C. and T.C. created the database of the project; H.H. carried out the analyses in collaboration with CZ and interpreted the data with T.C., A.H. and CZ; T.C. and H.H. led the manuscript with scientific and editorial input from A.H., C.Z., M.C. and R.S. All authors gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to H.H. or T.C.

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Erratum

The bibliographic reference of histological differences between wild and domestic specimens is cited in this paper without any criticism, yet there is literature that questions the methodology and interpretations of Drew et al. 1971. Indeed, a few months after its publication, a first paper (McConnell et al., 1971) expressed reviews, in particular on the interpretation of X-ray diffraction results, to which Drew et al. responded. Then, from 1975 onwards, much more important criticisms were made (Watson, 1975 ; Gilbert, 1989) :

- The irrelevant use of the "wild" and "domestic" categories, while the concept of *continuum* would have been more appropriate.
- The use of archaeological comparative material, whose status is uncertain by definition.
- A lack of discussion about other possible causes of the observed differences, including the possibility of alterations between death and burial.
- Some interpretation problems, especially in terms of optical observations. This suggests that these differences are more likely due to the quality of collagen preservation.

Moreover, at least two independent experimental protocols with archaeological and current material (Watson, 1975 ; Zeder, 1978) have failed to repeat the results obtained by Drew et al.

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CHAPITRE

— 4 —

PIG DOMESTICATION IN WESTERN
EUROPE : ASSESSING THE IMPACT OF
ANTHROPOGENIC CONTROL OVER
EARLY NEOLITHIC *SUS SCROFA*
POPULATIONS

4.1 Introduction

Archaeological studies have shown that pigs were independently domesticated in two separate places and periods : Firstly in the Near East around 8500 BCE, after managing wild boar populations for more than two millennia (Conolly et al., 2011 ; Ervynck et al., 2001 ; Vigne et al., 2009), and secondly in China around 6,500 BCE, but way much faster (Cucchi et al., 2016, 2011 ; Groenen, 2016 ; Jing and Flad, 2002). From the Near East, pigs were transported by Neolithic peoples associated with Pre-Pottery Neolithic B material culture towards Europe along two dispersal routes. The first is a maritime route that followed the coast of the Mediterranean Sea by cabotage to reach the Italian peninsula around 6000 BCE and the France coast around 5900 BCE (Manen et al., 2018). The second is a continental route that used the course of the Danube to penetrate Europe starting from the lower Danube towards 6000 BCE, through Eastern Europe during the 6th millennium BCE to reach the Parisian Basin by 5200 BCE (Guilaine, 2003 ; Ilett, 2010). The pigs that followed these Neolithic dispersals are all of Near Eastern origin (Larson et al., 2007), but mitochondrial genetic studies on current populations have shown paradoxical results : The mitochondrial genetic diversity of wild boars in Western Eurasia is well known and geographically structured, with two near-eastern clades and a European clade (Larson et al., 2007, 2005) but all current domestic pigs have a European mitochondrial signature (Larson et al., 2005 ; Ottoni et al., 2013), suggesting a local domestication in Europe which would contradict archaeological studies (Rowley-Conwy, 2003). The emergence of this paradox can be explained by two main factors. Firstly, interbreeding : the wild boars are still present throughout Eurasia, causing a genetic and morphological *continuum* between wild boars and domestic pigs, passing through all possible intermediaries such as wild pigs, hybrids etc ... Secondly, commensalism : in the case of the wild boar, the domestication process started with a long commensal history between wild boars and men (Zeder, 2012), leading to very gradual modifications, and an intentionality difficult to detect (Vigne, 2015).

Recently, part of this paradox has been solved thanks to large studies on the mitochondrial DNA of remains from Mesolithic and early Neolithic suines along the Danubian road (Caliebe et al., 2017 ; Larson et al., 2007). The results have shown that the first pigs found in Europe in the 6th millennium BCE bear the near-eastern mitochondrial signature, proving a diffusion of near-eastern pigs into Europe, in agreement with archaeological studies. This signature is found in the *Sus scrofa* remains up to the 4th millennium BCE, before being completely replaced by the European signature that is still observed in current pigs (Larson et al., 2007), which explains the current mitochondrial signatures, but raises the question of the origin of this change in mitochondrial signature. Two mains explanation have been proposed to explain this genetic turnover. It could be the result of either a local secondary domestication of European wild boars, or an hybridization of near-eastern pigs with females European wild boars (Frantz et al., 2015). Regarding the Mediterranean road, the archaeological data on pigs are less clear since the Neolithic populations which took this dispersal route were mainly cattle and sheep breeders (Rowley-Conwy et al., 2013). While there is strong evidence that primitive domestic pigs have been brought from the Near East up to Italy, Corsica and Sardinia, it is less clear wether they reached Liguria, Provence or Languedoc. Therefore, until further bioarchaeological studies, the status of the *Sus scrofa* remains in southern France remains unclear until the end of the Cardial (Rowley-Conwy et al., 2013).

Until recently, morphological evidence for the domestic or wild status of suines remains have relied on change in bone size (Rowley-Conwy et al., 2012). Following the domestication syndrome first described by Darwin (Darwin, 1868) and later experimentally proven to be the consequence of behavioral selection on tameness (Belyaev et al., 1985; Trut et al., 2009; Trut, 1999), leading to developmental perturbations (Wilkins et al., 2014), the reduction of size has been considered as a marker of an animal biologically domesticated. These domestication syndromes, considered to be shared among a wide range of phylogenetically unrelated species (Wilkins et al., 2014), are recently challenged (Lord et al., 2020) and remain questionable to explore early process of animal domestication in archaeology (Harbers et al., 2020b, 2020a; Mainland et al., 2007; Neaux et al., 2020). Geometric morphometric, allowing to measure change in bone shape unrelated to size (Cucchi et al., 2015), have shown that dental variation could detect phylogenetic signal for several mammalian taxa (Caumul and Polly, 2005; Cucchi et al., 2020, 2017; Hulme-Beaman et al., 2019) and early process of pig domestication in Neolithic China (Cucchi et al., 2017, 2011). However, this early process of pig domestication could be detected in China since early pigs management was probably less extensive in China than in Europe, preventing the gene flow between wild and domestic populations and therefore allowing the phenotypic expression of anthropogenic genetic isolation and selection (Cucchi et al., 2016; Price and Hongo, 2019). Therefore, despite their biosystematic resolution, these phenotypic dental markers could prove unable to track the early domestication of *Sus scrofa* during the Neolithisation of Europe. More recently, the impact of change in activity pattern due to human control on bone morphology has been experimented on wild boars (DOMEXP project) where morphometric studies showed that a plastic response to captivity could be detected in the variation of calcaneus form (Harbers et al., 2020a) as well as in the topography of the humerus cortical thickness (Harbers et al., 2020b). Such proof of concept that biomechanical stress induced by human control of wild animals movements leave an imprint in the bone morphology of a wild *suidae* provide new phenotypic markers to explore process of cultural control of animals (Hecker, 1982) in archaeology before any process of reproductive selection and isolation.

In this study we would like to associate the ecomorphological signals carried by the calcaneum form and the topography of the humerus cortical thickness to assess environmental stress of incipient domestication in the morphological variation of early Neolithic *Sus scrofa* from Northern and Southern France. To do so, we rely on a comparative material that attempt to encompass a wide range of genetic, selective and behavioural background in *Sus scrofa*, to cover as much phenotypic norm of reaction as possible. This includes a range of domestic populations from industrial breeds to extensive traditional breeds and a range of wild populations including wild caught wild boars and captive reared wild boars. This comparative material will also include Mesolithic wild boars from the North and South of France as reference for the wild phenotypic variation before the neolithization and the anthropization of the environments. The objective of this study is to assess how much Neolithic populations of *Sus scrofa* were under anthropogenic control in order to provide new insight into the current understanding of early pig domestication in Western Europe.

4.2 Material and methods

4.2.1 Comparative collection

In order to predict the status of archaeozoological remains, it is necessary to assemble a comparative collection made of specimens from diverse genetic origin and diverse degree of captivity, representing the entire *continuum* of the domestication process. Indeed, the predictions' accuracy mainly depends on the completeness of the comparative collection : We must be able to distinguish free wild boars and captive domestic pigs, but also to identify the intermediaries between the two extremes, which implies having a varied genetic and environmental panel, with for example hybrids or captive boars.

The extremes of the *continuum* were made of data from 28 archaeozoological remains of hunted Mesolithic boars (See the contexts of archaeological sites in section 4.2.2.), 40 current wild-caught wild boars from a control population in Urcier (Indre, France), and other populations in France and Switzerland, as well as 27 captive domestic pigs from the historical collections of the Museum für Haustierkunde Julius Kühn (MHK) in Halle (Germany), including specimens from traditional landraces and from recent improved breeds (SI 4.1).

To constitute the intermediaries of the domestication process *continuum*, we collected data from five captive hybrids, five free-range Corsican landrace pigs (U nustrale breed), which were bred according to the traditional extensive herding practice in Corsica where pigs can roam freely in large areas of maquis shrubland to access natural resources for their diet (Molenat and Casabianca, 1979), and 26 experimental captive wild boars, including 2 from the MHK and 24 two years captive boars from an experiment undertaken in the zoological reserve of La Haute Touche in Obterre (France) from wild boars in the control population in Urcier (France) (Harbers et al., 2020b, 2020a).

4.2.2 Archaeozoological material and context

Thirteen archaeological sites dated from the Mesolithic to the Neolithic were selected in three regions of Europe, corresponding to three archaeological contexts (Figure 4.1 page 79) : two sites in Cyprus island, which correspond to the beginning of the Neolithic expansion and a specific island context, four sites in the North of France, which correspond to the end of the Neolithic expansion in continental Europe, and six sites in the south of France, which correspond to the end of the Neolithic expansion in Mediterranean Europe. For each site, we collected all the analyzable humerus and calcaneus identified as swine. Calcaneus are considered analyzable if they are unfragmented and if the epiphysis is present. Since the calcaneus epiphysis begins to fuse at about 2 years of age in wild boar (Bridault et al., 2000), the vast majority of archaeological calcaneus comes from adult individuals. Humerus are considered analyzable when the distal half of the diaphysis and the distal metaphysis are present, in one piece and without holes.

All remains from sites or layers dated to the Mesolithic were included in the comparative collection, while all remains from sites or layers dated to the Neolithic were subjected to predictive tests.

In Chalain, the remains have been identified by their size and morphology as pigs or wild boars by archaeozoologists (Arbogast, 1997; Pétrequin, 1997). In Klimonas and Rouca-

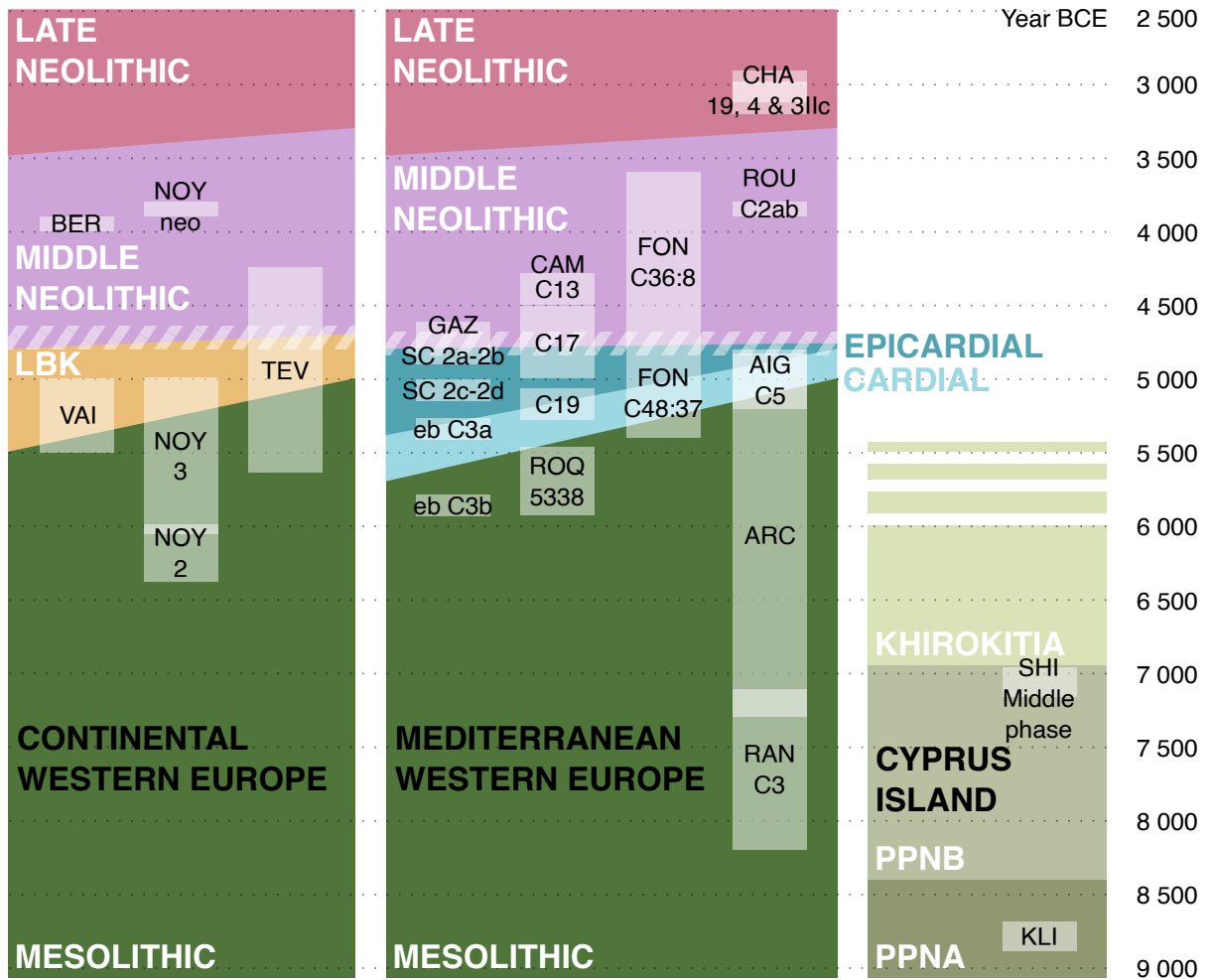
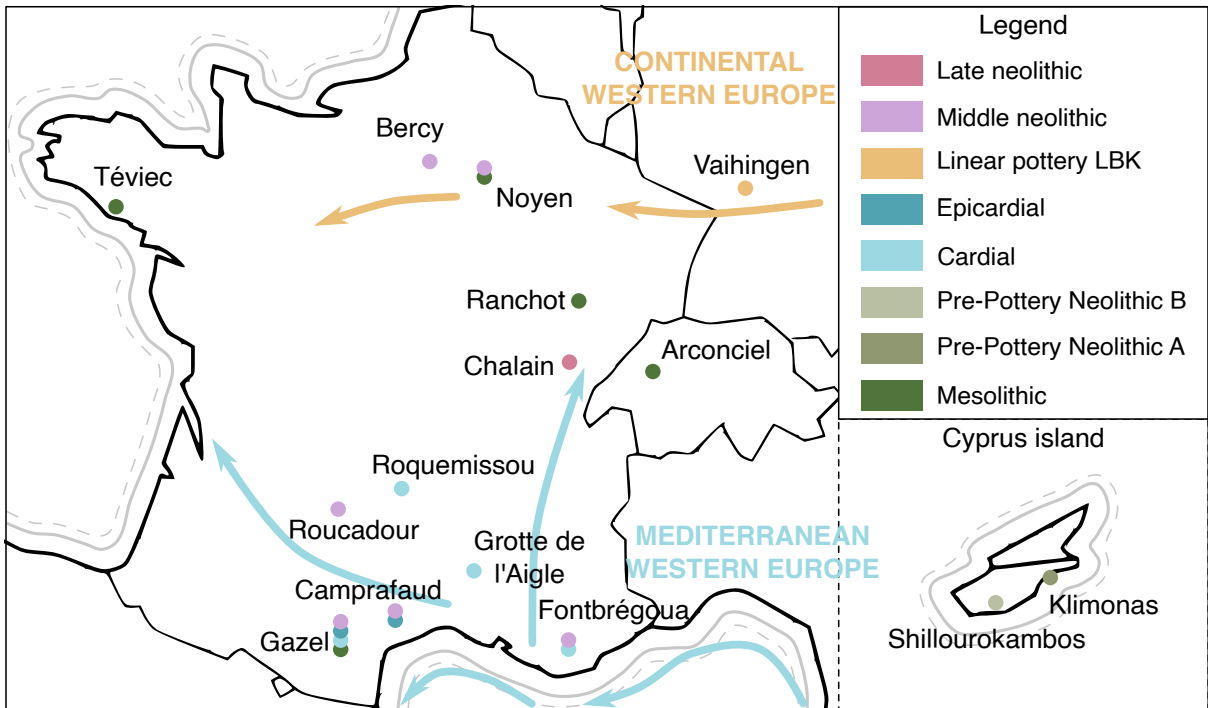


FIGURE 4.1 – Geographical, chronological and archaeological context of the selected sites.

The map show the geographical localisation of the 15 sites and their archeological context. The timeline show for each site the different layers selected in this study and their period of occupation. The sites are separated into two chronological period : Mesolithic and Neolithic, and then into three geographic groups. Cyprus island : Klimonas (KLI, Neo) and Shillourokambos (SHI, Neo). Western Europe under Mediterranean influence : Ranchot (RAN, Meso), Arconciel (ARC, Meso), Gazel (GAZ, Meso and Neo), Chalain (CHA, Neo), Fontbrégoua (FON, Neo), Roquemissou (ROQ, Neo), Grotte de l'Aigle (AIG, Neo), Camprafaud (CAM, Neo) and Roucadour (ROU, Neo). Continental Western Europe : Tévéc (TEV, Meso), Noyen (NOY, Meso and Neo), Vaihingen (VAI, Neo) and Bercy (BER, Neo).

dour, the archaeological context is explicit enough for archaeologists to identify all the remains as being wild boars (Lesur et al., 2001 ; Vigne et al., 2012). These identifications have been designated in this study as "assumptions based on archaeozoological analyses" and allow comparison with our predictions.

Mesolithic comparative collection

The oldest Mesolithic selected site is Les Cabônes rockshelter at Ranchot (RAN) on the western margin of the Jura range. Mesolithic occupations were identified in layer 3 (RAN C3), dated by several AMS radiocarbon dates ranging from around 8,200 – 7,100 cal BCE 2 sigma (Cupillard et al., 2015). The abundant mammalian archaeofauna (ca. > 4500 NISP) includes the three main species of wild ungulates (red deer, wild boar, roe deer) classically recorded during this period (Bridault, 1994), red deer and wild boar being the first two species hunted (Leduc et al., 2015). At Ranchot, as at other Mesolithic sites, the hunters mainly targeted sows with their piglets, and occasionally solitary males that would provide, in addition to meat and fat, the ivory from tusks (Leduc et al., 2015, 2013). Layer 3 provided four analyzable calcaneus and one analysable humerus which are integrated in our Mesolithic comparative material.

The second oldest Mesolithic selected site is the Arconciel rockshelter (ARC), located at the foot of the Pre-Alps of Fribourg was occupied by Mesolithic hunter-gatherers between 7,300 and 4,800 BCE 2 sigma (Guidez, 2018 ; Mauvilly, 2008). This site provided 3 calcaneus which are integrated in our Mesolithic wild boar comparative material.

The third Mesolithic selected site is Noyen (NOY), which provided the largest collection of archaeological suines in France dating from the Neolithic transition (Marinval-Vigne et al., 1993, 1989 ; Mordant et al., 2013 ; Tresset, 1988). The site is subdivided into three main layers : layer 2, layer 3, and a Neolithic layer (see section 2.3.3).

Middle Mesolithic layer Noyen 2 (NOY 2) is dated from 6,380 – 5,990 BCE and was occupied by people which practiced an intensive deer and wild boar hunting. This layer provided four calcaneus which are integrated in our Mesolithic comparative material.

Late Mesolithic layer Noyen 3 (NOY 3) is dated from 6,060 – 4,995 BCE and was occupied by different people from Noyen 2, and which practiced a very specialized wild boar hunting. This layer provided two calcaneus and 10 humerus which are integrated in our Mesolithic comparative material (Tresset and Vigne, 2007).

