RESEARCH ARTICLE

Size and shape of the semicircular canal of the inner ear: A new marker of pig domestication?

Allowen Evin[1] | Loïc David[1] | Antoine Souron[2] | Bastien Mennecart[3] |
Maeva Orliac[1] | Renaud Lebrun[1]

[1]ISEM, University of Montpellier, CNRS, EPHE, IRD, Montpellier, France

[2]University of Bordeaux, CNRS, MCC, PACEA, UMR 5199, Bordeaux, France

[3]Naturhistorisches Museum Basel, Basel, Switzerland

Correspondence
Allowen Evin, ISEM, University of Montpellier, CNRS-IRD-EPHE, Montpellier, 2 place Eugène Bataillon, CC065, 34095 Montpellier, Cedex 5, France.
Email: allowen.evin@umontpellier.fr

Abstract

Domestication has led to many changes in domestic animal biology, including their anatomy. The shape of the inner ear, part of the mammalian ear, has been found particularly relevant for discriminating domesticated species, their hybrids or differentiating the wild and domestic populations of a single species. Here we assessed the use of the size and shape of the semicircular canals (SCC) of the inner ear as a marker of pig domestication. We studied a total of 63 petrosal bones belonging to wild boar (*Sus scrofa*, two populations) and domestic pigs (extensively and intensively reared specimens) that were μCT-scanned and from which the size and the shape of the inner ear were quantified through geometric morphometrics, analyzing the 3D coordinates of 6 landmarks and 60 sliding semilandmarks localized on the SCC and the common crus. The domestic pigs have larger SCC than the wild boar from which they also strongly differ in shape (correct cross validation of 95.5%, confidence interval: 92.3%–98.1%). Strong shape differences were detected between the two populations of wild boar, as well as a sexual size dimorphism. All together the results highlight the taxonomic discriminant power of the SCC of the inner ear shape, and its relevance for domestication studies.

KEYWORDS
domestication, geometric morphometrics, petrosal bone, *Sus scrofa*, X-ray tomography

1 | INTRODUCTION

During domestication, animals are moved from the wild to a human-controlled environment. This change in life conditions, paired with intentional or nonintentional selection by human societies, have led to many changes in domestic animal biology. Main modifications include an increase in tameness, a decrease in brain size, or a change in coat colour (review in Sánchez-Villagra et al., 2016).

In the pig (*Sus scrofa*), osteological markers of domestication typically studied in archaeological remains correspond to a size reduction of bones and teeth (Rowley-Conwy et al., 2012), as well as changes in the shape of teeth (e.g. Cucchi et al., 2011; Evin et al., 2013, 2015) and skull (Evin et al., 2017; Owen et al., 2014a). In addition, research of new osteological markers of domestication and captivity is still ongoing, and recent studies on differences between wild and domestic populations revealed for example the use of limb

bone cortical morphology (Harbers, Zanolli, et al., 2020), or calcaneus size and shape (Harbers, Neaux, et al., 2020). Other bones, such as the petrosal bone, have received little attention so far despite their known taxonomical discriminant power (e.g., O'Leary, 2010; Orliac, 2013). The petrosal is a bilateral bone of the cranium that houses the bony labyrinth, which is a series of cavities that contains significant soft-tissue structures, such as the organs of hearing and balance of the inner ear, components of the central and peripheral nervous system, and major cranial arteries. In vertebrates, including mammals, the inner ear has two functional parts: the cochlea involved in hearing and the vestibular system involved in balance. The vestibular system is composed of three approximately orthogonal semicircular canals (SCC) contributing to coordination of body movements during loco-motion (reviewed in Spoor, 2003).

The relevance of the inner ear for domestication studies has been recently explored for the dog (Janssens et al., 2019; Schweizer et al., 2017) and equids (Clavel et al., 2021). The strong inner ear shape variation revealed between wolf (*Canis lupus*, i.e., the dog an-cestor), and modern and archaeological dogs (Schweizer et al., 2017), and between modern wolf-like dogs (i.e., mesaticephalic breeds) and modern Eurasian wolves (Janssens et al., 2019) highlighted the re-levance of using measurements of the structure as a marker of do-mestication. Dogs have, on average, a significantly smaller bony labyrinth than wolves although the two overlap (Janssens et al., 2019; Schweizer et al., 2017). In addition, dogs and wolves show a similar amount of bony labyrinth shape variation (Janssens et al., 2019; Schweizer et al., 2017), but smaller size variation in wolves than dogs (Schweizer et al., 2017).