The next Mesolithic selected site is Téviec (TEV). This is a necropolis station dating from the final Mesolithic around 5,640 – 4,250 cal. BCE according to AMS dating on human bones (Schulting and Richards, 2001). This necropolis provided one calcaneus which is integrated in our Mesolithic comparative material.

The latest Mesolithic material is coming from Gazel (GAZ), a cave occupied from the Mesolithic to the Neolithic. This site is divided into 3 sectors : Entrance, Scree (“Éboulis” abbreviated “eb”) and Central chamber (“Salle centrale” abbreviated “SC”) (Manen et al., 2018; Manen and Sabatier, 2003). We focused in this study on 4 chrono-cultural phases : one Mesolithic and three Neolithic phases (see section 2.3.3).

The Mesolithic layer is the 3b in the scree (GAZ eb C3b) which is dated to the late Mesolithic around 5,900 – 5,700 BCE and provided one calcaneus integrated in our Mesolithic comparative material.

Cyprus island

In Cyprus, wild boars are not endemic : they were introduced by populations of Natoufian /Khiamian hunter-gatherers around 10,550 BCE (Vigne et al., 2012). Animals were necessarily transported from the mainland on boats, and this transport indicates a certain control over wild populations very early on the continent. Indeed, the first indications of genuinely domesticated suines appear at the middle PPNB (Ervynck et al., 2001; Peters et al., 1999), nevertheless certain indices allow us to suppose first experiences of domestication from the PPNA (Rosenberg and Redding, 1998; Vigne et al., 2012).

The earliest selected site in Cyprus island is Klimonas (KLI), where we found two analyzables calcaneus from layers dated from around 8,800 BCE. This site was occupied by populations from the early neolithic (PPNA) who hunt the wild boars introduced on the island.

The second site is Shillourokambos (SHI), where we found six calcaneus from the middle phase dated around 7,100 BCE. This site was occupied by populations from the middle neolithic (PPNB) that owned domestic pigs, but the current state of research does not make it possible to define whether they are Cypriot boars domesticated on the island or a new introduction of domestic pigs from the mainland.

Continental Western Europe

The first Neolithic populations from the LBK (Linearbandkeramik) culture arrived in Western Europe around 5,500 BCE, bringing with them domestic pigs with near-eastern ancestry (Frantz et al., 2019; Larson et al., 2007).

The earliest selected Neolithic site in continental Europe is Vaihingen an der Enz (VAI), dated from 5,500 – 5,000 cal. BCE. This is a well-preserved, extensively excavated LBK site and it constitutes one of the largest LBK faunal assemblages (>39,000 specimens, including 400 fish remains) (Schäfer, 2011). The proportion of wild animals on this site is around 15%, while the proportion of domestic pig reaches up to 37% in the jüngere LBK. Pigs raised on the site are usually killed before one year.

The next selected site in continental Europe is Bercy (BER), dated from 4,000 – 3,900 BCE and occupied by a middle Neolithic agropastoralists from the Chasséen culture.

However, the practice of wild boar hunting continues and the occurrence of wild and domestic taxa is suggested by metric measurements on archaeological remains (Tresset, unpublished report). This site provided one humerus and one calcaneus.

The last selected material in continental Europe comes from the neolithic layer of Noyen sur Seine (NOY neo), dated from 3,900 – 3,800 BCE. It was occupied by a middle Neolithic society which practiced mainly beef and pig breeding, but hunting was still a non negligible activity. This layer provided one calcaneus and one humerus (Tresset, 1988).

Areas under Mediterranean influence

The Neolithic Cardial populations arrived in Western Europe around 5,600 BCE, bringing with them some domestic pigs, even if they practice relatively few breeding : hunting is actually much more important to them, specifically wild boar hunting (Manen et al., 2018; Rowley-Conwy et al., 2013; Tresset and Vigne, 2007; Vigne, 2008).

The earliest selected site in the Mediterranean area is Roquémisou (ROQ), where we focused on the layer 5338 (ROQ 5338) dated around 5,700 cal BCE, which correspond to just before the limit between Mesolithic and Neolithic. This layer is considered Mesolithic, but it has not been dated directly and is located just below Neolithic layers, so its situation remains hypothetical (Perrin, 2019). This layer provided one calcaneus.

Fontbrégoua (FON) is a settlement occupied from the Upper Palaeolithic to the end of the Neolithic, but most of the material come from the Neolithic layers between 5,400 and 3,600 cal BCE (Helmer, 1979). We focused on two sets of Neolithic layers.

Layers 48 to 37 (FON C48 :37) correspond to the Cardial layers. Both wild and domestic animals contributed to the diet during the Early Neolithic period (Helmer, 1979; Rowley-Conwy et al., 2013). These layers provided one calcaneus and one humerus.

Layers 36 to 8 (FON C36 :8) correspond to the Chasséen layers. The frequency of hunting decreased by half during this period, probably due to the more intensive farming of domestic livestock (Helmer, 1979). These layers provided one analyzable calcaneus.

Camprafaud (CAM) is one of the most complete stratigraphic sequences in the Hérault, from the Early Neolithic to the Bell Beaker culture, from 5,300 to 2,000 BCE. We focused in this study on three Neolithic horizons. These layers contained a large faunal accumulation, indicating hunting activities and the presence of domestic animals (Manen et al., 2018; Manen and Sabatier, 2003).

Early Epicardial layer 19 (CAM C19), dated around 5,280 – 5,070 cal BCE, which provided one calcaneus.

Late Epicardial layer 17 (CAM C17), dated from the first half of the 5th millenium BCE, which provided one humerus.

Chasséen layer 13 (CAM C13), dated from around 4,500 – 4,200 BCE, provided one calcaneus. (Manen, pers. com.)

The cave of Aigle (AIG) presents a stratigraphy from the Early Neolithic to the Bronze Age (Manen et al., 2018; Manen and Sabatier, 2003). The faunal assemblage consists mainly of *Sus* remains but their status, wild or domestic, remains unclear. We focused on the Cardial layer 5 (AIG C5), dated around 5110 – 4950 cal BCE which provided 3 calcaneus.

The next Neolithic material comes from three Neolithic phases of Gazel (GAZ) : Layer 3a in the scree (GAZ eb C3a), which provided one calcaneus, was initially attributed to the Mesolithic occupation of the site. Several sheep remains from this level have recently been dated, showing that material from the early and middle Neolithic occupations has been mixed with Mesolithic material (Manen et al., 2018). The *Sus* calcaneus was thus directly dated to secure the chrono-cultural attribution (unpublished direct 14C datation) : it corresponds to the beginning of the Cardial-Epicardial occupation, around 5,400 – 5,200 BCE (phase I of the Neolithic occupation). Layerc 2c and 2d in the central chamber (GAZ SC 2c-2d) belong to the Late Epicardial (phase III of the Neolithic occupation), dated around 5,200 – 5,000 BCE (Tornero et al., 2020), and provided one humerus and one calcaneus. Layers 2a and 2b in the central chamber correspond to the transition between early and middle Neolithic (GAZ SC 2a-2b) and date around 4,900 – 4,600 BCE (phase IV). They provided 5 humerus. During this phase pigs double in importance on the site (Rowley-Conwy et al., 2013).

Roucadour (ROU) is a specific Chasséen site, where 90% of the remains correspond to hunted wild animals. There are only three domestic remains, identified as cattle and goat (Lesur et al., 2001). It is interesting to note that the reference material which was used to determine the wild or domestic status of the remains in Roucadour comes from Chalain. The quality of identification in Roucadour therefore depends on the quality of identification in Chalain. We focused on layers C2a and C2b (ROU C2ab), dated around 3,900 – 3,800 BCE which provided three calcaneus.

The latest Neolithic site in the area under Mediterranean influence is Chalain (CHA), which is a complex of several partially contemporary villages around the Chalain lake occupied by some groups of farmers under the influence of Mediterranean neolithisation arrived in the Jura around 3,500 BCE (Pétrequin, 1997). We focused on three villages : 4, 19 and 3IIc. Chalain 4 (CHA 4) is occupied at least between 3,100 and 3,000 BCE and provided nine calcaneus and three humerus. Chalain 19 (CHA 19) is occupied around 3,200 – 2,910 BCE and provided 16 calcaneus and 5 humerus. Chalain 3IIc (CHA 3IIc) is occupied around 2,990 – 3,005 BCE and provided one humerus. On Chalain, swine remains seem to form two clusters by size of the bones. Small bones have been identified as domestic pig, while large bones have been identified as wild boar (Arbogast, 1997; Pétrequin, 1997).

4.2.3 Humerus cortical thickness topology and cross section area

For the cortical thickness topology protocol, we focused on the humerus since they are better preserved than other limb bones in archaeological deposits, mainly thanks to its earlier distal epiphyseal fusion and greater distal density (Lyman and Lyman, 1994).

Cortical thickness is defined here as the distance between each point of the periosteum and the closest point of the endosteum (Bondioli et al., 2010). Humerus 3D models were segmented using Avizo v 8.0 software (Visualization Sciences Group Inc., Bordeaux) in order to generate the two surfaces corresponding to the external (periosteum) and the internal (endosteum) surfaces of the bone. For each humerus, the portion corresponding to the diaphysis was defined and cut out using two homologous morphological landmarks : the extremity of the teres minor tuberosity (LM1) and the distal fork of the medullary

cavity (LM2). Then we remove from this portion 5% on the distal extremity and 10% on the proximal extremity to obtain the diaphysis. For fragmented archaeological specimens, LM1 and the proximal part of the diaphysis are sometimes missing. To compensate for the absence of LM1, we compare each fragmented bone to the current wild boars humerus, and the most similar in terms of size and shape is then aligned and resized on the archaeological remain to estimate the position of LM1. To compensate for the lack of the proximal part of some archaeological humerus, we decided to focus only on the distal half of the diaphysis for all of our dataset, since a previous study (Harbers et al., 2020b) showed that the areas of the mapping needed to distinguish free wild boars, captive wild boars and pigs are found in the distal half of the Humerus diaphysis. We then measured the cortical thickness, mapped it onto a plane, and standardised it. All this protocol is explained in the previous study (Harbers et al., 2020b).

Since archaeological specimens are fragmented and incomplete, it is impossible for us to use bone volume to quantify size. We therefore used for this study the cross section area at the distal end of the diaphysis, defined as 5% above LM2. The Pearson correlation coefficient shows that the two variables are almost perfectly correlated ($\rho = 0.965$), so the area of the cross section is a good alternative to bone volume.

4.2.4 Calcaneus three-dimensional shape and centroid size

For the bone three dimensional shape protocol, we focused on the calcaneus since it is a lever arm for the ankle extensors and so very important in terrestrial mammal locomotor behaviour (Bassarova et al., 2009; Carrano, 1997). Furthermore, this bone is well preserved in archaeological contexts thanks to its compacity, and it was not purposely broken to access the bone marrow (Binford, 1978).

The complexity of the calcaneus shape was captured using a three-dimensional sliding semi-landmark procedure (Gunz et al., 2005) with 14 anatomical type III landmarks on the maxima of curvature, 181 sliding semi-landmarks on seven curves, and 763 surface sliding semi-landmarks uniformly distributed over the surface were taken. All this protocol is explained in a previous study (Harbers et al., 2020a).

Only current specimens over one year old were included in the calcaneus shape protocol since the previous study (Harbers et al., 2020a) showed that the calcaneus epiphysis carries a large part of the deformations linked to captivity and domestication, and in an archaeological context only epiphysed individuals, therefore adults, can be analyzed.

4.2.5 Statistical analyses

Differences in humerus cross section area and calcaneus one size (Centroid size) between subgroups of wild boars and domestic pigs from the comparative collection were tested using an ANOVA and visualised with a boxplot. The humerus cortical thickness topography and calcaneus shape differences were tested with MANOVAs and visualized using Linear Discriminant Analyses (LDA); both were performed on reduced datasets after a Principal Component Analysis (PCA) performed on the Procrustes coordinates to keep 97% of the variance (Mitteroecker et al., 2005), and using 9 groups common to Calcaneus and Humerus : Mesolithic wild boars (WB meso), modern wild caught wild boars (WB wc), experimental

free wild boars (WB ctrl), pen experimental captive wild boars (WB pen), stall experimental captive wild boars (WB stall), captive hybrids (HYB), corsican free-ranging pigs (DP cor), traditional pig breeds (DP land), improved pig breeds (DP improv), and a tenth group for calcaneus only : MHK captive boars (WB mhk).

To visualize variations in humerus cortical thickness topography along the canonical axes, we calculated the theoretical minimum and maximum morphometric map for each axis. On each cartography, the four muscle attachment sites are displayed as visual cues. To visualize calcaneus shape deformations along the canonical axes, we calculated the theoretical minimum and maximum shapes for each axis, associated with a heatmap on landmarks corresponding to the distance between the minimum and maximum of the axis. Projections of Neolithic specimens into the discriminant morphospace of the LDA computed on modern specimens were performed using the LDA prediction to calculate their discriminant scores and their posterior probabilities using the Bayes theorem.

A second LDA was performed using only three : (1) modern and Mesolithic wild caught wild boars, (2) modern captive wild boars, and (3) modern domestic pigs and hybrids, in order to perform the classification of Neolithic *Sus scrofa* to one of the three groups using machine learning approach with a knn algorithm. The value of “k” was chosen as the square root of the number of specimens “n” in the comparative material, so $k = 9$ for the humerus dataset ($n = 85$) and $k=10$ for the calcaneus dataset ($n = 85$).

Among the two statistical methods that we tested for this study, LDA probabilities has the advantage of giving a result in percentages, which allows for a more nuanced interpretation. Conversely, knn prediction has the advantage of giving a clear and explicit prediction, more suitable for graphical visualization, that’s why we used the knn results on most graphics.

All the statistics were performed using R (R Core Team, 2017). ANOVA and PCA were performed using the R package "stat" (R Core Team, 2017). LDA and LDA prediction using the package “MASS” (Venables et al., 2002) and visualizations were performed by using “geomorph” (Adams and Otárola-Castillo, 2013) and “rgl” (Adler and Murdoch, 2017).

4.3 Results

4.3.1 Humerus cortical thickness topography in modern and archaeological *Sus scrofa*

Humerus cross section area (Figure 4.2 page 85) differed significantly among modern wild and domestic groups (ANOVA : $F = 10.81$; $P < 0.001$). Current pigs tend to have a larger cross section than current wild boars. Among current wild boars, captive specimens have greater values cross section area compared to wild caught ones. Mesolithic wild boars have an intermediate size of cross section between current wild boars and domestic pigs. Neolithic remains show a large range of cross section area, subdivided in 3 cluster by the mixture analysis : (1) a small with cross sections similar to small current wild boars, (2) a medium one with cross section similar to large current wild boars, and (3) a large one with cross section similar to current pigs or Mesolithic wild boars. Neolithic specimens previously identified as domestic pigs by archaeozoologists fall in the small and medium size cluster, while those identified as wild boars fall in the medium and large size cluster.

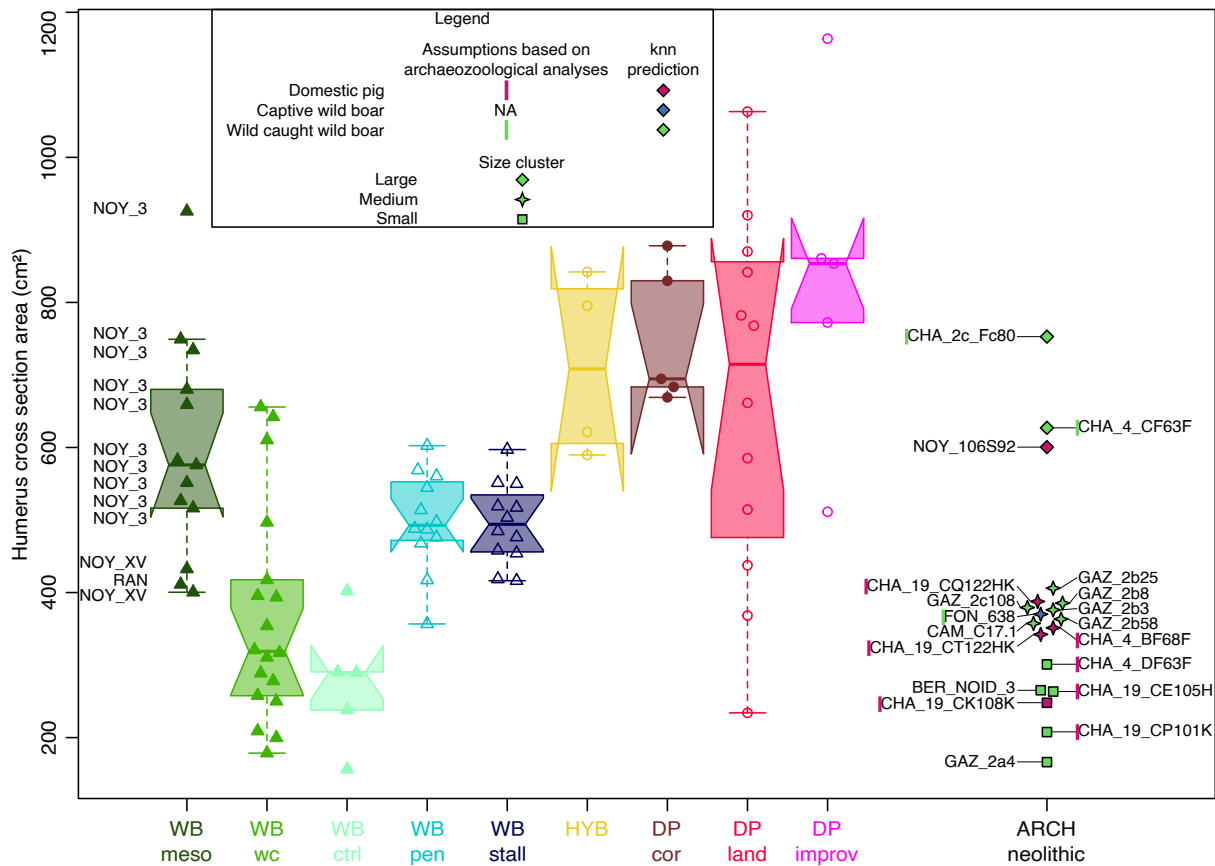


FIGURE 4.2 – Variation in humerus cross section area in Mesolithic, Neolithic and current specimens.

Variation in humerus cross section area in Mesolithic and current wild boars (triangles) and current pig breeds (circles) compared to Neolithic specimens. Size clusters are indicated by the symbols and the knn prediction computed from shape variables by the filling of the symbols. Assumptions based on archaeozoological analyses are indicated by a colored line next to the ID.

The knn prediction computed from shape variables identifies domestic pigs in the three clusters of Chalain and one captive wild boar in the medium size cluster of Fontbrégoua. The archaeological sites of Chalain have a wide range of sizes, while Gazel *Sus scrofa* has 5 humerus out of 6 in a very small range in the medium size cluster.

Topography of humerus cortical thickness differed significantly between the 9 comparison groups (MANOVA : $F = 2.4932$; $P < 0.001$). The first axis of the LDA (Figure 4.3 page 87) separates three main clusters with pigs in the negative part, captive wild boars in the positive part, and Mesolithic and current wild caught wild boars in between. The difference in cortical thickness topography along axis 1 between captive wild boars and domesticated pigs corresponds to a relative change between the insertion area of protractor/retractor (PEC and BRA) and extensor (ECR) : the two areas are relatively thick in captive boars while only the protractor/retractor (PEC and BRA) area is relatively thick in pigs. The second axis distinguishes free-ranging wild boars in the negative part from captive wild boars and domesticated pigs in the positive part. The changes along this axis are very similar to the axis 1. Variation in cortical thickness topography of Neolithic *Sus scrofa* in the discriminant space mainly spreads along the first axis and is mainly centred in the variation of modern and Mesolithic wild boars but spreads towards Landraces pigs' variation.

4.3.2 Variation in calcaneus size and shape in current and archaeological *Sus scrofa*

Calcaneus centroid size (Figure 4.4 page 88) differ significantly among the comparative groups (ANOVA : $F = 9.03$; $P < 0.001$). Current pigs tend to have a larger calcaneus than current wild boars, and among current pigs captive ones tend to have a larger calcaneus than free-ranging ones. Mesolithic wild boars have a similar calcaneus size than current pigs and in the range of the largest wild boars from our collection. Neolithic remains show a large range of calcaneus size clustered in two groups according to Bayesian mixture models : a small similar in size with current wild boars, and large, similar in size with current pigs and Mesolithic wild boars. Remains previously identified as domestic pigs by archaeozoologists are in the small size cluster and the smallest range of the large size cluster. While those previously identified as wild boars are mainly in the large size cluster. The archaeological sites of Chalain, Aigle and Shillourokambos have a range of sizes divided in two clusters. The three specimens from Roucadour are all in the large cluster.

Calcaneus shape between the 10 comparison groups differ significantly (MANOVA : $F = 3.318$; $P < 0.001$). The first axis of the LDA (Figure 4.5 page 89) separates the pigs in the negative part, wild boars in the positive part, and hybrids in between. The difference in calcaneus shape along axis 1 between wild boars and domesticated pigs is marked by an increase in calcaneus robustness and thickness with a medio-laterally wider calcaneus, particularly on the medial side. The coracoid process and the cuboid facet are also more robust and the epiphysis is longer in domestic pigs than in captive wild boars. The second axis distinguishes captive wild boars in the positive part from free ranging wild boars and domesticated pigs in the negative part. The shape divergence on the second axis was mainly localized on the proximal epiphysis, which was longer and curved towards the dorsal side in captive wild boars. The sustentaculum tali was also slightly shifted towards the distal end compared to wild-caught wild boars. Calcaneum shape variation of Neolithic *Sus scrofa* spreads beyond the norm of reaction of Mesolithic and current wild

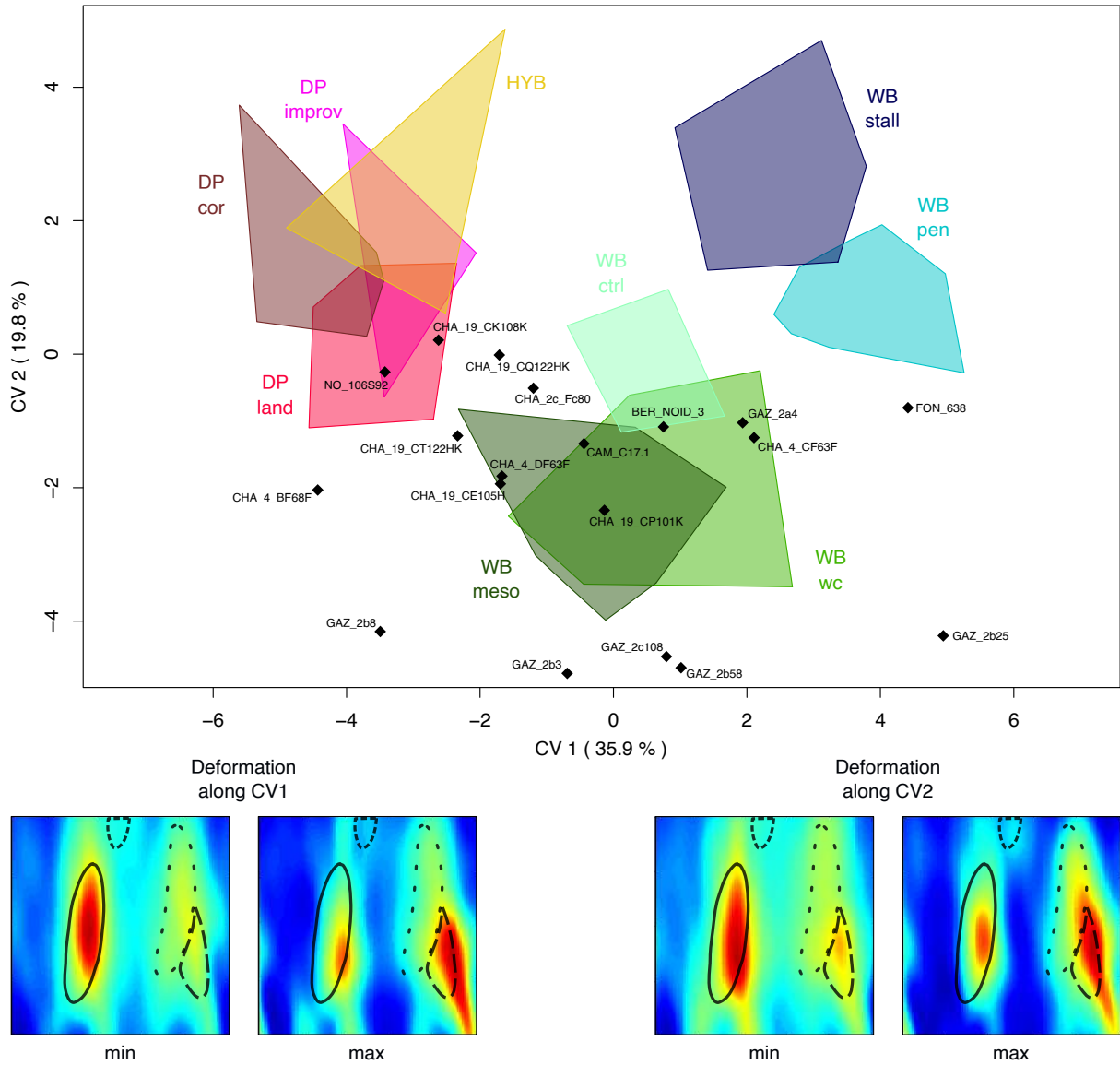


FIGURE 4.3 – Morphospace from LDA on humerus shaft cortical topography.

Morphospace from LDA two first canonical axes representing the pattern of humerus shaft cortical topography differentiation among wild boars and pigs living in free-ranging or captive environments. Neolithic archaeological humerus are projected on this morphospace and indicated by black dots. Minimum and maximum shaft cortical topography are shown for each axis. On each topography, the four muscle attachment sites are displayed as visual cues : pectoralis superficialis (PEC) and brachiocephalicus (BRA) in full line, extensor carpi radialis (ECR) in long dotted lines, coracobrachialis (COR) in tight short dotted lines, and anconeus (ANC) in distant short dotted lines.

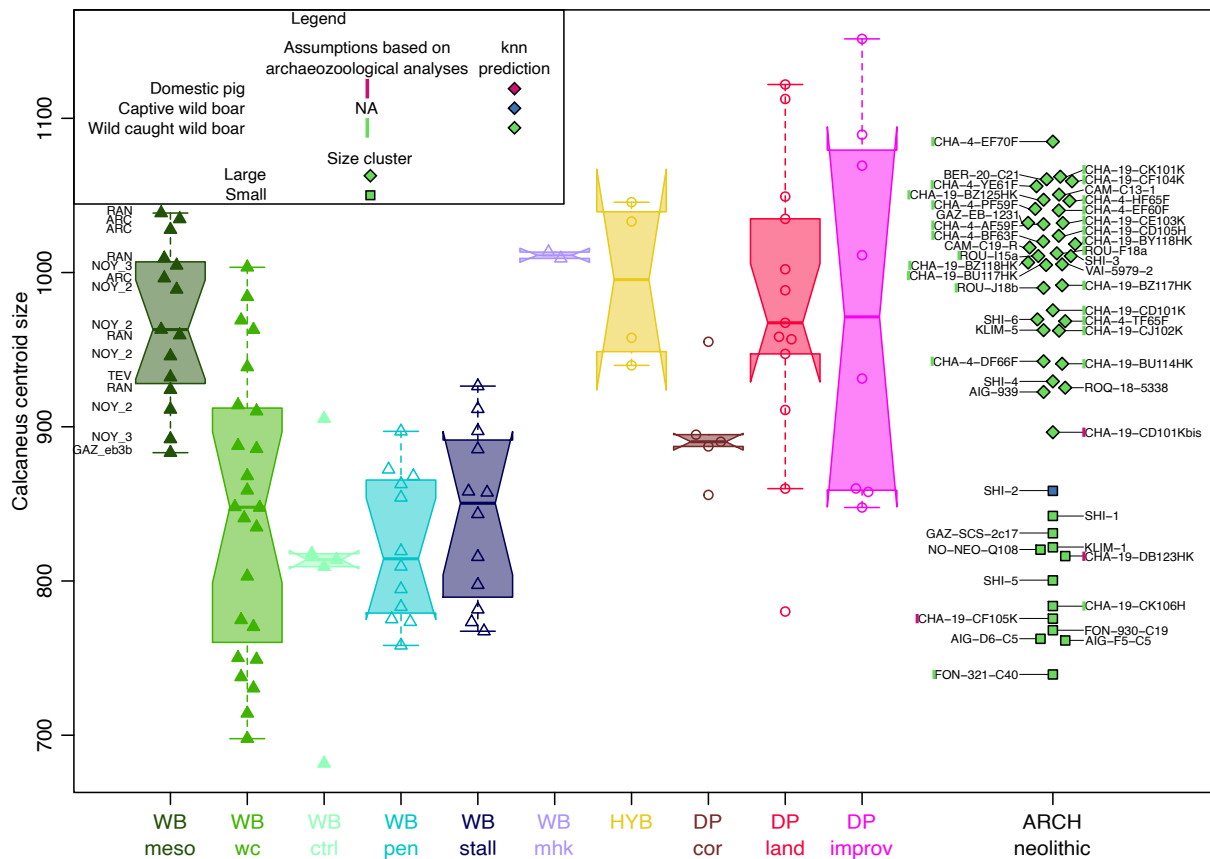


FIGURE 4.4 – *Calcaneus* centroid size variation in Mesolithic, Neolithic and current specimens.

Calcaneus centroid size variation in Mesolithic and current wild boars (triangles) and current pigs breeds (circles) compared to Neolithic specimens the result of size clustering is indicated by the shape of the dots and the result of knn prediction computed from shape variables is indicated by the color of the dots. Assumptions based on archaeozoological analyses are indicated by a colored line next to the ID.

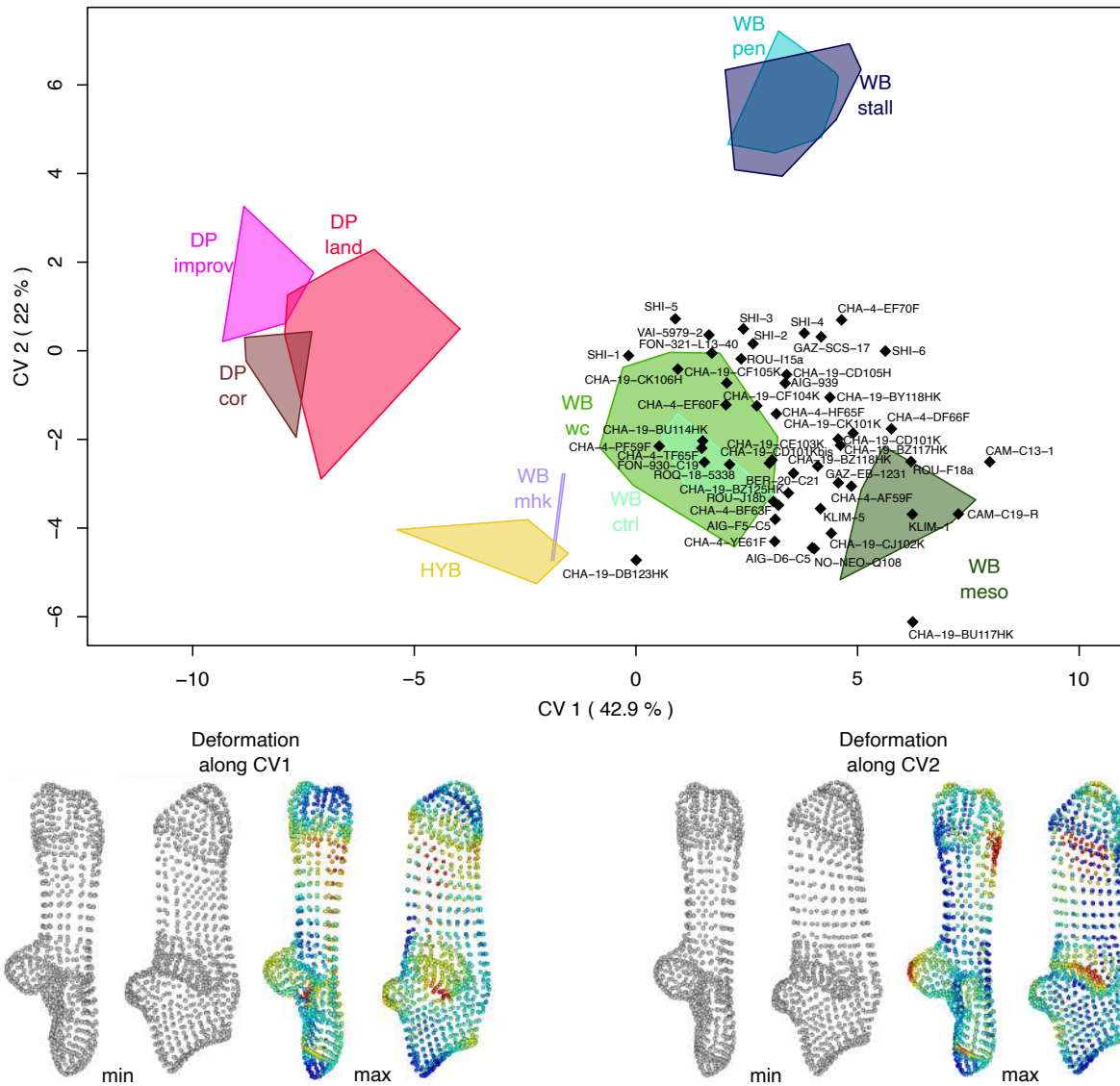


FIGURE 4.5 – Morphospace from LDA on calcaneus geometric morphometry.

Morphospace from LDA two first canonical axes representing the pattern of calcaneus geometric morphometry differentiation among wild boars and pigs living in free-ranging or captive environments. Neolithic archaeological calcaneus are projected on this morphospace and indicated by black dots. Minimum and maximum calcaneus shapes are shown for each axis. The heatmap on landmarks for positive extreme shapes represents the distance of each landmark from the negative extreme shape - the greater the distance the hotter the colour.

caught wild boars in the morphological space and we can notice that this variation is not directed towards the current phenotypic variation of domestic pigs.

4.3.3 Predicting the level of anthropogenic pressure on population of *Sus scrofa* in Western Europe

Knn predictions and LDA probabilities for the classification of the Neolithic *Sus scrofa* according to three morphotypes (domestic, wild caught wild boars and captive wild boars) provide identical results (100% similarity) for both the topography of humerus cortical thickness and the calcaneus shape (Figure 4.6 page 91). There is only one exception for a specimen for Chalain (HUM_CHA_4_CF63F) which is predicted as wild caught wild boar by knn but around 70% as captive wild boar by the LDA. The association of the predictive classification from both phenotypic markers clearly show that the vast majority of the Neolithic *Sus scrofa* are related to the wild caught wild boar morphotype. Only the humerus cortical thickness topography has associated Neolithic specimens to a domestic morphotype.

Bringing together the LDA and KNN predictions and size clustering from the calcaneus shape and the humerus topography (Figure 4.6 page 91 and Figure 4.7 page 93), we can observe the diversity of morphotypes and the degree of anthropogenic changes in the *Sus scrofa* phenotype in the course of the neolithisation of Cyprus and Western Europe. Starting with PPN Cyprus, we observe that all PPNA and PPNB calcaneum studied have been related to the phenotypic variation of free ranging wild boars, despite one PPNB specimen from the middle phase of Shillourokambos with large and a small wild caught wild boar morphotype that exists since the PPNA. For the *Sus scrofa* from sites in the Mediterranean area, we have observed that all the early Neolithic (Cardial and Epicardial) specimens belong to a large and a small free ranging wild boar morphotype, bare one specimen in Fontbrégoua identified as a medium size captive wild boar phenotype from humerus cortical topography. In Fontbrégoua, just like in PPN Cyprus, coexist a large and a small wild caught phenotype and a captive phenotype. The only domesticated phenotypes have been identified with the humerus topography from the late Neolithic in Chalain 4 and Chalain 19 which all correspond to specimens previously identified as domestic by zooarchaeologists. However, humerus cortical topography prediction identify two specimens previously identified as domestic as free ranging wild boars. Regarding specimens from sites in continental Europe, the few early Neolithic (LBK) calcaneum from Vaihingen have be identified as wild caught, while during the middle Neolithic, prediction from calcaneus shape and humerus cortical topography identify three morphogroups : a large wild caught phenotype in Bercy and small wild caught and domestic phenotypes in Noyen sur Seine.

The evolution of the calcaneus centroid size over time associated with its predicted size clusters and morphotypes (Figure 4.7 page 93) allows to observe the occurrence of two sizes cluster during the Neolithic among the wild caught boars : a really small morphotype, smaller than Mesolithic wild boars, that is found both in northern and southern sites in Western Europe as well as in Cyprus and a very large morphotype, larger than Mesolithic wild boars, that is found both in continental and Mediterranean Western Europe.

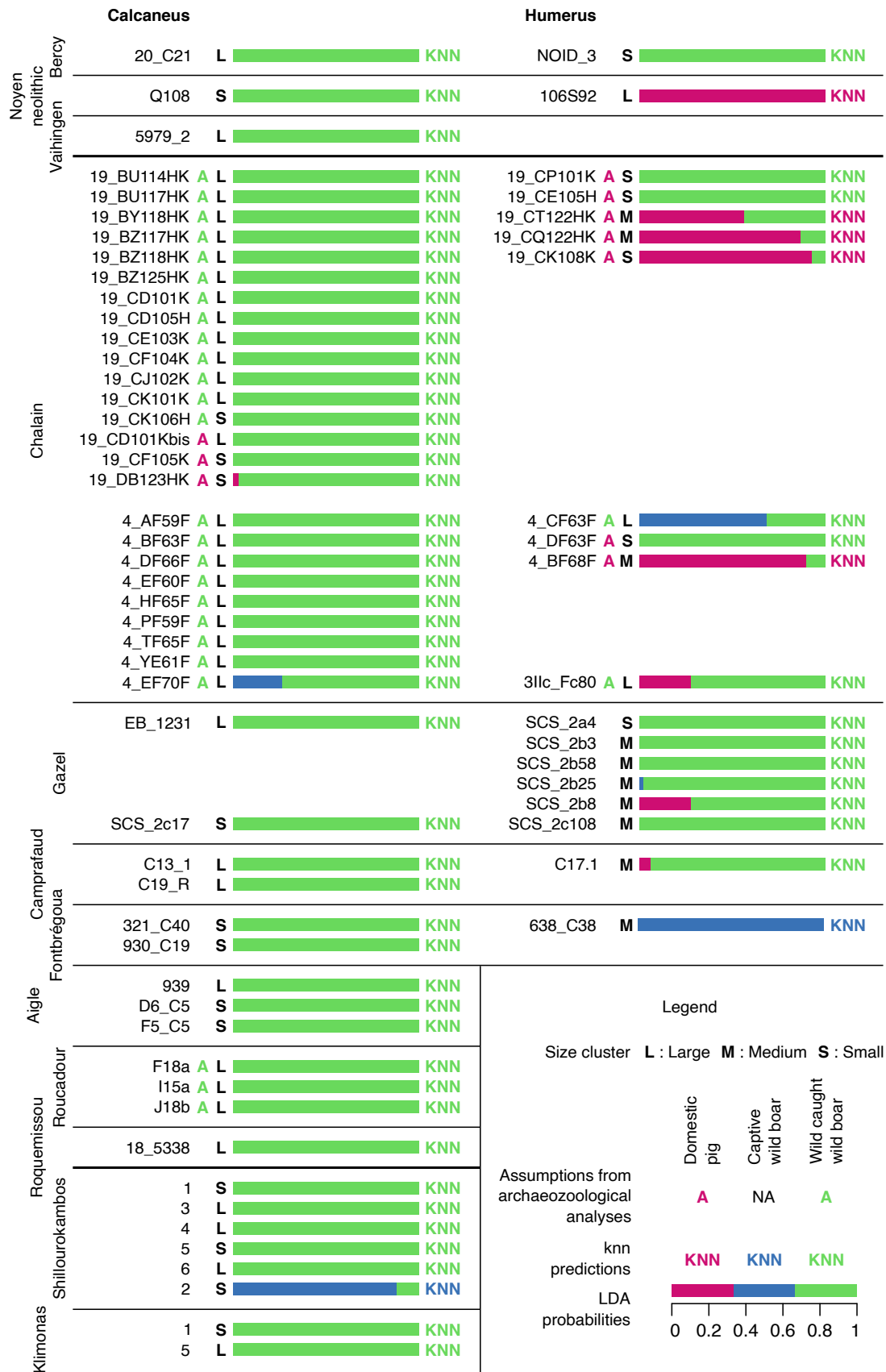


FIGURE 4.6 – Summary of LDA probabilities, knn prediction, size cluster, and assumptions based on archaeozoological analyses.