The bony labyrinth was also studied in the context of equids (*Equus* spp.) domestication and was found to be efficient for distin-guishing donkeys and horses, as well as their mule hybrids (Clavel et al., 2021). This last study also highlighted the better discriminant power of the SCC over the cochlea.

While few studies focus on domestic species, a large number have explored the variation of the human (*Homo sapiens*) bony labyrinth (e.g., Ponce de León et al., 2018; Spoor et al., 1994, 1996). Though the existence of sexual dimorphism in the inner ear is still debated (Braga et al., 2019; Ward et al., 2020), several studies have revealed differences between men and women (Braga et al., 2019; Miller, 2007; Osipov et al., 2013; Sato et al., 1991). In addition, though the bony labyrinth morphology has been traditionally documented not to change much after birth, some studies have revealed differences between subadults and adults in humans (Boucherie et al., 2021). In comparison, the impact of age and sex on the inner ear morphology of domestic species does not seem to have been studied so far and the value of the petrosal bone in discriminating between domestic pigs and wild boar is as yet unknown.

Thus, here we explored (1) the differences between extant wild boar and domestic pigs in their inner ear SCC size and shape, (2) the differences between two wild boar populations and between in-tensively and extensively reared domestic pigs, (3) the effect of age and sex on semicircular canal measurements.

1.1 | Material

A total of 63 petrosal bones of European suids (*Sus scrofa*) were studied and divided into four categories: two populations of wild boar (*n* = 37), one population of domestic pigs from extensive farming (*n* = 23), and a small series of domestic pigs of commercial origin (*n* = 3), most probably intensively reared without their precise origins being traceable.

The two wild boar populations came from the Occitanie region in southern France, one from the Cevennes (Mialet, Gard, France) that included 18 specimens housed at ISEM-Univ. Montpellier, and a second from the footstep of the Pyrenees (Tautavel, Pyrénées-Orientales, France) with 19 specimens housed at PACEA-Univ, Bor-deaux. Both populations were collected by hunters and one petrosal bone per skull was extracted before µCT scanning. The environment of the two populations is characterized by a frank Mediterranean climate and the two areas are predominantly constituted by forests and semi-natural environments (87.3% and 50.7%, respectively; Ministère de la transition Écologique, 2021).

A single population of 23 domestic pigs, now housed at ISEM-Univ. Montpellier, was collected from an extensive livestock farm from the south of the Massif Central (Gard, France) with similar cli-mate and main land occupation as the two wild populations of 57.4% of forest and semi-natural environments. The breed(s) involved in the breeding of these specimens is/are not known, but the herd origi-nates from a mixture of rustic and traditional breeds according to the owner. All specimens for which the sex could be determined were female.

In addition, three domestic pigs obtained from shops were in-cluded: one originating from the Czech Republic, the two others from France. Though their exact origin cannot be tracked, they very likely grew in intensive farms and belong to intensively bred breeds.

The specimens were divided into three age categories according to the eruption stages of their maxillary and/or mandibular teeth (SI Table 1). The juveniles had their second molars erupted and corre-sponded approximately to specimens younger than 14 months. The sub-adults had their third molars partially erupted, corresponding to approximately 14–22 months old. Finally, the adult specimens had their lower third molars fully erupted, which occurred approximately around 22 months.

When possible, the sex of the specimens was determined ac-cording to the morphology of the canine, or of the canine alveoli (Mayer & Brisbin, 1988) (Table S1).

2 | METHODS

2.1 | 3D model acquisition

The petrosal bones from Tautavel were µCT-scanned using a General Electrics Vtome x|s X-ray microtomograph at PACEA at a resolution of 14–15 µm; all others were µCT-scanned using an EasyTom 150 system (RX-Solutions) at a resolution of 44.91 µm

at ISEM. For the specimens scanned at ISEM, the bony labyrinths were subsequently segmented using a two-step approach involving smart interpolation: (i) presegmentation one slice out of around 20 slices in Avizo; (ii) Biomedisa smart interpolation tool (Lösel et al. 2020). The segmentation of Tautavel specimens was performed within the Avizo 9.1 (Thermo Fisher Scientific) workspace. All extracted left and right bony labyrinths were then exported as surface PLY files.

2.2 | Landmark and semilandmark protocol

The 3D surface models were imported into MorphoDig 1.6 (Lebrun, 2018) for landmark and semilandmark digitization. Before landmark and semilandmark digitization, all left labyrinths were mirrored. Three-dimensional coordinates of 6 landmarks and 60 sliding semilandmarks were digitized on the SCC of the right and left-mirrored labyrinths following Schweizer et al. (2017) (Figure 1). All coordinates were acquired by the same operator (LD). A total of 23 sliding semilandmarks were digitized on the lateral semicircular canal, 16 on the anterior and posterior SCC and five for the common crus (Figure 1). Coordinates were superimposed with a Generalized Procrustes Analysis (Adams et al., 2013; Rohlf & Slice, 1990) using the Procrustes distance criterion for optimizing semilandmarks position. Analyses of size variation were based on the centroid size, while shape variation was investigated using the coordinates after superimposition, i.e., Procrustes residuals.

2.3 | Statistics

Differences in size were tested with Kruskall–Wallis and pairwise Wilcoxon tests and visualized with boxplots. Shape variation was first explored and visualized using a Principal Component Analysis. Differences between groups were then tested using multivariate analysis of variance (MANOVA) and visualized using canonical variate analyses. Correct cross-validation percentages (CVP) of the discriminant analysis were calculated following Evin et al. (2013) based on a resampling procedure (100 runs) of the largest groups to match the size of the smallest, rendering the size of the groups balanced. CVP are provided as the mean, and a confidence interval limited by the minimum and maximum of 90% of the distribution.

Between groups homogeneity of variance was compared for shape using a morphological disparity approach (Adams et al., 2019; Zelditch et al., 2012) and Fligner–Killeen tests for size. Allometry, the relationship between size and shape, was analyzed by testing the homogeneity of the allometric pattern between wild boar and domestic pigs, and between the two wild boar populations, using MANCOVAs with shape as the dependent variable, centroid size as a covariate, and the group (wild or domestic) as a factor.

All statistical analyses were performed in R v3.6.2 (R Core Team, 2021), primarily with the package Morpho (Schlager et al., 2018).

3 | RESULTS

Overall domestic pigs had larger SCC than wild boar ($W = 862$, $p = 7e\text{-}9$), though the two overlap (Figure 2a). The linear discriminant analysis succeeds to correctly identify 82.5% (confidence interval [CI]: 78.8%–84.6%) of the specimens. No size difference was detected between intensively and extensively reared domestic pigs ($\chi^2 = 3.26$, $p = 0.07$), nor between the two wild boar populations ($\chi^2 = 0.18$, $p = 0.67$) (Figure 2b). Wild boar and domestic pigs did not differ in size variance ($\chi^2 = 0.035$, $p = 0.8512$).

The first axis of the principal component analysis (32.76% of variance) tends to separate the wild boar and domestic pigs with little overlap between the two (Figure 3a). The same analysis visualizing the four populations (Figure 3b) reveals that while the two domestic groups strongly overlap on axes 1 and 2 (45.28% of total variance), the two wild populations tend to be separated, with the specimens from the Pyrenees being more localized on the positive side of axis one and the negative side of axis 2. Along the two first axes (Figure 3c,d), the shape changes appeared to spread over the three SCC without a specific location. Based on the SCC shape, 95.5% (CI: 92.3%–98.1%) of the specimens are correctly classified as wild or domestic by the discriminant analysis. A similar success is shown for the SCC form providing a correct cross-validation of 95.9% (CI: 92.3%–98.1%). Again, the shape differences between wild boar and domestic pigs are spread over the three SCC (Figure 4).

Domestic pigs are more diverse in term of SCC shape than wild boars ($p = 0.005$, domestic pig Procruste variance = 0.002923443, wild boar Procruste variance = 0.002247815). Allometries were found to be homogeneous between wild boar and domestic pigs (interaction term of the MANCOVA, $F_{(59,1)} = 9.9$, $p = 0.248$).
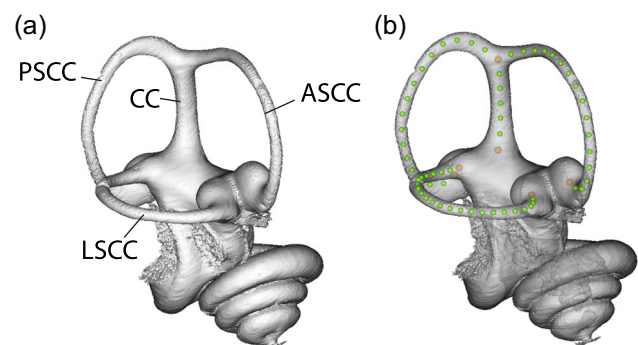