Calcaneus are in the left column, Humerus are in the right column.

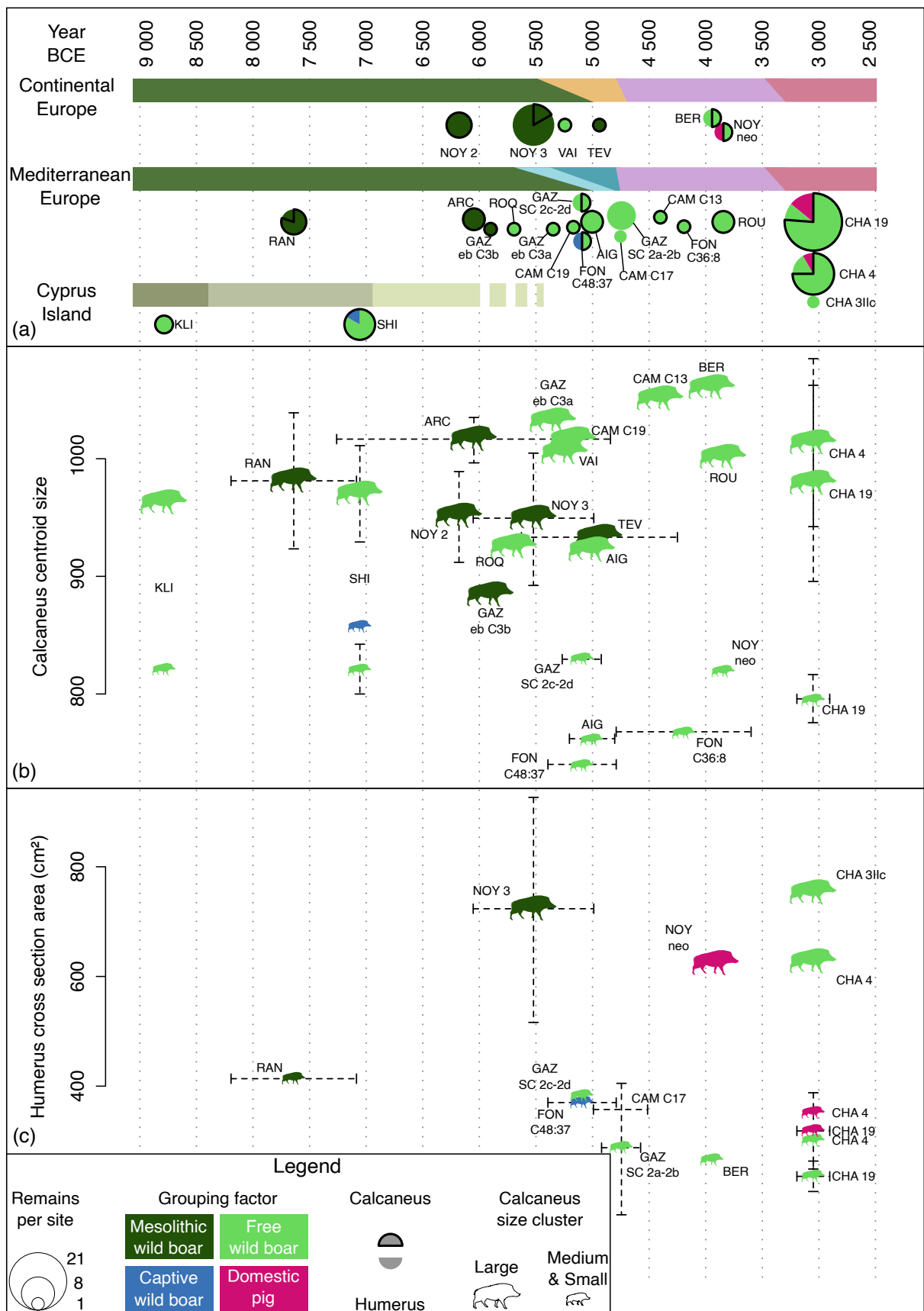


FIGURE 4.7 – Timeline of calcaneus centroid size and humerus cross section area for each period of each site in their chronological context.

The timeline (a) display the number (circle area) and proportion of calcaneus and humerus for each period of each site in their chronological context. The proportions of remains determined as « Mesolithic » and by knn as « Free ranging wild boar », « Captive wild boar » and « Domestic pig » are indicated using colors. The graphs (b and c) display the change in calcaneus centroid size and humerus cross section area of *Sus scrofa* for each site from Mesolithic to the Middle Neolithic. For each calcaneus and humerus information for their size cluster and their knn prediction to the three morphotypes (domestic, wild caught wild boar, captive wild boar) is provided. The horizontal dotted bars indicate the period of occupation of the layer from which the calcaneus come. The vertical dotted bars indicate the extent of the centroid size or cross section area data.

4.4 Discussion

4.4.1 Methodological consideration

Predictions on the shape of calcaneus did not identify any domestic phenotype, whereas several calcaneus from Chalain 19 were considered domestic by archaeozoologists. Conversely, the humerus protocol identified a significant proportion of domestic phenotype. This difference in prediction between the two methods, beyond random effect and statistical effect, suggests that there are methodological discrepancies between the two markers, but also possible differences in their ability to identify lifestyle changes.

The first bias concerns their applications : the protocol for studying the calcaneus shape requires an adult fully fused calcaneus to be applied in an archaeological context. Epiphysis fusion in *Sus scrofa*' calcaneus happens from 24 months (Barone, 1986). All calcaneus from young specimens under two years of age will be found separated from the epiphysis (Bridault et al., 2000) and therefore impossible to analyse. This exclude a great part of the population that could be under the domestication target. On the one hand, this specificity can be a disadvantage, because on many sites we found a large number of non-fused calcaneus which could not be analyzed, which greatly reduced our data set. On the other hand, this can be an advantage : since all the specimens analyzed are adults, we can study the part of the phenotypic variation that is far less impacted by growth : small remains belong to small adult specimens. Conversely, the protocol for studying the humerus cortical thickness topography works whatever the degree of epiphysation of the bone, and even tolerates many fragmentation degrees since most of the morphofunctional signal is observable on the most robust distal part of the diaphysis (Harbers et al., 2020b). This allows to include a maximum of remains in our dataset, but makes it more complicated to analyse since age complicates the signal.

The second bias relates to their results, and follows the first bias : breeders tend to slaughter their animals relatively early, around one or two year of age, to avoid wasting too much resources by feeding them, and therefore the remains of domestic pig come most of the time from young individuals, none fused. Conversely, hunters will have a mixed strategy, slaughtering sows and piglets, but also adult males, which will provide more meat, in addition to valued items such as large canines (Leduc et al., 2015, 2013).

Since the humerus protocol can analyze the remains whatever the level of epiphysation or fragmentation, it can identify hunted wild boars as often as wild boars in captivity. Conversely, the calcaneus protocol will tend to identify mainly hunted specimens and very few reared specimens. Our results are totally in this direction since the humerus protocol identified 26.3% pigs and 5.3% captive boars, while the calcaneus protocol identified 98% free wild boars.

It is also possible that the humerus cortical thickness topography is much more effective than the calcaneus external morphology in registering a change in lifestyle, via a variation in muscle activity. Indeed, a previous study has shown that captivity produces changes in muscle activity that have a direct impact on the bone structure of long bones in wild boar (Harbers et al., 2020b), but also in primates (Morimoto et al., 2011) and reindeer (Salmi and Niinimäki, 2016). However, in another study the external morphology of calcaneus showed the same ability to identify changes in muscle activity induced by captivity in wild boar (Harbers et al., 2020a). It is therefore more likely that methodological biases are responsible for these differences in prediction.

4.4.2 Revisiting the status of *Sus scrofa* remains from early Neolithic contexts in Cyprus and Western Europe

Cyprus island

In Cyprus island, the main issue is whether the pigs found from the PPNB are the result of an introduction of domesticated pigs from the continent, or a local domestication of Cypriot wild boars. Our results highlighted the presence of a captive boar on Shillourokambos at the end of the PPNB, which could suggest the beginning of a local domestication. Note that in the PPNA there is at least one very small wild boar comparable in size to domestic pigs. Its size cannot be explained by a very young age because the calcaneus is already fused, but it can be explained by the strong control of wild populations involved by the introduction of wild boars on the island by boats.

Continental Western Europe

In continental Western Europe, Neolithic societies are known for practicing mainly pig husbandry, while perpetuating wild boar hunting in a significant way (Schäfer, 2011; Tresset, 1988; Whittle, 1996). Furthermore, the total replacement of near-eastern pigs by new pigs of European wild boars ancestry from the 5th millennium BC would indicate potential local domestication during this period (Frantz et al., 2019; Larson et al., 2007). Our results are consistent with archaeological analyzes : we find both free wild boars and domestic pigs. On the other hand, no captive wild boar was identified, which could have made it possible to directly attest to a secondary local domestication. However, this absence of identification is easily explained by the small number of Neolithic remains analysed in the Danubian road, and does absolutely not constitute a proof of the absence of local domestication.

Note that even if an Archaeological mtDNA analysis (Krause-Kyora, 2011) detected hybrids between wild boars and domestic pigs in Vaihingen, the calcaneus analyzed in this study is probably not, since the hybrids rather have a domestic shape calcaneus (SI 4.2).

Early and middle Neolithic in the Mediterranean area

During the beginning of the Neolithic transition in the west of the Mediterranean road, archaeological and paleogenetic data suggest that the Neolithic populations bred a few pigs brought from the Middle East, but that most of their suine resources are based on hunting (Frantz et al., 2019; Helmer, 1979; Rowley-Conwy et al., 2013). Our results confirm the archaeological data, but above all provide completely new food for thought : all the remains from early and middle Neolithic sites (ROQ, CAM, FON, AIG, GAZ) are identified as free wild boars, except one Humerus in Fontbrégoua, identified as a captive wild boar. This captive specimen, as well as the five small free wild boar calcaneus of GAZ SC 2c, FON and AIG could be indicators of an increased selection pressure exerted by humans on wild boar populations, and of a possible beginning of local domestication.

Middle and late Neolithic in areas under Mediterranean influence

Concerning the late Neolithic in Chalain, our results are entirely consistent with archaeological data : we find both free wild boar and domestic pig. However, our predictions differ from archaeozoological determinations : some of the specimens previously considered as domestic pig were predicted by our analyses as free wild boar. By looking directly at the misinterpreted remains, we can notice that for the humerus, they are very young individuals with bone still in growth, while for the calcaneus, the misinterpreted specimens are adults but small. Thus, it is possible that the proportion of domestic pigs was slightly overestimated compared to the proportion of wild boars in Chalain. Concerning Roucadour, we must keep in mind that the archaeozoological identifications were made using the remains from Chalain as reference material to distinguish wild and domestic specimens. So it is possible that the proportion of pigs was overestimated too. Despite this, almost all of the Roucadour specimens were initially identified as wild, and our results fully support these identifications.

On the low prediction rate of captive specimens

Of 68 Neolithic remains studied, only two were predicted to be captive wild boar : one calcaneus and one humerus. These results could show that the control level of wild boar populations in the Neolithic period was much less constraining than the one we set up for our experimental comparative specimens, which was 0.3 ha for the least constrained group. Wild boar population control was therefore probably to be carried out in semi-freedom, which is not sufficient to induce the changes in muscle activity that cause bone modifications.

4.4.3 Neolithisation and phenotypic diversification in Western Europe *Sus scrofa*

A diversification of phenotypes has been observed among western European wild boar from the Cardial-Epicardial Neolithic of southern France, with several size groups present. In the earliest contexts such as Roquemissou, Gazel eb C3a and Camprafaud C19, only large size specimens are present. From 5200 BCE, a group of very small suines is identified at Fontbrégoua and l'Aigle, and then at Gazel, Camprafaud C17 and Chalain. This suggests that during Cardial-Epicardial, the anthropogenic impact on wild boar populations is changing. This can be explained either by a new population control or by the

introduction of non-native populations. A study on the dental forms of suins during neolithisation in Romania also showed that there were three morphogroups of suins during the sequence according to a dichotomous classification method based on dental forms (Evin et al., 2015).

This approach allowed the recognition of two large morphotypes, one identified as wild and the other as domestic based on their hereditary dental characters. The third group is a group of small suins identified as domestic based on dental shapes. The genetic and isotopic data associated with these specimens clearly showed that they had an evolutionary history linked to the suins introduced from the Near East (Larson et al., 2007) and that their diet was under anthropogenic supply (Balasse et al., 2018, 2016).

It is possible that the group of small suins observed from the Neolithic period in Western Europe is similar to the small Romanian "domestic" suine. To answer this question it would be necessary to analyse their teeth and identify their oxygen/nitrogen isotopic signature. But if we accept that these small suins came from a lineage originating from the Near East, potentially admixed with local wild boars and that their diet was highly reliant on resources from anthropogenic ecosystems, we can hypothesize that their management was extensive enough to allow them to express the locomotor behaviour of current wild boar populations, as shown by their reaction norm more centred on the phenotypes of current wild boar, but not to the extent of Mesolithic wild boars.

4.5 Conclusion and perspectives

Understanding the human-suine relationship during the Neolithization of Europe is very complex since these early process of intensification of their relationships have probably left not genetic or morphological hereditary traces. This is why our approach relied on plastic morphological changes that could account for an intensification of the relationship at the scale of the animal's behaviour without relying on a framework of multigenerational reproductive isolation imposed by genetic markers. In this study we have shown that the morphology of Western European suins changed during the neolithic period, leading to a diversification of phenotypes observable from the cardinal in the South of France. In this area and at this period, this diversification could be considered as the consequence of arrival of new management system based on an extensive control of populations of near-eastern Origin , which cohabited with the persistence of wild boar hunting practices. These hypotheses are now to be tested by associating these approaches with isotopic and genomic proxies to provide a more complete vision of the human-suine relationship at the beginning of the Neolithic period in Western Europe.

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CHAPITRE

5

CONCLUSIONS ET PERSPECTIVES
GÉNÉRALES

Préambule

Étudier et caractériser les conséquences morphologiques osseuses de la croissance en captivité chez le sanglier est essentiel pour identifier les marqueurs du tout début du processus de domestication et pour comprendre par quels phénomènes biologiques ces marqueurs sont engendrés. L'objectif de cette thèse était d'identifier ces marqueurs de la captivité et de les confronter à des restes archéozoologiques pour déterminer le niveau de contrôle anthropique auquel étaient soumises les populations de sangliers au cours du Néolithique.

Ce chapitre vise à résumer les principales réponses apportées aux problématiques soulevées dans le chapitre introductif, et à explorer pour chaque problématique les perspectives de recherche.

5.1 Conclusions

5.1.1 Chapitre 2

Le chapitre 2 se concentre sur l'impact que peut avoir la croissance en captivité sur la morphologie externe d'un os du tarse chez des sangliers sauvages, en utilisant les méthodes de morphométrie géométrique surfacique 3D.

Le comportement locomoteur d'un sanglier en captivité peut-il induire des modifications de conformation osseuse au-delà de la norme de réaction des sangliers sauvages ?

La plupart des études précédentes ont pu montrer que la captivité, via des changements d'alimentation, d'exercice et de stress, a un impact sur la morphologie. Mais elles ont été conduites sur plusieurs générations, confondant donc les modifications plastiques au cours de la vie avec les différences héréditaires induites par la sélection (Frankham et al., 1986 ; O'Regan and Kitchener, 2005 ; Schulte-Hostedde and Mastromonaco, 2015). Nous avons pu montrer que dès la première génération en captivité, les sangliers montrent des modifications dans la conformation du calcaneus au-delà de la norme de réaction des sangliers sauvages. En revanche, la taille du calcaneus ne semble pas impactée par la captivité.

À quel point ces modifications sont impactées par le lien fonctionnel entre os et muscles ?

Nous avons mis en évidence un fort lien entre la réduction de la mobilité, les déformations du calcaneus qui en résultent et l'augmentation de la force musculaire des muscles du membre postérieur. Ce qui nous laisse penser que les comportements locomoteurs stéréotypés liés à la captivité induisent une augmentation de l'activité des extenseurs de la cheville et favorisent des fibres musculaires à contraction plus rapide avec une plus large section transversale, ce qui entraîne une réorientation du calcaneus et une augmentation de la force exercée par les muscles sur l'os, et donc une modification de sa conformation.

Comment ces modifications diffèrent-elles de celles induites par la sélection artificielle pratiquée chez le cochon au cours des 200 dernières années ?

Nos résultats ont montré que les modifications plastiques induites par la captivité sont bien différentes des modifications induites par la sélection artificielle exercée sur les cochons au cours de deux derniers siècles. Ces dernières consistent en une augmentation de la robustesse générale de l'os et sont plutôt liées à une augmentation de la masse des individus (Frost, 1997) induite par des programmes de reproduction pour obtenir des cochons plus grands, plus gros, et avec une plus grande production de muscles (Wilkinson et al., 2013).

5.1.2 Chapitre 3

Le chapitre 3 vise à identifier des marqueurs du stress biomécanique induit par la captivité au niveau de l'endostructure de la diaphyse des os longs des membres appendiculaires en étudiant la topographie de l'épaisseur corticale de l'humérus chez le sanglier.

La réduction de la mobilité au cours de la croissance chez le sanglier peut-elle induire des variations mesurables dans la structure corticale des os des membres au-delà de la norme de réaction des sangliers sauvages ?

Nos résultats permettent de mettre en évidence que le volume osseux et la topographie de l'épaisseur corticale de l'humérus sont impactés par la captivité, suffisamment pour que les modifications soient mesurées expérimentalement.

À quel point ces modifications sont impactées par le lien fonctionnel entre os et muscles ?

Cette étude vient corroborer la précédente puisqu'elle a permis de montrer que la captivité provoque une augmentation globale de la taille de la section transversale des muscles attachés à l'humérus, identique à celle observée pour les muscles attachés au calcaneus. Cette augmentation est probablement due à une augmentation de la masse corporelle, une alimentation plus riche en protéines, et des comportements stéréotypés qui augmentent l'utilisation des muscles. L'analyse de la topographie de l'épaisseur corticale nous a permis de voir que la captivité induit une diminution relative de l'utilisation des muscles extenseurs du membre antérieur par rapport aux autres muscles.

5.1.3 Chapitre 4

Le chapitre 4 consiste en une application des deux méthodes développées dans les deux chapitres précédents sur des restes de suinés du Mésolithique et du Néolithique de l'Europe de l'Ouest et de Chypre. L'objectif étant de tester leur applicabilité en contexte archéologique et d'apporter un nouvel éclairage sur :

La question d'une potentielle domestication du sanglier endémique de Chypre.

L'influence du Mésolithique et de la Néolithisation sur la diversité phénotypique des populations de *Sus scrofa* en Europe Occidentale.

Quelles limites méthodologiques ont pu être mises en évidence par cette application archéozoologique ?

Premièrement, le protocole de morphométrie géométrique sur le calcanéus nécessite des os entièrement épiphysés, et ne peut donc s'appliquer qu'à des restes d'adultes. Dans le cas du sanglier, cette épiphysation ne se fera pas avant l'âge de deux ans, voire plus tard en fonction des auteurs (Zeder et al., 2015). Ce qui exclut une bonne partie des spécimens potentiellement en captivité. En revanche, cette limite nous permet d'étudier la variation phénotypique sans l'influence de la croissance. À l'inverse, le protocole de cartographie de l'épaisseur corticale fonctionne avec des spécimens de tous âges, ce qui inclue un grand nombre de spécimens mais rend le signal morphofonctionnel plus complexe à interpréter à cause de l'influence de ce dernier.