FIGURE 1 Landmark and sliding semilandmark protocol used in the study, illustrated on the right bony labyrinth of a wild boar (ISEM-851). (a) 3D surface of the bony labyrinth presenting the positions of the anterior semicircular canal (ASCC), of the posterior semicircular canal (PSCC), of the lateral semicircular canal (LSCC), and of the common crus (CC); (b) Landmarks and semilandmarks. Brown: fixed curve extremities for the ASCC, PSCC, LSCC, and CC, which correspond to type-I landmarks. Green: sliding semilandmarks along each curve
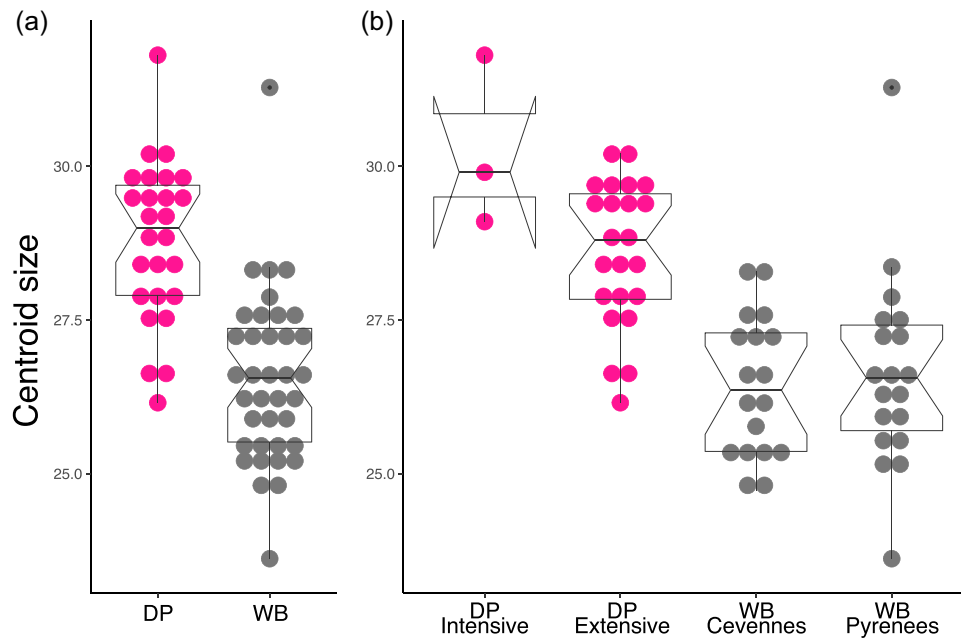
FIGURE 2 Differences in centroid size of the semicircular canals. Centroid size differences are shown in boxplots between wild boar and domestic pigs (a) and between the intensive and extensive pig populations and the two wild populations (b). DP, domestic pig (pink dots); WB, wild boar (gray dots)
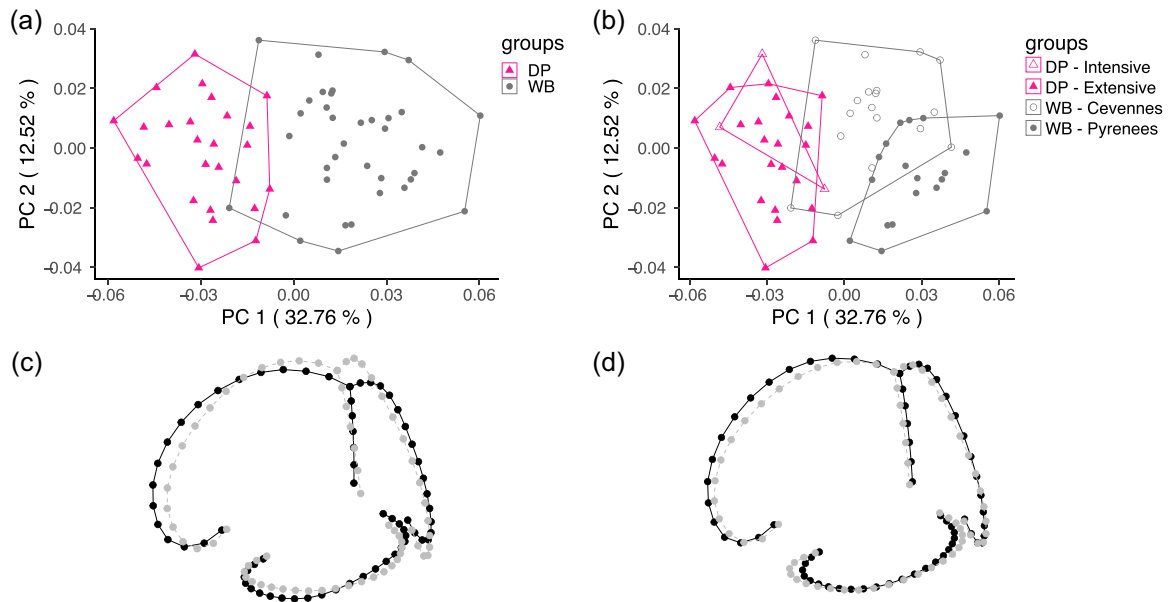