La seconde limite vient s'associer à la première : l'âge d'abattage des bêtes diffère en fonction de leur statut. Les éleveurs ont tendance à tuer les bêtes jeunes ayant atteint un optimum pondéral alors que les chasseurs ont une stratégie plus variée. Ainsi l'analyse du calcanéus, qui nécessite des os d'adultes, aura moins l'occasion d'identifier des spécimens en captivité que celle de l'humérus. Néanmoins, les motivations de productivité pour une carcasse de cochon propre aux sociétés d'économie de marché actuelles ne s'appliquent pas aveuglément aux sociétés des éleveurs du début du Néolithique, pour lesquelles la séparation entre les pratiques de chasse et d'élevage n'est pas facile à discerner (Rowley-Conwy et al., 2012). Non seulement le taux de croissance pondérale pour les premiers élevages de cochons est incomparable avec celui des races même traditionnelles, obligeant certainement les éleveurs néolithiques à garder leurs cochons certainement au-delà de la deuxième année. L'exemple ethnographique des sociétés d'éleveurs de cochons de Papouasie-Nouvelle-Guinée nous éclaire notamment sur le fait que ce sont les plus gros spécimens et donc les plus vieux qui sont consommés dans les banquets (Sillitoe, 2007).

La troisième limite est liée à notre définition de "captivité". Les spécimens captifs expérimentaux dont nous disposons ont été élevés dans un enclos de 0,3ha pour le groupe le moins contraint, or il est avéré par les études isotopiques que les premiers élevages du Néolithique européens ont été menés selon un mode extensif dans les milieux forestiers d'Europe septentrionale (Benecke, 1994 ; Hamilton et al., 2009) comme dans la péninsule ibérique (Navarrete et al., 2017). Cette pratique n'ayant changé qu'avec l'ouverture du paysage à la fin de l'Age du Fer en Europe, forçant les éleveurs de porc à se tourner davantage vers un élevage en semi ou complet confinement (Ervynck et al., 2007 ; Hamilton et al., 2009) comme c'est désormais le cas dans la majorité des élevages porcins à l'échelle de l'Europe, mis à part dans quelques îles méditerranéennes (Albarella et al., 2007). Les variations morphologiques liées au confinement du bétail porcine seraient alors bien moins importantes, ce qui limiterait notre capacité à les identifier. Néanmoins, nous pensons que le contrôle anthropogénique des mouvements d'un groupe de suidés sauvages, même s'il se fait en libre parcours comme pour les cochons, perturbe néanmoins l'expression du répertoire des comportements locomoteurs de ces suidés. Même si ces animaux peuvent parcourir d'importantes distances pour rejoindre leur aire de pâturage, la diversité des interactions avec leur environnement et avec les autres espèces de leur écosystème, via la prédation ou la compétition, sera modifiée par l'éleveur. D'après ce que l'on sait du libre parcours des troupeaux de porcins à l'époque médiévale, cet élevage extensif implique la présence du porcher (Edlin, 1970). Or il est possible d'envisager que les premiers élevages extensifs de suinés en Europe Néolithique nécessitaient également la présence de

l'éleveur pour protéger le troupeau des prédateurs ou éviter qu'ils ne saccagent les zones de cultures. L'exemple ethnographique d'élevage extensif de cochons (*Sus scrofa vittatus*) pratiqué en économie de subsistance par des sociétés de Papouasie-Nouvelle-Guinée nous éclaire également sur ce point (Sillitoe, 2007). En effet, ces sociétés spécialisées dans le « management » de troupeaux de cochons à des fins de subsistance, mais aussi et surtout dans le cadre d'échanges socio-politiques, pratiquent un élevage qui, en fonction des communautés, varie du mode extensif où les cochons sont en libre parcours dans la forêt jouxtant le village la journée et rentrent en fin de journée pour être nourris et passer la nuit, à un mode totalement parqué, que ce soit par des enclos (Hide, 1981) ou dans une zone naturellement enclavée (Feachem, 1973). Un management des suinés de type extensif, comme cela a pu se pratiquer au début du Néolithique, même s'il implique des croisements avec des sangliers sauvages et un libre parcours, ne signifie pas pour autant que le comportement locomoteur déployé par ces individus soit comparable à celui des sangliers sauvages. Cependant, dans l'état actuel de notre étude, nous ne savons pas à partir de quel degré de restriction de l'espace disponible peut-on commencer à observer les changements plastiques. Notre expérimentation a drastiquement restreint la mobilité et l'on a observé des changements plastiques quasiment identiques pour l'enclos de 3000 m² et la stabulation de 100 m². Néanmoins, la population de contrôle de l'expérimentation est issue d'un élevage de sangliers vivant dans 10 hectares de forêt, ce qui représente une importante réduction du potentiel de mobilité pour une population de sangliers dont l'espace vital s'étend plutôt autour de 500 hectares et parfois beaucoup plus pour les mâles solitaires (Étienne, 2003). Or cette population de sangliers d'élevage ne présente pas de changement morphologique par rapport aux autres populations de sangliers chassés du Nord de la France. Ce qui suggère donc que la réduction de mobilité capable d'entraîner des changements morphologiques au cours de la croissance des sangliers se situerait entre 3000 m² et 10 ha.

Quelles nouvelles données ont pu être apportées par ce réexamen du statut des suinés du début du Néolithique en Europe occidentale ?

Dans l'ensemble, nos analyses ont montré qu'il existe une grande diversification des phénotypes chez les populations de suinés en Europe de l'Ouest à partir de la moitié du 6^e millénaire AEC. Cette diversification se caractérise par l'émergence de deux morphotypes de grande et de petite taille à l'âge adulte, qui présentent tous deux les caractéristiques morphofonctionnelles de populations vivants dans un habitat naturel, sans contrôle anthropogène, mis à part pour le site de Fontbrégoua où un individu présente une topographie corticale typique de sangliers ayant vécu en captivité. Il faut attendre la fin du Néolithique et l'utilisation des marqueurs de la topographie de l'épaisseur corticale des diaphyses de l'humérus pour observer l'arrivée d'un troisième morphotype, de petite taille également, mais présentant des caractères typiques des cochons modifiés biologiquement par la sélection artificielle. En l'occurrence, notre étude sur les facteurs majeurs influençant la topographie de l'épaisseur corticale d'une population de sanglier étant la masse corporelle, il s'agirait peut-être de l'émergence de premiers spécimens engraisés et dont le surpoids aurait pu provoquer des changements dans la façon de se mouvoir, comme il a été démontré que l'obésité impactait la démarche des humains (Browning, 2012).

La présence de petits et de grands morphotypes parmi les premiers suinés d'Europe n'est pas nouvelle car elle a été déjà observée dans les contextes néolithiques roumains dès 5500 AEC (Evin et al., 2015), dans les contextes du Sud de la France à la

Baume d' Oullen dès 5300 cal AEC (Vigne and Helmer, 1999) mais aussi dans les premiers contextes néolithiques de Chine (Cucchi et al., 2016). Dans le premier et le dernier cas, le petit morphotype a été identifié comme ayant un statut domestique grâce à un signal isotopique typique d'une alimentation anthropogène (Balasse et al., 2016; Cucchi et al., 2016). Dans le second, le petit morphotype a été considéré comme étant issu de petits suinés domestiques sans autre élément de preuve. Dans l'état actuel de notre étude, ces petits morphotypes de suinés n'ont été identifiés que dans les contextes néolithiques cardiaux et épicaux du Sud de la France. Cependant, nos effectifs pour le Nord de la France ne nous permettent pas d'évacuer la possibilité qu'ils aient pu exister également dans le Nord. En effet, la paléogénétique a démontré que des spécimens issus de populations d'origine proche-orientale de petite taille ont été introduits par le courant danubien jusque dans le bassin parisien (Frantz et al., 2019; Larson et al., 2007). Néanmoins, cette interprétation est plus difficile à tenir pour le Sud de la France. En effet, il n'a pas été encore formellement démontré que le courant méditerranéen de néolithisation ait entraîné l'introduction de cochons d'origine proche orientale dans la région du Languedoc Roussillon depuis la zone Tyrrhénienne avant la fin du Néolithique voir l'Age du Bronze, comme le suggèrent les études paléogénétiques dans cette zone (Lega et al., 2017). Les seules données paléogénétiques pour le Sud de la France proviennent du site cardial de Pendimoun (Binder et al., 2020). Or pour ce site, un des huit spécimens de suiné identifié comme potentiellement domestique d'après sa forme dentaire a pu être génotypé comme appartenant à l'haplotype des sangliers originaires de méditerranée septentrionale centrale. Ce qui soutient l'hypothèse que l'introduction de cochons d'origine proche orientale en Languedoc Roussillon est un processus tardif (Rowley-Conwy et al., 2013), potentiellement déconnecté du processus de néolithisation. Donc comment interpréter la présence de petits sangliers dès le milieu du 6e millénaire AEC dans le Sud de la France ?

L'hypothèse que nous proposons est celle d'une trajectoire commensale de sangliers présentant des caractères développementaux de populations commensales vivant à proximité des occupations humaines et bénéficiant des espaces cultivés et des zones de rejets pour acquérir tout ou partie de leur nourriture. Ces individus auraient pu vraisemblablement être acquis par une chasse de contrôle pour protéger les cultures. Leur petite taille pourrait s'expliquer par les conséquences développementales d'une sélection d'individus plus adaptés à la proximité humaine (Wilkins et al., 2014), aussi nommé « syndrome de domestication » mais que l'on pourrait ici appeler syndrome « d'auto-domestication ». En effet, cette trajectoire commensale aurait impliqué un groupe d'individus déjà peu farouches et capables de se rapprocher des occupations humaines. La sélection indirecte d'individus les plus tolérants au stress de la proximité humaine, aurait rapidement favorisé l'émergence d'individus de plus petite taille. Dans ce sens, une étude longitudinale récente a montré que des populations sauvages de souris grises (*Mus musculus domesticus*) régulièrement exposées à la proximité humaine ont développé, en une dizaine d'années, des syndromes de domestication dont l'un étant la réduction de leur taille corporelle (Geiger et al., 2018).

5.2 Perspectives

5.2.1 Avenir du projet expérimental DOMEXP

Le projet Domexp, qui a consisté à faire grandir en captivité des sangliers issus d'une population semi-sauvage à partir de 6 mois jusqu'à leurs 2 ans, et à leur faire passer un scanner médical et une IRM tous les 3 mois pendant leur croissance, a généré une très grande quantité de données. Il sera donc essentiel de mettre à profit ces séries longitudinales de scanners *in vivo* au cours de la croissance pour mieux comprendre les processus développementaux d'apparition de ces réponses plastiques liées à la captivité identifiés dans cette thèse.

De plus, il est possible de mesurer un équivalent de la ACSA à partir des IRM, il serait donc intéressant d'étudier l'évolution de la force musculaire au cours du développement en fonction de la réduction de mobilité. Nos données ACSA sont d'ailleurs très lacunaires concernant les sangliers sauvages, il pourrait être intéressant de prendre ces mesures sur de nouveaux spécimens sauvages pour pouvoir construire un vrai modèle biomécanique. Enfin, comme expliqué dans le chapitre introductif, on peut s'attendre à ce que la captivité induise des modifications au niveau de la structure trabéculaire des os. Les scan effectués au cours de la croissance ne sont pas assez précis pour étudier ces structures, mais des scan au micro-CT ont déjà été effectués sur les os des individus en fin de croissance (2 ans), et leur analyse pourrait révéler des nouveaux marqueurs dont l'étude est actuellement en cours.

5.2.2 Perspectives de l'analyse du calcaneus en morphométrie géométrique tridimensionnelle

Concernant le protocole de morphométrie géométrique appliquée au calcaneus, la principale limite à résoudre se situe dans la pose manuelle des *landmarks* anatomiques, qui est relativement chronophage. La pose manuelle nécessite d'apprendre à identifier les *landmarks*, et est surtout très sensible à l'effet opérateur, c'est-à-dire qu'en changeant la personne qui réalise la pose des points, le résultat risque de ne pas être comparable. L'objectif à long terme étant que n'importe qui puisse réaliser le protocole. Pour que les archéozoologues puissent ajouter et prédire eux-même leurs restes archéologiques, il est nécessaire d'aller vers plus d'automatisation de l'acquisition des données de forme 3D. L'automatisation a déjà été envisagée dans plusieurs publications, selon plusieurs méthodes. La première consiste en une pose automatisée de *landmarks* via des algorithmes de reconnaissance automatique (Boyer et al., 2011 ; Gao et al., 2019), et serait à mon avis tout à fait applicable à notre problématique, ce qui permettrait d'automatiser totalement le protocole. La seconde méthode consiste en revanche à comparer les conformations en mesurant les distances entre les surfaces, sans passer par la pose de *landmarks* (Koehl and Hass, 2015), ce qui selon moi ne permet pas de prendre en compte toutes les déformations possibles. En effet une structure anatomique peut se décaler le long d'une surface sans que la surface ne se déforme, ce qui ne serait pas détectable avec ce genre de méthode et nécessite de placer un *landmark* spécifiquement sur cette structure, manuellement ou par des algorithmes. C'est justement le type de déformation qui a été mis en évidence dans cette thèse au niveau de l'épiphyse du calcaneus entre des individus chassés et des individus captifs : La jonction entre l'épiphyse et le reste du calcaneus se décale vers la partie distale de l'os et change légèrement d'orientation en réponse à la captivité. Cette déformation n'aurait pas pu être détectée en mesurant les distances entre les surfaces.

Au-delà de l'automatisation, il pourrait être intéressant de tester l'effet opérateur, qui pourrait tout à fait être relativement faible, d'autant que dans notre protocole, les *landmarks* les plus compliqués à placer ne sont pas les plus diagnostiques. C'est le cas des *landmarks* 4, 6 et 14 (Voir figure 2.1 et table 2.2) qui sont situés sur des maximums de courbure relativement aplatis mais qui ne font pas partie des déformations diagnostiques de la captivité ou de la domestication. À l'inverse les *landmarks* situés au niveau de l'épiphyse (9, 11 et 12) et des surfaces articulaires (1, 2, 3, 5, 7, 8) sont relativement intuitifs à positionner et sont situés au niveau des déformations diagnostiques. Seuls les *landmarks* 10 et 13 peuvent éventuellement poser problème puisqu'ils sont situés à la jonction de l'épiphyse mais nécessitent un peu d'entraînement pour les positionner avec précision.

Enfin, maintenant que les déformations induites par la captivité ont été identifiées et localisées, il pourrait être envisageable de mettre en place un nouveau protocole extrêmement simplifié avec quelques *landmarks* ou quelques mesures basiques aux bons endroits pour être capable de distinguer les spécimens libres des captifs très rapidement et simplement.

5.2.3 Perspectives de l'analyse de la topographie de l'épaisseur corticale de l'Humérus

Les limites du protocole de cartographie de l'épaisseur corticale de l'humérus sont assez similaires à celles énoncées pour le calcaneus. En effet, ce dernier repose sur de nombreuses étapes manuelles, comme des alignements d'os ou des découpes, qui sont relativement complexes et chronophages. Encore une fois, il est nécessaire d'aller vers plus d'automatisation.

Par chance, le package R *morphomap* a été publié cette année (Profico et al., 2020) et propose de réaliser des cartographies de l'épaisseur corticale de façon totalement automatique. Cependant, avant d'arriver au protocole actuel présenté dans cette thèse, nous avons fait plusieurs essais de protocoles, le premier étant particulièrement simple à réaliser mais assez peu précis et chaque itération a permis d'augmenter la précision au prix de nouvelles étapes manuelles. Le protocole automatique proposé dans le package *morphomap* correspond point par point au premier protocole élaboré dans le cadre de cette thèse, ce qui nous permet de relativiser l'intérêt de l'utilisation de ce package dans notre situation. En effet, le protocole automatique présente plusieurs problèmes :

- La hauteur des découpes transversales est définie par des pourcentages de l'os, et dépend donc de la conformation de l'os. Ce paramètre a probablement peu d'impact sur des os très longilignes comme le fémur d'hominidé présenté dans l'article, mais beaucoup plus important sur des os plus compacts comme l'humérus dans notre cas ou les épiphyses représentent une grosse proportion de l'os. Si les épiphyses sont plus longues sur un spécimen, les découpes vont être décalées et ne seront plus du tout homologues d'un individu à l'autre.

Pour pallier à cela, nous avons défini les découpes avec des *landmarks* anatomiques qui ont l'avantage d'être homologues, mais nécessitent une étape manuelle.

- L'inclinaison des découpes transversales se fait en fonction de l'alignement général de l'os dans l'espace. Étant donné que l'alignement est fait de façon géométrique il dépend de la conformation de l'os. Ainsi, si une épiphyse est projetée sur un côté, l'os

sera aligné de façon légèrement inclinée, les découpes seront également inclinées et ne seront plus homologues d'un individu à l'autre. De plus cet alignement nécessite quand même une étape manuelle avant de pouvoir procéder aux découpes, limitant son caractère « totalement automatique ».

Pour remédier à ce problème, notre protocole nécessite de réaliser l'alignement sur la diaphyse pré-découpée, ce qui implique une nouvelle étape manuelle mais nous assure d'avoir un alignement homologue au niveau de la diaphyse.

- Enfin la découpe longitudinale se fait géométriquement et en fonction de l'alignement général de l'os, ce qui pose les mêmes problèmes que les deux points précédents.

Nous avons pu résoudre cet écueil en définissant la découpe longitudinale par un *landmark* anatomique placé manuellement. À noter que nous avons pu tester l'influence de ce paramètre et comparer les résultats avec les deux types de découpe longitudinale, les résultats sont quasiment identiques, donc il est probablement possible de se passer de cette étape.

5.2.4 Avenir de l'évaluation de l'impact anthropogénique sur les populations archéologiques de *Sus scrofa* par l'étude de la forme des os et de la topographie de l'épaisseur corticale

L'application archéologique a permis de voir qu'il serait nécessaire d'augmenter la proportion de matériel archéozoologique utilisable dans nos protocoles. Pour cela deux possibilités : élargir les protocoles à plus de matériel fragmenté, et développer les protocoles sur de nouveaux os.

Dans le cas du protocole de morphométrie géométrique appliquée au calcaneus, un test préliminaire a déjà été effectué sur l'os sans l'épiphyse, pour pouvoir rajouter les spécimens non-épiphyse. Le test préliminaire sur un jeu de données réduit a montré des résultats encourageants, mais beaucoup moins précis qu'avec l'épiphyse. Il pourrait être intéressant de pousser ce test sur le jeu de données complet et avec des analyses plus poussées, mais l'intérêt reste maigre vu la faible quantité d'os concernés.

Le protocole de cartographie de l'épaisseur corticale de l'humérus est en revanche déjà bien avancé en termes de fragmentation puisqu'il inclut les spécimens dont la partie proximale de la diaphyse est fragmentée jusqu'à la moitié, c'est-à-dire la grosse majorité des restes d'humérus potentiellement analysables. De plus les zones d'insertions musculaires s'étendent sur toute la moitié distale de la diaphyse. Réduire encore la zone d'étude pour intégrer plus de matériel nous amènerait forcément à perdre une partie importante de l'information d'épaisseur corticale. La marge de progression est donc relativement faible.

Outre le calcaneus et l'humérus, il pourrait être intéressant d'étudier l'impact de la captivité sur le talus. Il est en effet fortement impliqué dans la locomotion et risque d'être directement influencé par le type de mobilité, comme le calcaneus avec lequel il s'articule (Barone, 1986 ; Popkin et al., 2012 ; Zeder et al., 2015). De plus, il est également très bien conservé en contexte archéologique. Sa forme et sa structure permettraient par ailleurs de coupler à la fois la morphométrie géométrique sur sa surface externe, et l'étude des trabécules de sa structure interne. La structure trabéculaire est en effet susceptible d'être modifiée par les contraintes externes et a déjà été utilisée pour identifier des modifications du mode de vie (Adachi et al., 1997 ; Bass et al., 2005 ; Chirchir et al., 2015 ; Djukic et

al., 2015 ; Gosman et al., 2011 ; Tsubota et al., 2002 ; Wallace et al., 2017).

Enfin, il serait intéressant de coupler toutes ces études avec des analyses isotopiques et génomiques ciblées :

- sur le morphotype des petits spécimens observés dans les contextes cardiaux et épicaux à partir du milieu du 6^e millénaire AEC afin de tester l'hypothèse de la trajectoire commensale pour ces spécimens.
- sur les spécimens de Chalain qui présentent des topographies corticales typiques de cochons domestiques actuels afin de tester l'hypothèse d'un engraissement.