FIGURE 3 Variation in semicircular canals shape. Variation is shown between wild boar and domestic pigs (a) and between the intensive and extensive pig populations and the two wild boar populations (b) as the two first axes of principal component analyses (a,b) with the visualization of the most extreme shape changes along principal component 1 (PC 1) (c) and PC 2 (d) with the positive side of the axis depicted in black, the negative side in gray. DP, domestic pig (pink triangles); WB, wild boar (gray dots)

The two wild boar populations clearly differed in their SCC shape ($F_{(13,23)}$ = 17.334, p = 7e-9), with a correct cross validation of 97.7% (CI: 97.2%–100%, Figure 5), with again, the main shape variation within wild boar being spread over the three SCC (Figure 5b,c). The two wild boar populations did not differ in their SCC shape variance (p = 0.458).

There were not enough domestic males to test for sexual dimorphism in domestic pigs. Pooling the two populations of wild boar revealed that females had smaller SCC than males (χ^2 = 4.6, p = 0.03, Figure 6a). However, the SCC size of the two sexes strongly overlap (Figure 6a) and the correct cross validation percentage between sexes was 64.2% (CI: 61.8%–67.6%). No difference in SCC shape was
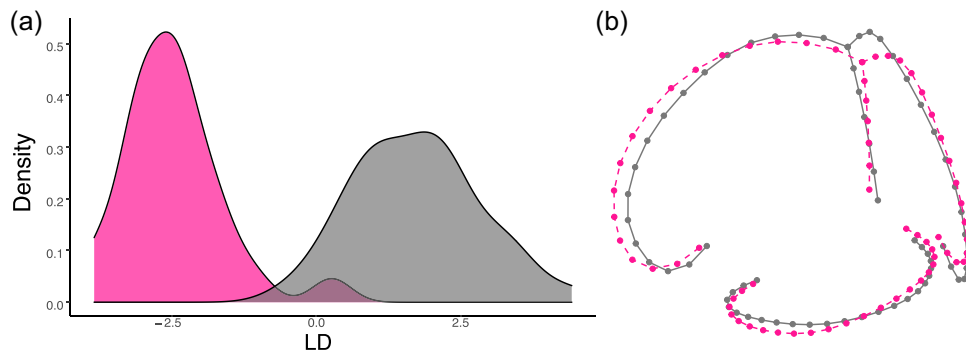
FIGURE 4 Visualisation of the shape differences between wild boar and domestic pigs. Density distribution of the specimens (a) and visualisation of the shape differences (b) along the linear discriminant (LD) axis are shown in pink for domestic pigs, grey for wild boar
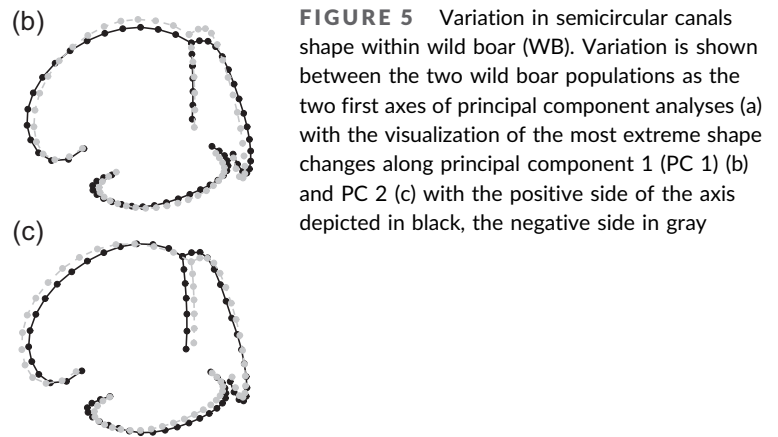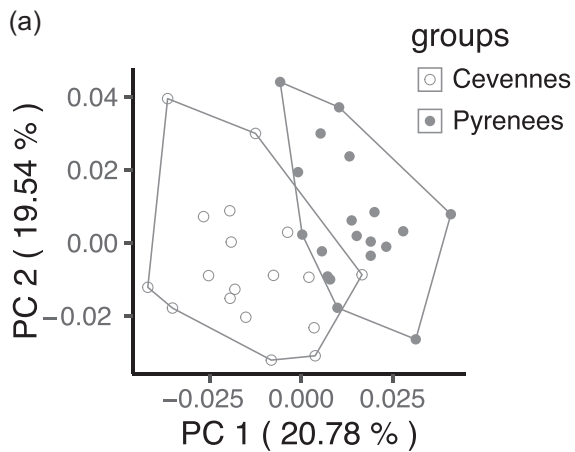

FIGURE 5 Variation in semicircular canals shape within wild boar (WB). Variation is shown between the two wild boar populations as the two first axes of principal component analyses (a) with the visualization of the most extreme shape changes along principal component 1 (PC 1) (b) and PC 2 (c) with the positive side of the axis depicted in black, the negative side in gray
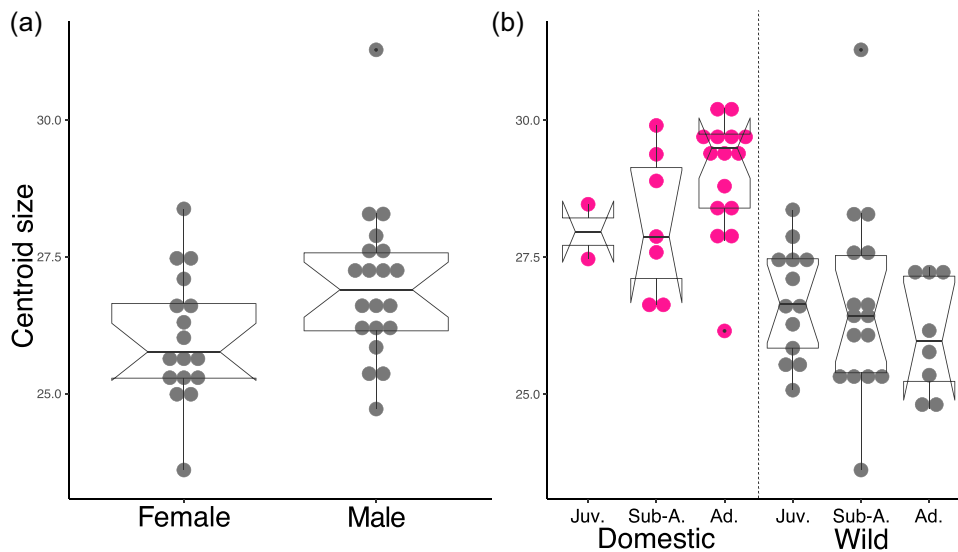

FIGURE 6 Analysis of centroid size by sexual and age categories. Boxplots of the centroid size are shown for sexual size dimorphism in wild boar semicircular canals (a) and by age groups in wild boar and domestic pigs (b). Ad, adult; Juv, juvenile; Sub-Ad, sub-adult

detected between wild boar males and females ($F_{(7,29)} = 1.45$, $p = 0.22$).

Because of the shape differences between wild boar and domestic pigs, of the differences between the two wild boar populations, and unbalanced samples among groups, we explored the size differences between age categories for each group separately. No differences due to age were identified within the wild boar populations from the Cevennes (shape: $F_{(3,14)} = 0.76$, $p = 0.53$; size:

$\chi^2 = 1.3$, $p = 0.25$, Figure 6b) or the Pyrenees (shape: $F_{(3,15)} = 1$, $p = 0.50$; size: $\chi^2 = 0.769$, $p = 0.38$) (Figure 6b). Conversely, adult extensive domestic specimens show larger SCC than their sub-adult counterparts ($W = 72$, $p = 0.036$, Figure 6b) without detected shape differences ($F_{(3,17)} = 0.3$, $p = 0.8$).

4 | DISCUSSION

The bony labyrinth morphology has been proven to be a very efficient marker for the reconstruction of mammal phylogeny (e.g., Mennecart et al. 2016, 2017; Urciuoli et al., 2021). Though based on only two geographically close wild boar populations and a limited number of domestic pigs (especially for the intensively bred category), extant wild boar and domestic pigs differ in their semicircular canal size and shape. This result, in addition to previous works on dogs (Janssens et al., 2019; Schweizer et al., 2017) and equids (Clavel et al., 2021), confirms the relevance of the structure for domestication studies and between populations comparison.