Ces études ciblées permettront ainsi d'apporter une vision plus complète de la relation Homme-suiné au début de la période Néolithique en Europe occidentale.

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ANNEXES

Supplementary Information 2.1

ID	GP1	GP2	Mass (kg)	Age (month)	Sex	PCSA.Gastro.Lat (cm ²)	PCSA.Gastro.Med (cm ²)	PCSA.Soleus (cm ²)	C.Size	Available.Area (m ²)
PRA-172	Control	Wild boar	23	23 F	NA	NA	NA	NA	681.6857	20000
PRA-175	Control	Wild boar	53	20 M	5.24109014675052	4.95283018667925	1.94070080862534	817.6660	20000	
PRA-185	Control	Wild boar	52	20 M	4.68923418423973	5.59531554977228	2.94117647058824	813.8565	20000	
PRA-187	Control	Wild boar	110	84 F	7.08697653014266	7.95512493625701	3.77358490566038	905.2820	20000	
PRA-188	Control	Wild boar	60	96 F	NA	NA	NA	809.3200	20000	
H279	Stall	Wild boar	92.5	25 F	5.71587125416204	6.49278579356271	4.46871896722939	797.5253	50	
H285	Stall	Wild boar	72	25 M	NA	NA	NA	858.0960	50	
H288	Stall	Wild boar	89	25 M	7.34856007944389	8.03234501347709	4.2573778422835	911.5906	50	
H286_H291	Stall	Wild boar	73	25 M	7.97169811320755	7.80922431865828	2.97914597815293	857.4095	50	
H315	Stall	Wild boar	89	25 F	4.92662473794549	8.93081761006289	4.55049944506104	815.6484	50	
H316	Stall	Wild boar	53.5	25 F	3.82323733862959	5.53459119496855	2.88915094339623	767.4235	50	
H318	Stall	Wild boar	61.5	25 F	6.88424273329934	7.15679895901106	2.09077001529932	781.6003	50	
H319	Stall	Wild boar	111	25 F	NA	NA	NA	843.4329	50	
H320	Stall	Wild boar	91	25 F	5.60796645702306	8.07783018667925	4.14046121593291	773.3655	50	
H330	Stall	Wild boar	77.5	25 M	7.80214176440592	7.2142064372919	3.19706498951782	897.2820	50	
H334	Stall	Wild boar	96	25 M	9.88083416087388	9.69601677148847	2.87735849056604	926.3647	50	
H335	Stall	Wild boar	84	25 M	5.61320754716981	8.37264150943396	4.354136429660813	885.4634	50	
H282	Pen	Wild boar	84	25 M	5.66037735849057	7.49167591564928	4.61676766613704	897.0203	3000	
H283	Pen	Wild boar	66.5	25 F	5.92243186582809	5.77830186679245	2.89308176100629	783.2168	3000	
H289	Pen	Wild boar	91.5	25 M	5.92243186582809	8.21309655937847	4.644412191582	862.8328	3000	
H333_H292	Pen	Wild boar	67	25 M	9.39108061749571	9.64360587002096	3.12810327706058	868.0063	3000	
H287_H293	Pen	Wild boar	67	25 M	6.19946091644205	7.12788259958071	4.32852386237514	809.3973	3000	
H312	Pen	Wild boar	57.5	25 F	6.81341719077568	6.96161353285621	2.59433962264151	773.5184	3000	
H313	Pen	Wild boar	65.5	25 F	5.5256064690027	4.80682839173405	2.49722530521643	758.2220	3000	
H314	Pen	Wild boar	71.5	25 F	3.39622641509434	8.04661487236404	1.2909632571996	819.4100	3000	
H317	Pen	Wild boar	67	25 F	5.70754716981132	6.00343053173242	4.16061925495888	794.7564	3000	
H321	Pen	Wild boar	90.5	25 F	6.85203574975174	7.10691823899371	1.9364448857994	775.2456	3000	
H331	Pen	Wild boar	86.5	25 M	7.14995034756703	8.57632933104631	4.63611859838275	854.1342	3000	
H332	Pen	Wild boar	141	25 M	8.95222802087515	8.05031446540881	3.55795148247978	872.3359	3000	
BDB-826.9-2001.106	Free ranging	Wild boar	137	168 M	NA	NA	NA	1003.401	10000	
BDB-826.9-2001.111	Free ranging	Wild boar	120	216 M	NA	NA	NA	938.7275	10000	
BDB-826.9-2001.60	Free ranging	Wild boar	50 14.4	162 F	NA	NA	NA	984.2907	10000	
BDB-826.9-2001.95	Free ranging	Wild boar	85 33.6	F	NA	NA	NA	774.7734	10000	
BDB-826.9-2001.97	Free ranging	Wild boar	92	M	NA	NA	NA	887.7248	10000	
DAR-826.9-2001.105	Free ranging	Wild boar	92	18 M	NA	NA	NA	962.9402	2250000	

Supplementary Information 2.1

DAR-826.9-2001.33	Free ranging	Wild boar	128	60 F	NA	NA	NA	914.0804	2250000
SJA-826.9-2001.14	Free ranging	Wild boar	60	24 F	NA	NA	NA	834.8443	10000000
SJA-826.9-2001.15	Free ranging	Wild boar	75	54 F	NA	NA	NA	885.7540	10000000
SJA-826.9-2001.28	Free ranging	Wild boar	70	20.4 M	NA	NA	NA	858.7704	10000000
SJA-826.9-2001.32	Free ranging	Wild boar	96	33.6 M	NA	NA	NA	868.1373	10000000
SJA-826.9-2001.44	Free ranging	Wild boar	60	18 M	NA	NA	NA	840.7813	10000000
SJA-826.9-2001.53	Free ranging	Wild boar	83.2	28.8 M	NA	NA	NA	848.0310	10000000
CO-2013-1264-G	Free ranging	Wild boar	60.8	12 F	NA	NA	NA	803.0009	150000000
CO-2013-1265-G	Free ranging	Wild boar	120	21 M	NA	NA	NA	969.0790	150000000
CO-2013-1270-D	Free ranging	Wild boar	86	17 M	NA	NA	NA	910.0914	150000000
CO-2013-1285-G	Free ranging	Wild boar	61.2	17.5 F	NA	NA	NA	749.0919	150000000
CH-383-D	Free ranging	Wild boar	78.976	17.5 M	NA	NA	NA	750.1994	54400000
CH-418-D	Free ranging	Wild boar	35.328	17 M	2.60247234873129	4.00943396226415	1.54986522911051	697.7746	54400000
CH-429-D	Free ranging	Wild boar	54.912	20 F	NA	NA	NA	730.4641	54400000
CH-508-D	Free ranging	Wild boar	31.744	18 F	NA	NA	NA	714.1338	54400000
CH-515-D	Free ranging	Wild boar	68.48	F	NA	NA	NA	770.3001	54400000
CH-660-D	Free ranging	Wild boar	49.792	19 F	NA	4.75192173305381	2.43457090687766	737.7593	54400000
S erp wid 262	MHK Stall	Wild boar	NA	185 M	NA	NA	NA	1013.244	50
S erp wid 268	MHK Stall	Wild boar	NA	118 M	NA	NA	NA	1009.186	50
S bay lds 1	MHK Stall	Traditional pig	NA	13 F	NA	NA	NA	988.4910	50
S bay lds 2	MHK Stall	Traditional pig	NA	33 F	NA	NA	NA	958.3690	50
S bay lds 3	MHK Stall	Traditional pig	NA	33 M	NA	NA	NA	1034.800	50
S bay lds 4	MHK Stall	Traditional pig	NA	33 M	NA	NA	NA	1121.925	50
S bay lds 6	MHK Stall	Traditional pig	NA	18 F	NA	NA	NA	780.1943	50
S hv br 5	MHK Stall	Traditional pig	NA	23 M (castrat)	NA	NA	NA	1002.134	50
S hv br 6	MHK Stall	Traditional pig	NA	22 F	NA	NA	NA	859.8969	50
S hv br 9	MHK Stall	Traditional pig	NA	51 F	NA	NA	NA	910.8904	50
S lcn 1	MHK Stall	Traditional pig	NA	24 M	NA	NA	NA	1112.526	50
S tmw 9	MHK Stall	Traditional pig	NA	112 F	NA	NA	NA	956.7395	50
S tmw 10	MHK Stall	Traditional pig	NA	36 F	NA	NA	NA	1049.260	50
DOM-COR-14396	Free ranging	Traditional pig	NA	13 NA	NA	NA	NA	855.8134	2000000
DOM-COR-14397	Free ranging	Traditional pig	NA	13 NA	NA	NA	NA	890.2894	2000000
DOM-COR-14398	Free ranging	Traditional pig	NA	13 NA	NA	NA	NA	894.8631	2000000
DOM-COR-14399	Free ranging	Traditional pig	NA	13 NA	NA	NA	NA	887.2618	2000000
DOM-COR-14400	Free ranging	Traditional pig	NA	13 NA	NA	NA	NA	955.1212	2000000
S bks 6	MHK Stall	Improved pig	NA	33 M (castrat)	NA	NA	NA	857.7658	50

Supplementary Information 2.1

S bks 9	MHK Stall	Improved pig	NA	32 F	NA	NA	847.6614	50
S bks 10	MHK Stall	Improved pig	NA	49 F	NA	NA	859.9891	50
S bks 71	MHK Stall	Improved pig	NA	61 M	NA	NA	931.2417	50
S dt eds 41	MHK Stall	Improved pig	NA	F	NA	14.7	1089.397	50
S dt eds 100	MHK Stall	Improved pig	NA	87 M	NA	NA	1151.508	50
S vd lds 33	MHK Stall	Improved pig	NA	43 F	NA	NA	1011.245	50
S vd lds 82	MHK Stall	Improved pig	NA	42 M	NA	NA	1069.328	50

Supplementary Information 2.2

procD.lm(f1 = shape ~ genotype * sex, iter = 999, RRPP = T, SS.type = "II")

	Df	SS	MS	Rsq	F	Z	Pr(>F)	
genotype	1	38042	38042	0.191436	17.0393	7.2914	0.001	**
sex	1	3827	3827	0.019256	1.7140	2.5133	0.012	*
genotype:sex	1	2819	2819	0.014185	1.2626	1.5090	0.071	.
Residuals	69	154048	2233					
Total	72	198717						

Signif. codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Supplementary Information 4.1

Collection	Collection_ID	Project_ID	Sex	Age (M/Mass (kg)	Population / Site	Breed	Status	Available areHumerus volume (tHumerus cross	Calculus centroid size
LHT	H282	OL5_282	M	20 80.5	Experimental enclosur	Wild boar	Captive	3000 174.476	568.8 NA
LHT	H282	OL6_282	M	25	84 Experimental enclosur	Wild boar	Captive	3000 NA	897.02036456337
LHT	H283	OL4_283	F	14	43 Experimental enclosur	Wild boar	Captive	3000 98.176	356.7 NA
LHT	H283	OL6_283	F	25 66.5	Experimental enclosur	Wild boar	Captive	3000 NA	783.216868175077
LHT	H287_H293	OL4_293	M	14 44.5	Experimental enclosur	Wild boar	Captive	3000 108.507	417.2 NA
LHT	H287_H293	OL6_293	M	25	67 Experimental enclosur	Wild boar	Captive	3000 NA	809.397385463298
LHT	H289	OL6_289	M	25	90 Experimental enclosur	Wild boar	Captive	3000 179.3	862.832866598372
LHT	H312	OL6_312	F	25 57.5	Experimental enclosur	Wild boar	Captive	3000 130.945	773.518420233302
LHT	H313	OL6_313	F	25 65.5	Experimental enclosur	Wild boar	Captive	3000 138.285	758.22202890719
LHT	H314	OL5_314	F	20	81 Experimental enclosur	Wild boar	Captive	3000 147.86	487.1 NA
LHT	H314	OL6_314	F	25	77 Experimental enclosur	Wild boar	Captive	3000 NA	819.410051285105
LHT	H317	OL4_317	F	14 50.5	Experimental enclosur	Wild boar	Captive	3000 127.94	467.9 NA
LHT	H317	OL6_317	F	25 71.5	Experimental enclosur	Wild boar	Captive	3000 NA	794.756490820523
LHT	H321	OL5_321	F	20	67 Experimental enclosur	Wild boar	Captive	3000 127.195	476.1 NA
LHT	H321	OL6_321	F	25	67 Experimental enclosur	Wild boar	Captive	3000 NA	775.245634036753
LHT	H331	OL4_331	M	14	73 Experimental enclosur	Wild boar	Captive	3000 148.975	513.8 NA
LHT	H331	OL6_331	M	25 90.5	Experimental enclosur	Wild boar	Captive	3000 NA	854.134215530968
LHT	H332	OL5_332	M	20 73.5	Experimental enclosur	Wild boar	Captive	3000 170.108	544.5 NA
LHT	H332	OL6_332	M	25 86.5	Experimental enclosur	Wild boar	Captive	3000 NA	872.33598247299
LHT	H333_H292	OL6_292	M	25 91.5	Experimental enclosur	Wild boar	Captive	3000 194.574	868.006300178078
LHT	H279	OL6_279	F	25 92.5	Experimental stabulati	Wild boar	Captive	50 149.603	797.525355558987
LHT	H285	OL5_285	M	20	59 Experimental stabulati	Wild boar	Captive	50 140.49	503.4 NA
LHT	H285	OL6_285	M	25	72 Experimental stabulati	Wild boar	Captive	50 NA	858.096033214266
LHT	H286_H291	OL4_291	M	14	50 Experimental stabulati	Wild boar	Captive	50 133.488	857.409543544501
LHT	H286_H291	OL6_291	M	25	73 Experimental stabulati	Wild boar	Captive	50 NA	857.409543544501
LHT	H288	OL4_288	M	14 56.5	Experimental stabulati	Wild boar	Captive	50 152.732	911.590617232135
LHT	H288	OL6_288	M	25	89 Experimental stabulati	Wild boar	Captive	50 NA	911.590617232135
LHT	H315	OL5_315	F	20	77 Experimental stabulati	Wild boar	Captive	50 128.91	454.2 NA
LHT	H315	OL6_315	F	25	89 Experimental stabulati	Wild boar	Captive	50 NA	815.648443429481
LHT	H316	OL5_316	F	20	59 Experimental stabulati	Wild boar	Captive	50 124.299	458.1 NA
LHT	H316	OL6_316	F	25 53.5	Experimental stabulati	Wild boar	Captive	50 NA	767.423502786301
LHT	H318	OL4_318	F	14	45 Experimental stabulati	Wild boar	Captive	50 107.22	416.3 NA
LHT	H318	OL6_318	F	25 61.5	Experimental stabulati	Wild boar	Captive	50 NA	781.600391330624
LHT	H319	OL6_319	F	25	111 Experimental stabulati	Wild boar	Captive	50 154.306	843.43293138985
LHT	H320	OL4_320	F	14	54 Experimental stabulati	Wild boar	Captive	50 102.229	418.6 NA
LHT	H320	OL6_320	F	25	91 Experimental stabulati	Wild boar	Captive	50 NA	773.365522304813
LHT	H330	OL6_330	M	25 77.5	Experimental stabulati	Wild boar	Captive	50 174.31	897.282051850573
LHT	H334	OL5_334	M	20 95.5	Experimental stabulati	Wild boar	Captive	50 199.376	551.3 NA
LHT	H334	OL6_334	M	25	96 Experimental stabulati	Wild boar	Captive	50 NA	597.1 NA
LHT	H335	OL6_335	M	25	84 Experimental stabulati	Wild boar	Captive	50 181.526	885.463400701432
MHK	S erp wld 262	S erp wld 262	M	185 NA	MHK Stabulation	Wild boar	Captive	50 NA	1013.24498372024

Supplementary Information 4.1

MHK	S erp wld 288	S erp wld 268	M	118 NA	MHK Stabulation	Wild boar	Captive	50 NA	NA	1009.18658837645
MNHN	Pradat-172	PRA172	F	23	23 Urcier Experimental cc	Wild boar	Free	100000 55.27	238.1	854.134215530968
MNHN	Pradat-173	PRA173	M	5	15 Urcier Experimental cc	Wild boar	Free	100000 28.337	156.3	872.33598247299
MNHN	Pradat-174	PRA174	F	7	28 Urcier Experimental cc	Wild boar	Free	100000 70.854	289.7	681.685703432093
MNHN	Pradat-175	PRA175	M	20	53 Urcier Experimental cc	Wild boar	Free	100000 106.648	402.1	817.666025174236
MNHN	Pradat-185	PRA185	M	20	52 Urcier Experimental cc	Wild boar	Free	100001 NA	NA	813.856543261603
MNHN	Pradat-186	PRA186	M	8	30 Urcier Experimental cc	Wild boar	Free	100002 70.879	290.5	NA
MNHN	Pradat-187	PRA187	F	84	110 Urcier Experimental cc	Wild boar	Free	100003 NA	NA	905.28209196532
MNHN	Pradat-188	PRA188	F	96	60 Urcier Experimental cc	Wild boar	Free	100004 NA	NA	809.320067854789
MNHN	CH-129	CH129	F	4.5	13.952 Chambord	Wild boar	Free	54400000 36.349	178.6	NA
MNHN	CH-132	CH132	NA	9 NA	Chambord	Wild boar	Free	54400000 66.42	257.9	NA
MNHN	CH-138	CH138	F	9 NA	Chambord	Wild boar	Free	54400000 61.166	278.1	NA
MNHN	CH-150	CH150	M	10	16.768 Chambord	Wild boar	Free	54400000 67.456	310.6	NA
MNHN	CH-151	CH151	M	5 NA	Chambord	Wild boar	Free	54400000 42.564	209.0	NA
MNHN	CH-77	CH77	F	7	20.864 Chambord	Wild boar	Free	54400000 53.449	250.1	NA
MNHN	CH-81-VF	CH81VF	F	NA	117.76 Chambord	Wild boar	Free	54400000 123.398	395.6	NA
MNHN	CH-84	CH84	M	6.5	17.92 Chambord	Wild boar	Free	54400000 37.077	199.7	NA
MNHN	CH-383-D	CH383	M	17.5	78.976 Chambord	Wild boar	Free	54400000 118.365	417.5	750.199493726821
MNHN	CH-418-D	CH418	M	17	35.328 Chambord	Wild boar	Free	54400000 85.795	320.9	697.774671235194
MNHN	CH-429-D	CH429	F	20	54.912 Chambord	Wild boar	Free	54400000 106.567	393.5	730.46413997866
MNHN	CH-508-D	CH508	F	18	31.744 Chambord	Wild boar	Free	54400000 77.737	288.8	714.133887534015
MNHN	CH-515-D	CH515	F	18.5	68.48 Chambord	Wild boar	Free	54400000 108.265	354.0	770.300199750966
MNHN	CH-660-D	CH660	F	19	49.792 Chambord	Wild boar	Free	54400000 88.771	316.9	737.759343323334
MNHN	2013-1264-G	CO1264	F	9	60.8 Compiegne	Wild boar	Free	150000000 137.709	496.7	NA
MNHN	2013-1265-G	CO1265	M	25	120 Compiegne	Wild boar	Free	150000000 244.607	610.3	NA
MNHN	2013-1270-D	CO1270	M	17	86 Compiegne	Wild boar	Free	150000000 201.447	642.3	NA
MNHN	2013_1273_G	CO1273	M	36 NA	Compiegne	Wild boar	Free	150000000 197.11	655.8	NA
MNHN	CO-2013-1285-G	CO1285	F	17.5	61.2 Compiegne	Wild boar	Free	150000001 NA	NA	749.091919040815
MHNG	BDB-826.9-2001.1	BDB106	M	168	141 Bois-de-la-Bâtie	Wild boar	Free	10000 NA	NA	1003.40112573879
MHNG	BDB-826.9-2001.1	BDB111	M	216	137 Bois-de-la-Bâtie	Wild boar	Free	10000 NA	NA	938.72752652415
MHNG	BDB-826.9-2001.1	BDB60	F	162	120 Bois-de-la-Bâtie	Wild boar	Free	10000 NA	NA	984.290767754356
MHNG	BDB-826.9-2001.1	BDB95	F	14.4	50 Bois-de-la-Bâtie	Wild boar	Free	10000 NA	NA	774.773440223467
MHNG	BDB-826.9-2001.1	BDB97	M	33.6	85 Bois-de-la-Bâtie	Wild boar	Free	10000 NA	NA	887.724842991741
MHNG	DAR-826.9-2001.1	DAR105	M	18	92 Dardagny	Wild boar	Free	2250000 NA	NA	962.940232976435
MHNG	DAR-826.9-2001.1	DAR33	F	60	128 Dardagny	Wild boar	Free	2250000 NA	NA	914.080434567044
MHNG	SJA-826.9-2001.1	SJA14	F	24	60 Saint-Jean-d'Aulps	Wild boar	Free	1000000 NA	NA	834.844366146574
MHNG	SJA-826.9-2001.1	SJA15	F	54	75 Saint-Jean-d'Aulps	Wild boar	Free	10000000 NA	NA	885.754080378808
MHNG	SJA-826.9-2001.1	SJA28	M	20.4	70 Saint-Jean-d'Aulps	Wild boar	Free	10000000 NA	NA	858.770484991629
MHNG	SJA-826.9-2001.1	SJA32	M	33.6	96 Saint-Jean-d'Aulps	Wild boar	Free	10000000 NA	NA	868.137369089935
MHNG	SJA-826.9-2001.1	SJA44	M	18	60 Saint-Jean-d'Aulps	Wild boar	Free	10000000 NA	NA	840.781320045584
MHNG	SJA-826.9-2001.1	SJA53	M	28.8	83.2 Saint-Jean-d'Aulps	Wild boar	Free	10000000 NA	NA	848.031071326749
MHNG	S erp wld 13	erpwld13	M	43.7 NA	Captive hybrid	Hybrid	Captive	50 255.025	795.2	1045.61016983315