Despite significant differences, the size of the inner ear overlaps between the wild and domestic populations of dog (Janssens et al., 2019; Schweizer et al., 2017) and suids (this study). While dogs have smaller inner ears than wolves (Janssens et al., 2019; Schweizer et al., 2017), domestic pigs have larger SCC than wild boar, suggesting that domestication does not result in a similar size change across species. This difference cannot be directly explained by skull size differences since for both species, as for other large mammals, a size decrease is a classical marker of domestication (Vigne et al., 2005). However, for both species, a large diversity of size exists and some domestic breeds have the same skull size than their wild counterparts (e.g., Evin et al., 2017; Owen et al., 2014b). A future line of research would be therefore to explore the link between inner ear and skull sizes acquired on the same specimens.

However, our analyses on domestic pig/wild boar focus only on the SCC morphometrics while the ones on dogs/wolves also include the cochlea. Further studies including morphometric differences between wild boar and domestic pigs based on their cochlea are therefore needed for more in-depth comparison. In addition, it will be necessary to contrast the size of the inner ear, or more globally the petrosal bone, with the skull size of the specimens, as it has been demonstrated in ruminants that the size of the inner ear correlates with body mass and skull length (Costeur et al., 2019).

Analyses of semicircular canal shape revealed strong differences (not due to allometries) between wild boar and domestic pigs. Unfortunately, any adaptive or functional explanations for the differences in semicircular canal shape would be highly speculative. It might be tempting to propose an explanation linked to the locomotor changes of the animals during domestication and captivity known to have impacted the skeleton (e.g., Harbers, Neaux, et al., 2020; Harbers, Zanolli, et al., 2020; Pelletier et al., 2020; Pelletier et al., 2021), but it is just as possible that the changes in skull morphology (Evin et al., 2017; Owen et al., 2014b) led to changes of the inner ear, or that drift was also involved.

Our approach succeeded to identify more than 95% of the specimens to the correct group, thus it could be used as an identification tool. This would be particularly important for archeozoological studies for which the identification of the wild or domestic status of the specimen is important but not always easy. In comparison, 100% of the specimens can be attributed to mesaticephalic dogs or extant Eurasian wolves (Janssens et al., 2019).

The bony labyrinth morphology is specific and succeeds to separate closely related species (Mennecart & Costeur 2016b, 2016a; Mennecart et al., 2017). We show here that within a species, wild and domestic representatives can be distinguished on the basis of the SCC morphology. Similarly, in equids, though belonging to different species with much older divergence time than between wolves-dogs and wild boar-domestic pigs, the inner ear shape succeeds to separate horse, donkey and their mule hybrid (Clavel et al., 2021) with high correct cross validation percentages. This last study also highlights the better discriminant power of the semicircular shape over the cochlea shape, which would deserve to be investigated further in suids.

Strong differences between populations are also observed in SCC shape, with 97.7% of the specimens being assigned to the correct group. Although the two wild boar populations lived in the same broad area, micro-local environmental differences or differences in past history of the populations may explain these morphometric differences and cannot be excluded. At least in Cevennes, local hunters say that interbreeding between wild populations and hybrid and/or domestic specimens has occurred, however tracing these admixture events is not possible without in-depth genetic analysis. Admixture between wild boar and domestic pigs is known to have been important in pig domestication history (Frantz et al., 2019). It seems therefore possible that the closer morphometric proximity of the wild boar population from the Cevennes to domestic pigs result from a greater genetic proximity.

A sexual size dimorphism in the inner ear was detected in wild boar. This dimorphism is however not strong enough to be used as a tool for sex determination since only ~64% of the specimens were correctly assigned to the right sex using predictive analysis. While several studies mentioned sexual size dimorphism in humans (Braga et al., 2019; Miller, 2007; Osipov et al., 2013; Sato et al., 1991), such difference has not been found in equids (Clavel et al., 2021). It would be of prime interest to further explore this sexual dimorphism by increasing the sample size, especially for the less numerous domestic pigs, and to assess whether these size differences can result solely from skull size dimorphism. While males and females of domestic pigs differ in their skull size and shape, the wild boar do not (Owen et al., 2014a).

No strong differences linked to age were identified in wild boar, in agreement with that reported for other artiodactyls (Costeur et al., 2017; Mennecart & Costeur, 2016b). Conversely, adult domestic pigs appeared to have larger SCC than sub-adult specimens, though the two groups largely overlapped. In humans, the cochlea and the SCC reach their adult size and shape in utero, between the 17th and 25th fetal weeks (Jeffery & Spoor, 2004;

Richard et al., 2010), suggesting no size and shape variation after birth. Since the age of all specimens was estimated according to the eruption stages of their teeth, a difference in skeletal and dental maturity between wild boar and domestic pig may explain the observed differences, but this should be confirmed with specimens of known age. In addition, it cannot be excluded that the differences observed between age categories of domestic pig were the result of our sampled population that correspond, according to the owner, to a mixed population of rustic and traditional breeds. Therefore, studies of additional ontogenetic series of various domestic breeds are needed to confirm this finding.