Supplementary Information 4.1

HKM	S	erp wld 15	erpwld15	M	122 NA	Captive hybrid	Hybrid	Captive	50 273.717	842.1	1033.12224976308
HKM	S	erp wld 16	erpwld16	F	122 NA	Captive hybrid	Hybrid	Captive	50 191.513	621.4	957.6906444430423
HKM	S	erp wld 16	erpwld25	F	36 NA	Captive hybrid	Hybrid	Captive	51 185.806	589.7	NA
HKM	S	erp wld 113	erpwld113	F	61 NA	Captive hybrid	Hybrid	Captive	50 NA	NA	939.817988046449
MNHN	1850-435-D		mnhn435	NA	NA	Captive pig	Intensive pig bree	Captive	135.45	511.3	NA
HKM	S	bks 1	bks1	F	NA	Captive pig	Intensive pig bree	Captive	50 234.243	860.7	NA
HKM	S	bks 6	bks6	M (cas	33 NA	Captive pig	Intensive pig bree	Captive	50 179.337	853.6	857.765887441064
HKM	S	bks 8	bks8	M	18 NA	Captive pig	Intensive pig bree	Captive	50 236.32	772.3	NA
HKM	S	bks 9	bks9	F	32 NA	Captive pig	Intensive pig bree	Captive	50 NA	NA	847.661412423178
HKM	S	bks 10	bks10	F	49 NA	Captive pig	Intensive pig bree	Captive	50 NA	NA	859.989143709163
HKM	S	bks 71	bks71	M	61 NA	Captive pig	Intensive pig bree	Captive	50 292.426	1163.6	931.241745770616
HKM	S	dt eds 41	dt eds 41	F	14.7 NA	Captive pig	Intensive pig bree	Captive	50 NA	NA	1089.39751855554
HKM	S	dt eds 100	dt eds 100	M	87 NA	Captive pig	Intensive pig bree	Captive	50 NA	NA	1151.5080175743
HKM	S	vd lds 33	vd lds 33	F	43 NA	Captive pig	Intensive pig bree	Captive	50 NA	NA	1011.24502740644
HKM	S	vd lds 82	vd lds 82	M	42 NA	Captive pig	Intensive pig bree	Captive	50 NA	NA	1069.32889158806
HKM	S	bay lds 1	baylds1	F	13 NA	Captive pig	Traditional pig b	Captive	50 266.172	767.9	988.491062267287
HKM	S	bay lds 2	baylds2	F	33 NA	Captive pig	Traditional pig b	Captive	50 263.142	870.2	958.369035025498
HKM	S	bay lds 3	baylds3	M	33 NA	Captive pig	Traditional pig b	Captive	50 339.922	1063.1	1034.80079804978
HKM	S	bay lds 4	baylds4	M	33 NA	Captive pig	Traditional pig b	Captive	50 NA	NA	1121.9257493846
HKM	S	bay lds 5	baylds5	F	11.2 NA	Captive pig	Traditional pig b	Captive	50 153.35	585.2	NA
HKM	S	bay lds 6	baylds6	F	18 NA	Captive pig	Traditional pig b	Captive	50 97.792	368.3	780.194344725674
HKM	S	hv br 3	hvbr3	M	5.1 NA	Captive pig	Traditional pig b	Captive	50 116.342	437.6	NA
HKM	S	hv br 4	hvbr4	M	5.1 NA	Captive pig	Traditional pig b	Captive	50 52.456	234.1	NA
HKM	S	hv br 5	hvbr5	M (cas	23 NA	Captive pig	Traditional pig b	Captive	50 311.84	841.7	1002.13489278359
HKM	S	hv br 6	hvbr6	F	22 NA	Captive pig	Traditional pig b	Captive	50 190.869	514.4	859.896986552679
HKM	S	hv br 9	hvbr9	F	51 NA	Captive pig	Traditional pig b	Captive	50 238.412	661.5	910.89045026456
HKM	S	ma 18	ma18	M	NA	Captive pig	Traditional pig b	Captive	50 259.05	920.2	NA
HKM	S	pol 2	pol2	F	NA	Captive pig	Traditional pig b	Captive	50 220.189	782.1	NA
HKM	S	lcn 1	lcn 1	M	24 NA	Captive pig	Traditional pig b	Captive	50 NA	NA	1112.526483544486
HKM	S	tmw 9	tmw 9	F	112 NA	Captive pig	Traditional pig b	Captive	50 NA	NA	956.739508447872
HKM	S	tmw 10	tmw 10	F	36 NA	Captive pig	Traditional pig b	Captive	50 NA	NA	1049.26048634739
MNHN	DOM-COR-1439€	COR14396		NA	13 NA	Corsica	Traditional pig b	Free	2000000 184.422	683.5	855.813424069959
MNHN	DOM-COR-1439€	COR14397		NA	13 NA	Corsica	Traditional pig b	Free	2000000 230.943	694.6	890.289411916067
MNHN	DOM-COR-1439€	COR14398		NA	13 NA	Corsica	Traditional pig b	Free	2000000 230.541	829.8	894.863132470503
MNHN	DOM-COR-1439€	COR14399		NA	13 NA	Corsica	Traditional pig b	Free	2000000 194.828	669.1	887.261867537904
MNHN	DOM-COR-1440€	COR14400		NA	13 NA	Corsica	Traditional pig b	Free	2000000 312.584	878.1	955.121203150135
Strasbourg	ARC-15402	ARC-15402		NA	NA	Arconciel	Mesolithic wild bo	Free	NA	NA	1034.70579981294
Strasbourg	ARC-21723	ARC-21723		NA	NA	Arconciel	Mesolithic wild bo	Free	NA	NA	996.341690262767
Strasbourg	ARC-29712	ARC-29712		NA	NA	Arconciel	Mesolithic wild bo	Free	NA	NA	1027.79455430363
MNHN	GAZ-CAL-EB-3b-	GAZ-EB-831		NA	NA	Gazel	Mesolithic wild bo	Free	NA	NA	883.198700219892
MNHN	Ens2-XVI-3133-2-	NO-2-3133		NA	NA	Noyen 2	Mesolithic wild bo	Free	NA	NA	945.817599926108
MNHN	Ens2-XVI-B144-8-	NO-2-B144		NA	NA	Noyen 2	Mesolithic wild bo	Free	NA	NA	911.188784102377

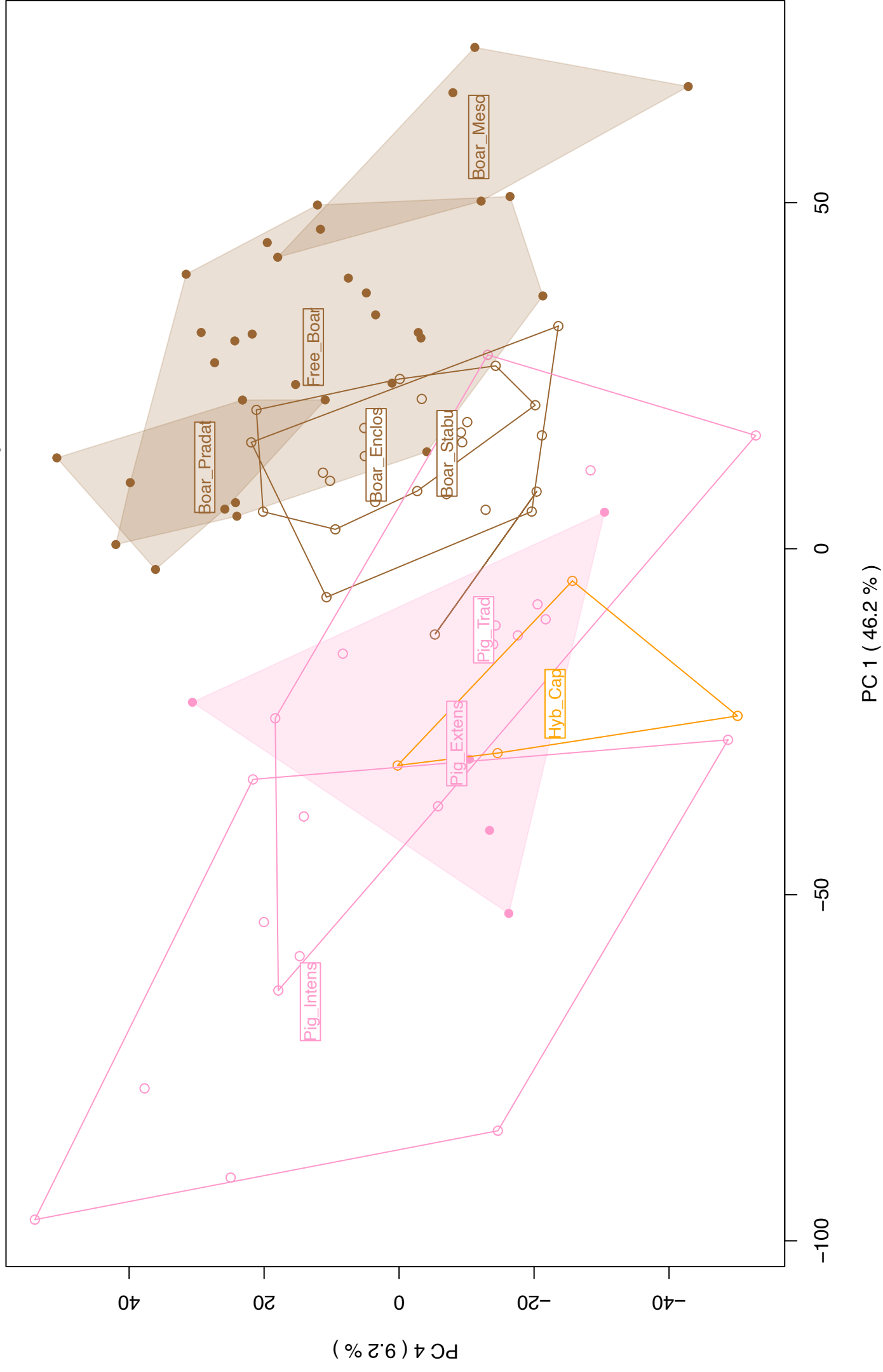
Supplementary Information 4.1

MNHN	Ens2-XVI-E137-1;NO-2-E137	NA	NA	Noyen 2	Mesolithic wild boFree	NA	NA	989.029524814106
MNHN	Ens2-XVI-L132-GNO-2-L132	NA	NA	Noyen 2	Mesolithic wild boFree	NA	NA	963.025043840474
MNHN	Ens3-XVI-G235-2NO-3-G235-25-;NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	NA	892.035616559767
MNHN	Ens3-XVI-Q214-7NO-3-Q214	NA	NA	Noyen 3	Mesolithic wild boFree	NA	NA	1004.61007025362
MNHN	Ens3-XVI-G235-2NOY-3_G235_2NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	659.0	NA
MNHN	Ens3-XVI-G235-2NOY-3_G235_2NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	516.4	NA
MNHN	Ens3-XVI-H234-;NOY-3_H234	NA	NA	Noyen 3	Mesolithic wild boFree	NA	680.0	NA
MNHN	Ens3-XVI-H236-;NOY-3_H236	NA	NA	Noyen 3	Mesolithic wild boFree	NA	575.9	NA
MNHN	Ens3-XVI-L232-2NOY-3_L232	NA	NA	Noyen 3	Mesolithic wild boFree	NA	526.6	NA
MNHN	Ens3-XVI-N212-;NOY-3_N212_2NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	925.6	NA
MNHN	Ens3-XVI-N212-;NOY-3_N212_2NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	734.4	NA
MNHN	Ens3-XVI-Q211-;NOY-3_Q211	NA	NA	Noyen 3	Mesolithic wild boFree	NA	551.4	NA
MNHN	Ens3-XVI-Q216-;NOY-3_Q216	NA	NA	Noyen 3	Mesolithic wild boFree	NA	749.2	NA
MNHN	Ens3-XVI-R217-;NOY-3_R217	NA	NA	Noyen 3	Mesolithic wild boFree	NA	582.5	NA
MNHN	XV-Fd12-U-72-83NOY-3_XV_Fd1NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	432.5	NA
MNHN	XV-Fd8-L134 NOY-3_XV_Fd8NA	NA	NA	Noyen 3	Mesolithic wild boFree	NA	400.4	NA
Nanterre	RAN-C9-37 RAN_C9_37	NA	NA	Ranchot	Mesolithic wild boFree	NA	411.2	NA
Nanterre	RAN-A10-674 RAN-A10-674	NA	NA	Ranchot Cabônes	Mesolithic wild boFree	NA	NA	1038.58218068971
Nanterre	RAN-C10-484 RAN-C10-484	NA	NA	Ranchot Cabônes	Mesolithic wild boFree	NA	NA	924.001843756267
Nanterre	RAN-D7-263 RAN-D7-263	NA	NA	Ranchot Cabônes	Mesolithic wild boFree	NA	NA	959.419618847095
Nanterre	RAN-Z10-661 RAN-Z10-661	NA	NA	Ranchot Cabônes	Mesolithic wild boFree	NA	NA	1009.20772331107
MNHN	THE-297 THE-297	NA	NA	Thevies	Mesolithic wild boFree	NA	NA	932.127895102238
MNHN	AIG-CAL-939 AIG-939	NA	NA	Aigle	NA	NA	NA	922.564006529377
MNHN	AIG-CAL-D6-C5 AIG-D6-C5	NA	NA	Aigle	NA	NA	NA	762.513072251
MNHN	AIG-CAL-F5-C5 AIG-F5-C5	NA	NA	Aigle	NA	NA	NA	761.430505275957
MNHN	BER-QS-NO-ID-3BER_NOID_3	NA	NA	Bercy	NA	265.3	NA	NA
MNHN	QS-LXIX-20-c215BER-20-C21	NA	NA	Bercy	NA	NA	NA	1060.47816583411
MNHN	CAM-C17-1 CAM_C171	NA	NA	Camprafaud	NA	NA	NA	NA
MNHN	CAM-CAL-C13-1 CAM-C13-1	NA	NA	Camprafaud	NA	357.4	NA	1050.55481150745
MNHN	CAM-C19-R CAM-C19-R	NA	NA	Camprafaud	NA	NA	NA	1016.23090154271
Lons-Le-Saun	CHA-19HK-CE10-CHA-19_CE105NA	NA	NA	Chalain 19	NA	263.5	NA	NA
Lons-Le-Saun	CHA-19HK-CK10-CHA-19_CK108NA	NA	NA	Chalain 19	NA	248.0	NA	NA
Lons-Le-Saun	CHA-19HK-CP10-CHA-19_CP101NA	NA	NA	Chalain 19	NA	207.6	NA	NA
Lons-Le-Saun	CHA-19HK-CQ12-CHA-19_CQ122NA	NA	NA	Chalain 19	NA	387.7	NA	NA
Lons-Le-Saun	CHA-19HK-CT12-CHA-19_CT122NA	NA	NA	Chalain 19	NA	342.3	NA	NA
Lons-Le-Saun	CHA-19-BU114HICHA-19-BU114INA	NA	NA	Chalain 19	NA	NA	NA	940.858273261553
Lons-Le-Saun	CHA-19-BU117HICHA-19-BU117INA	NA	NA	Chalain 19	NA	NA	NA	1004.91223603093
Lons-Le-Saun	CHA-19-BY118HICHA-19-BY118INA	NA	NA	Chalain 19	NA	NA	NA	1018.4945289964
Lons-Le-Saun	CHA-19-BZ117HICHA-19-BZ117INA	NA	NA	Chalain 19	NA	NA	NA	991.742683665368
Lons-Le-Saun	CHA-19-BZ118HICHA-19-BZ118INA	NA	NA	Chalain 19	NA	NA	NA	1006.51328175806
Lons-Le-Saun	CHA-19-BZ125HICHA-19-BZ125INA	NA	NA	Chalain 19	NA	NA	NA	1047.20525080633
Lons-Le-Saun	CHA-19-CD101K CHA-19-CD101INA	NA	NA	Chalain 19	NA	NA	NA	975.524128767358

Supplementary Information 4.1

Lons-Le-SaunCHA-19-CD101KI	CHA-19-CD101INA	NA	Chalain 19	NA	NA	NA	NA	NA	896.443344937837
Lons-Le-SaunCHA-19-CD105H	CHA-19-CD105INA	NA	Chalain 19	NA	NA	NA	NA	NA	1023.83935958498
Lons-Le-SaunCHA-19-CE103K	CHA-19-CE103INA	NA	Chalain 19	NA	NA	NA	NA	NA	1032.13468745871
Lons-Le-SaunCHA-19-CF104K	CHA-19-CF104INA	NA	Chalain 19	NA	NA	NA	NA	NA	1059.13925982892
Lons-Le-SaunCHA-19-CF105K	CHA-19-CF105INA	NA	Chalain 19	NA	NA	NA	NA	NA	775.58889282073
Lons-Le-SaunCHA-19-CJ102K	CHA-19-CJ102INA	NA	Chalain 19	NA	NA	NA	NA	NA	962.329718857862
Lons-Le-SaunCHA-19-CK101K	CHA-19-CK101INA	NA	Chalain 19	NA	NA	NA	NA	NA	1062.14764365678
Lons-Le-SaunCHA-19-DB123H	CHA-19-DB123INA	NA	Chalain 19	NA	NA	NA	NA	NA	783.757890258986
Lons-Le-SaunCHA-11c-Fc80-I1c	CHA-3I1c_Fc80	NA	Chalain 3I1c	NA	NA	NA	NA	NA	816.154145112985
Lons-Le-SaunCHA-4-BF68F	CHA-4_BF68F	NA	Chalain 4	NA	NA	NA	NA	752.8	NA
Lons-Le-SaunCHA-4-CF63F	CHA-4_CF63F	NA	Chalain 4	NA	NA	NA	NA	351.4	NA
Lons-Le-SaunCHA-4-DF63F	CHA-4_DF63F	NA	Chalain 4	NA	NA	NA	NA	627.1	NA
Lons-Le-SaunCHA-4-AF59F	CHA-4_AF59F	NA	Chalain 4	NA	NA	NA	NA	300.9	NA
Lons-Le-SaunCHA-4-BF63F	CHA-4_BF63F	NA	Chalain 4	NA	NA	NA	NA	NA	1031.39735323558
Lons-Le-SaunCHA-4-DF66F	CHA-4_DF66F	NA	Chalain 4	NA	NA	NA	NA	NA	1020.14934202234
Lons-Le-SaunCHA-4-EF60F	CHA-4_EF60F	NA	Chalain 4	NA	NA	NA	NA	NA	942.475788746202
Lons-Le-SaunCHA-4-EF70F	CHA-4_EF70F	NA	Chalain 4	NA	NA	NA	NA	NA	1040.29755473018
Lons-Le-SaunCHA-4-HF65F	CHA-4_HF65F	NA	Chalain 4	NA	NA	NA	NA	NA	1084.90992279601
Lons-Le-SaunCHA-4-PF59F	CHA-4-PF59F	NA	Chalain 4	NA	NA	NA	NA	NA	1046.50300855197
Lons-Le-SaunCHA-4-TF65F	CHA-4-TF65F	NA	Chalain 4	NA	NA	NA	NA	NA	1041.2940786819
Lons-Le-SaunCHA-4-YE61F	CHA-4-YE61F	NA	Chalain 4	NA	NA	NA	NA	NA	968.472439880112
Quinson	FON-638	NA	Fontbregoua	NA	NA	NA	NA	370.1	NA
Quinson	FON-321-L13-40	NA	Fontbregoua	NA	NA	NA	NA	NA	739.400144250805
Quinson	FON-930-P3-19-C	NA	Fontbregoua	NA	NA	NA	NA	NA	768.091769711829
MNHN	GAZ-HUM-SCN-2GAZ_2a4	NA	Gazel	NA	NA	NA	NA	166.2	NA
MNHN	GAZ-HUM-SCN-2GAZ_2b25	NA	Gazel	NA	NA	NA	NA	406.0	NA
MNHN	GAZ-HUM-SCN-2GAZ_2b3	NA	Gazel	NA	NA	NA	NA	376.1	NA
MNHN	GAZ-HUM-SCN-2GAZ_2b58	NA	Gazel	NA	NA	NA	NA	363.4	NA
MNHN	GAZ-HUM-SCN-2GAZ_2b8	NA	Gazel	NA	NA	NA	NA	385.4	NA
MNHN	GAZ-HUM-SCN-2GAZ_2c108	NA	Gazel	NA	NA	NA	NA	379.3	NA
MNHN	GAZ-CAL-EB-3a- GAZ-EB-1231	NA	Gazel	NA	NA	NA	NA	NA	1032.19379566021
MNHN	GAZ-CAL-SCS-2cGAZ-SCS-17	NA	Gazel	NA	NA	NA	NA	NA	830.95798662705
Cyprus	US-6039-KL15-KIKLIM-1	NA	Klimonas	NA	NA	NA	NA	NA	821.857773207891
Cyprus	US-10.3E38-KL11KILIM-5	NA	Klimonas	NA	NA	NA	NA	NA	962.653532021023
MNHN	106-S-92	NOY_106S92	Noyen Neolithic	NA	NA	NA	NA	600.5	NA
MNHN	XV-Fd15-Q108-3	NO-NEO-Q108	Noyen Neolithic	NA	NA	NA	NA	NA	820.302748928421
NA	ROQ-18-5338	ROQ-18-5338	Roquemissou	NA	NA	NA	NA	NA	925.337020175888
MNHN	ROU-F18a-C2b	ROU-F18a	Roucadour	NA	NA	NA	NA	NA	1012.45870702983
MNHN	ROU-I15a-C2a	ROU-I15a	Roucadour	NA	NA	NA	NA	NA	1010.71633938469
MNHN	ROU-J18b-C2b	ROU-J18b	Roucadour	NA	NA	NA	NA	NA	990.068792144871
Cyprus	SHILL-1-sect3-USSH1-1	SHILL-1-sect3-USSH1-1	Shillourouambos	NA	NA	NA	NA	NA	842.187575080827

Supplementary Information 4.2 BG-PCA on calcaneus shape



ÉVALUATIONS DES RAPPORTEURS ET
CORRECTIONS



MNHN Paris
soutenance-these@mnhn.fr
fassa@mnhn.fr
cc thomas.cucchi@mnhn.fr

Prof. Dr. Marcelo R. Sánchez-Villagra
Institute Director
Research Group Leader
Telefon +41 44 634 23 42
Telefax +41 44 634 49 23
m.sanchez@pim.uzh.ch

Zurich, 11. December 2020

Re: Evaluation of the PhD Thesis by Hugo Harbers entitled "*Identification des marqueurs morphofonctionnels du processus de domestication en archéozoologie: approche tridimensionnelle de la variation endostructurale de la diaphyse humérale et de la forme du calcaneus*"

Experimental studies of animal domestication have been mostly about intense selective breeding for a trait and the consequences – as in the celebrated silver fox experiment in Siberia or the tracing of changes in egg production in some breeding lines of chicken. What has been missing are experiments that evaluate the effects of anthropogenic environments in conditions that resemble the first phases of domestication. This kind of work would be particularly important for zooarchaeology, which uses largely morphological markers to study the domestication process. Much of the attention on studies of domestication these days are on genomics - fine morphological studies are then relevant to bring that area of investigation also to the next level of testing and exploration. The doctoral thesis of Hugo Harbers attempts that and succeeds. It does so with detailed studies of pigs and critical discussions on the subject.

Hugo Harbers thesis consists of five chapters, including two of three core ones that have already been published in peer-reviewed Journals. As such, most of the core of this thesis has passed the scrutiny of evaluation by scientists in the field and editorial boards. Of the three papers presented in this thesis, Mr. Harbers is first author of all of them. I find the illustrations across this thesis clear and nicely done and the whole presentation professionally done.



The Introductory chapter contains an overview of basic concepts on evolution, but most importantly on developmental plasticity. This provides the proper framework to situate the aspects of the domestication process that the thesis discusses. This includes a critical assessment of the (rapidly moving subject of) domestication syndrome, the pathways to domestication, and the definition of domestication to start with. These are so complex subjects with so much literature around them, it is a truly challenging task to present them properly. This chapter manages to survive this dangerous territory with an original and useful overview. The Introductory chapter also contains, very importantly, an introduction to the methods used in the thesis, including geometric morphometrics and the quantification of differences in cortical bone shape and volume. A brief introduction to the subject of archaeological research and pig domestication complete this section of the thesis.

In chapter 2 the calcaneus shape is used as a phenotypic marker of captivity and domestication, in an experimental approach involving mobility reduction. This work involved sophisticated 3D morphometrics that quantified differences in shape variation and covariation in wild-caught wild boars and captive-reared ones. Important variables such as sex and body mass were accounted for. It was shown that the alteration of locomotor behaviour – and with that the biomechanical environment - had an impact on the shape of the calcaneus, and that this shape is beyond the reaction norm of wild-caught populations. It is a very significant discovery that this experiment resulted in no bone size reduction in captive-reared wild boars – size is usually taken to be the variable most prone to change. The changes recorded in calcaneus shape for the animals in captivity differs from those induced by selective breeding – the latter had a much greater effect.

Chapter 3 is a careful examination of the effects of captivity and domestication in pigs with another original experimental approach. An advantage of the developed protocol for studying the humerus cortical thickness topography is that it works with any degree of epiphysation of the bone, and with fragmented specimens, as the morphofunctional signal is observable on the most robust distal part of the diaphysis. The study contains several kinds of multivariate statistical analyses, muscle dissections to generate data used to estimate muscle force, in addition to the 3D morphometrics of sectioned bones.



In chapter 3, it is correctly pointed out how some previous works have made claims on bone histological differences between wild and domestic forms, citing for example the work of Drew et al 1971. Here it would be appropriate also as critique to cite these two works that question the methods and interpretations of Drew et al. 1971:

Watson 1975 Domestication & bone structure in sheep and goats. *J Archaeol Sci* 2:375-83.
Gilbert 1989 Microscopic bone structure in wild and domestic animals: a reappraisal. In Crabtree et al (Eds.), *Early Animal Domestication and Its Cultural context* (Vol. 6, pp. 47-86). University of Pennsylvania Museum of Archaeology.

In chapter 4 much of what was learned in chapters 2 and 3 with the experimental approach is used to address a zooarchaeological question, namely assessing anthropogenic control of early pig populations in Western Europe. The calcaneum form and the topography of the humerus cortical thickness have an ecomorphological signal as shown in chapters 2 and 3. The morphological variation of early Neolithic wild boar/pig from diverse localities is assessed with this perspective. The study results in a comprehensive graph of the spatial and temporal distribution in central Europe in several thousand years of Mesolithic wild boar, free wild boar, captive wild boar and domestic pig. Limitations of sampling are discussed: importantly, as only calcanei with fused epiphyses are studied, this excludes all individuals under 2 years of age, a large age group targeted by domestication. The study of calcanea from continental Western Europe, provided independence evidence to that of molecular studies that suggested that Neolithic societies practiced pig husbandry, while perpetuating wild boar hunting.

Chapter 5, the conclusions, is a synthesis of the different chapters, pointing out the main conclusions in a critical light. Here methodological aspects are discussed. For example, the nature of the changes of the shape of the calcanei documented in some populations and how these can be captured by 3 D morphometrics and not by comparison of linear measurements, the traditional approach of zooarchaeology. The critical landmarks for the differentiation of wild and captive boar are identified in a critical dissection of the method and the results, making specific recommendations on how to approach with a simple method this question. In chapter 5 also issues of automatization versus manual work in capturing data and avoiding errors are discussed.



I was impressed by the thoughtfulness and forward-looking recommendations in chapter 5. I would have found appropriate a discussion of how the approach of this thesis could be applied to the study of other species. But to focus on pigs is justified.

I provide here a few final comments:

- Throughout the work the literature cited seems to me to be appropriate and comprehensive. Although certainly not essential given the concentration on postcranial anatomy, I think it would be worth in a review of issues of phenotypic plasticity and functional anatomy using pigs as a model, to cite some works on Sue Herring on the subject as it concerns mastication.
- The thesis refers to 'ungulates', with the pigs as example of that. It is acceptable but suboptimal in my personal opinion to use a term referring to a non-natural group that in reality does not include groups with deep similarities. Pigs have in general a locomotory apparatus similar to cattle and horses, but they are different in many ways in this regard, not to mention the dietary differences.
- The title of the thesis does not promise more than what is delivered – these days titles tend to exaggerate the importance and reach of the published work – I find it positive this is not the case here.

The work is a significant contribution in functional anatomy, examining osteological correlates of habitat change. The approach is experimental and the results are relevant for zooarchaeological and for phenotypic plasticity research. In view of all of the above, I recommend the approval of this excellent thesis without any hesitation.

The candidate is authorized to defend his thesis.

Yours sincerely,

Marcelo Sánchez-Villagra

TEL : 33 (0)1 40 79 56 86
FAX : 33 (0)1 40 79 54 22
email : soutenance-these@mnhn.fr
fassa@mnhn.fr

de : **Monsieur ou Madame** Joris Peters

qualité : Professeur

Lieu d'exercice : Université de Munich, Institut für Paläoanatomie, Domestikationsforschung
und Geschichte der Tiermedizin, Kaulbachstraße 37,

sur la thèse présentée par : Mr. Hugo Harbers

ayant pour sujet : *Identification des marqueurs morphofonctionnels du processus de domestication en archéozoologie : approche tridimensionnelle de la variation endostructurale de la diaphyse humérale et de la forme du calcaneus*

Le candidat est autorisé à défendre sa thèse.
The candidate is authorized to defend his (her) thesis.

Le manuscrit ne répond pas aux normes requises pour une soutenance à la date prévue.
The manuscript does not meet the standards required for a defense on the scheduled date.

Argumentation (1 à 5 pages)

The doctoral thesis submitted by H. Harbers comprises five chapters and one appendix. The study follows the classical order starting with an introductory (chapter 1) and a concluding chapter (chapter 5). Chapters 2 to 4 carry the headings "*The mark of captivity: plastic responses in the ankle bone of a wild ungulate*", "*Investigating the impact of captivity and domestication on limb bone cortical morphology: an experimental approach using a wild boar model (Sus scrofa)*", and "*Pig domestication in Western Europe: assessing the impact of anthropogenic control over Early Neolithic Sus scrofa populations*". Chapter 2 differs from the others in that it is composed of two publications in peer-reviewed journals. Both papers are an integral part of H. Harbers' study and give the thesis a cumulative character.

The introductory chapter opens with general considerations regarding the domestication phenomenon. They are followed by explanatory notes regarding potential domestication trajectories and terminate with the domestication syndrome elucidating some of the biological adaptations as well as parallel morphological phenomena and behaviours in the various domestic animal species. As far as the proof of domestication in the archaeological record is concerned, several criteria are briefly touched, such as a reduction in sexual dimorphism, morphometric changes in the size and shape of bones and teeth, shifts in slaughter age profiles and stable isotope signatures, etc. These approaches all have the disadvantage that they only become visible archaeologically after an unknown delay in time, which is why they do not necessarily mark initial anthropogenic management of wild animals. In this respect, mesoscopic arthropathies recently described for early Neolithic sheep and goats in Anatolia and related to their penning could provide new clues relative to early human interaction with livestock.

With the same objective, H. Harbers pursues an innovative approach aiming at evaluating phenotypic plasticity in wild boar living under different conditions. Starting point is the assumption that different *Sus* phenotypes would emerge in case of changing patterns of mobility under the conditions of the wild *versus* human-controlled environments. To be able to test this hypothesis, it turned out necessary in a first step to investigate wild individuals from different populations in Western Europe in order to quantify and with the aid of morphometric approaches the 'standard response' of wild boars to their respective natural environments. In a second step, these results were then compared with similar data obtained from a modern wild boar population raised under controlled conditions. The latter comprised 84 individuals of homogenous genetic ancestry raised ca. 20 months under two distinct modes of reduced mobility and associated diets, i.e. free pasturing in a wooded area covering 3,000m² or stabled in areas measuring 4m². With these data sets at hand, it would be possible to test whether the population raised under the conditions of the anthropogenic environment exhibited quantifiable morphological change and thus patterns of phenotypic plasticity beyond the standard response found in free-roaming wild boar. With this thoughtful research design in hand and assuming that initial *Sus* management went along with reduced mobility in the animals, H. Harbers thus evaluated the constraints affecting growth and variability of two skeletal elements essential to an efficient functioning of the musculoskeletal system, more precisely the calcaneus and the humerus (Chapter 2). In the first element, deformations in the external morphology have been studied (publication 1), whereas in the second the topography of the cortical thickness was in focus (publication 1).

The calcaneus study published in the peer-reviewed journal Royal Society Open Science (Harbers et al. 2020, IF 2.68) thus analyses and discusses shape variation and covariation in this ankle joint bone thereby comparing spatially managed *versus* free ranging (hunted) wild boar. It allows concluding that the plastic signal differs significantly in the two *Sus* populations, whereby the observed correlation linking reduced mobility to increased muscle forces seems counterintuitive at first in view of the more varied behavioural repertoire in free-living wild boar including, e.g., wide-range feeding and fleeing instances to escape predators. From an osteomorphological viewpoint, hunted and captive individuals can be separated by the changed orientation of the junction between the epiphysis and the remaining part of the calcaneus. This adaptation is interpreted as resulting from a difference in locomotor strain due to stereotypical movements adopted by pigs confined lifelong to enclosures, a phenomenon reported in many other taxa confined to limited areas, e.g., those living in zoological gardens.

Turning to the humerus, Harbers and colleagues (2020; Scientific Reports, IF 4.0) used a 3D mapping approach to evaluate shaft cortical thickness in modern captive wild boar (n=24), free-ranging wild boar (n=23) and a set of individuals representing modern breeds (n=24). These results illustrate that locomotor behaviour in the captive environment produces a cortical bone pattern that is clearly distinct from the one observed in wild boar allowed to roam freely. Moreover, cortical thickness topography in captive wild boar is also unparalleled by that of animals resulting from selective breeding measures. Both findings allow concluding that two key elements in the cultural history of domestic animals affect cortical thickness in the humerus in a distinct manner, namely (i) human restrictions regarding spatial behaviour and (ii) selective breeding measures.

The next logical step was the application of the aforementioned osteological markers to relevant early Neolithic assemblages to track incipient management and intensification of the human-pig relationship across Europe (chapter 4). Being a process of learning by doing, the challenges of maintaining viable herds of pigs at the cost of lowered mobility likely represented a major challenge to Neolithic communities, an assumption that H. Harbers tested with modern and archaeological *Sus* populations from Mesolithic and Neolithic contexts. Morphotype classification encompassed three groups, i.e. domestic, caught in the wild, and captive wild. Interestingly, predictions turned out different for humerus and calcaneus, the latter element showing a higher contribution of free-ranging wild boar compared to the first. This is explained by the fact that the protocol for the calcaneus requires fully fused specimens, while that for the humerus allows investigating all specimens independent of their state of epiphyseal fusion. Many results and aspects presented in this chapter could be cited with profit, but we will limit ourselves to two particularly interesting findings, namely the occurrence of captive wild boar at Late PPNB Shillourokambos (Cyprus) and the presence of small-sized wild *Sus* morphotypes in different parts of Europe early in the process of Neolithisation. This is interpreted as evidence for commensal populations of local wild boar.

The synthesis chapter 5 recapitulates the innovative aspects as well as main results and conclusions of the preceding chapters 2 to 4. It also addresses potential venues of research and improvements for data acquisition, analysis and interpretation. The latter include, among other things, a more detailed look at the data obtained with the aid of imaging techniques, the use of machine learning approaches to replace manual setting of landmarks on calcanei and automation of cortical thickness mapping in the humerus.

In conclusion, H. Halbers' doctoral thesis fully meets the criteria required and expected by the scientific community, whereby the novel approaches presented by the candidate merit particular attention. The doctoral thesis convincingly demonstrates the advantages of an interdisciplinary research approach and can therefore serve as a source of information and inspiration for similar research both within and beyond the discipline of zooarchaeology.

I strongly recommend defense of this thesis.

Munich, 14 December 2020



Prof. Dr. Joris Peters

Corrections

1 Général

L'utilisation du terme « ongulés » a été réduite. Étant donné que les espèces qui constituent ce clade sont très diverses, sans profondes similarités, le cochon ne représente pas particulièrement un bon exemple pour le représenter. Nous avons donc préféré le remplacer par le terme « suidés », dont le cochon est bien plus représentatif.

2 Chapitre 1, Section 1.2.4, Plasticité osseuse

Ajout d'un paragraphe pour discuter de la plasticité phénotypique au niveau du crâne, notamment concernant les travaux de Sue Herring sur la mastication chez le porc.

« [...]Dans le cas de la domestication, le nouvel environnement engendre deux principaux changements :

- Un changement d'alimentation, qui pourrait induire des modifications au niveau de l'appareil masticatoire. En effet des aliments plus robustes vont induire chez le cochon une augmentation de l'activité musculaire masticatoire, ainsi que de la durée et de l'amplitude du cycle de mastication (Herring, 1977, 1976), mais également plus de variabilité individuelle dans les mouvements alors que les aliments moins robustes induisent des mouvements plus stéréotypés (Montuelle et al., 2018). Cependant, une étude qui s'est penché sur les conséquences morphologiques de ces modifications comportementales n'a pas pu démontrer d'impact sur l'épaisseur ou la densité de l'os cortical de l'arc zygomatique, auquel s'attachent les muscles masticateurs, ni sur les éléments du neurocrâne (Franks et al., 2016). Ces études nous permettent d'ailleurs de mettre en évidence le fait que toutes les structures ne sont pas forcément plastiques, certaines peuvent être surtout contrôlées génétiquement, mais également que parfois la plasticité n'impacte pas les caractères eux même, mais plutôt la variabilité de ces caractères.
- Une limitation de l'espace disponible [...] »

3 Chapitre 3, *Erratum*

Ajout d'une critique de l'article de Drew et al, 1971, sous forme d'*erratum* à la fin du chapitre 3, en s'appuyant notamment sur les travaux de Watson 1975 et Gilbert 1989.

« The bibliographic reference of histological differences between wild and domestic specimens is cited in this paper without any criticism, yet there is literature that questions the methodology and interpretations of Drew et al. 1971. Indeed, a few months after its publication, a first paper (McConnell et al., 1971) expressed reviews, in particular on the interpretation of X-ray diffraction results, to which Drew et al. responded. Then, from 1975 onwards, much more important criticisms were made (Watson, 1975 ; Gilbert, 1989) :

- The irrelevant use of the "wild" and "domestic" categories, while the concept of *continuum* would have been more appropriate.
- The use of archaeological comparative material, whose status is uncertain by definition.

- A lack of discussion about other possible causes of the observed differences, including the possibility of alterations between death and burial.
- Some interpretation problems, especially in terms of optical observations. This suggests that these differences are more likely due to the quality of collagen preservation.

Moreover, at least two independent experimental protocols with archaeological and current material (Watson, 1975 ; Zeder, 1978) have failed to repeat the results obtained by Drew et al. »

Références complémentaires

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