The petrosal bone is regularly sampled for palaeogenetic studies due to its good DNA preservation (see review in Pálsdóttir et al., 2019) and it has been advocated to preserve 3D models of the bone as an archive before its destruction for later study including morphometric analyses (Evin et al., 2020; Pálsdóttir et al., 2019; Sykes et al., 2020). After DNA sampling, 80% of the inner ears of equids can be studied with a geometric morphometric approach (Clavel et al., 2021). The same is likely not true for smaller species whose petrosal bones are also smaller and do not permit DNA sampling without destruction of the relevant area.

All together, these results highlight the taxonomic discriminant power of the SCC of the inner ear shape, and its relevance for pig domestication studies, in particular for bioarchaeology, where the wild versus domestic status of the specimens is often unknown and no discrete criteria exist so far for discriminating petrosal bones of wild boar and domestic pigs. The study of Schweizer et al. (2017) includes archaeological specimens in addition to modern breeds and reveals a great proximity between the two groups in their inner ear shape compared to those of wolves, suggesting that changes in inner ear morphology during dog domestication likely did not result from the recent improvement of dog breeds. It would be therefore of prime interest to include archaeological specimens of various chrono-cultural periods and geographic regions to assess the place and timing of emergence of the wild/domestic differentiation on the structure, not only on pigs but also on dogs and other domestic mammals. Though pig petrosal bones are not the most commonly found among archaeological remains, the relevance of the inner ear morphology for differentiating between wild and domestic populations of other species (e.g., auroch/ cattle discrimination), or for between species identification (e.g., sheep and goat, also not always easily identified in bioarchaeology), is a promising future line of research.

CONFLICT OF INTERESTS

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

All data used in this study are included in Table S1.

ORCID

Allowen Evin http://orcid.org/0000-0003-4515-1649
Antoine Souron http://orcid.org/0000-0001-7384-4974
Bastien Mennecart http://orcid.org/0000-0002-9669-2907
Maeva Orliac http://orcid.org/0000-0002-8922-8356
Renaud Lebrun http://orcid.org/0000-0002-5819-2653

PEER REVIEW

The peer review history for this article is available at https://publons. com/publon/10.1002/jez.b.23127.

REFERENCES

Adams, D., Rohlf, J., & Slice, D. (2013). A field comes of age: Geometric morphometrics in the 21st century. *Hystrix*, 24(1), 7–14. https://doi. org/10.4404/hystrix-24.1-6283

Adams, D. C., Collyer, M. L., & Kaliontzopoulou, A. (2019). Geomorph: Software for geometric morphometric analyses. R package version 3. 1.0.

Boucherie, A., Polet, C., Lefèvre, P., & Vercauteren, M. (2021). Sexing the bony labyrinth: A morphometric investigation in a subadult and adult Belgian identified sample. *Journal of Forensic Sciences*, 66(3), 808–820. https://doi.org/10.1111/1556-4029.14663

Braga, J., Samir, C., Risser, L., Dumoncel, J., Descouens, D., Thackeray, J. F., Balaresque, P., Oettlé, A., Loubes, J. M., & Fradi, A. (2019). Cochlear shape reveals that the human organ of hearing is sex-typed from birth. *Scientific Reports*, 9(1), 1–9. https://doi.org/10. 1038/s41598-019-47433-9

Clavel, P., Dumoncel, J., Der Sarkissian, C., Seguin-Orlando, A., Calviere-Tonasso, L., Schiavinato, S., Chauvey, L., Perdereau, A., Aury, J. M., Wincker, P., Onar, V., Clavel, B., Lepetz, S., Braga, J., & Orlando, L. (2021). Assessing the predictive taxonomic power of the bony labyrinth 3D shape in horses, donkeys and their F1-hybrids. *Journal of Archaeological Science*, 131, 105383. https://doi.org/10.1016/j. jas.2021.105383

Costeur, L., Mennecart, B., Müller, B., & Schulz, G. (2017). Prenatal growth stages show the development of the ruminant bony labyrinth and petrosal bone. *Journal of Anatomy*, 230(2), 347–353. https://doi.org/ 10.1111/joa.12549

Costeur, L., Mennecart, B., Müller, B., & Schulz, G. (2019). Observations on the scaling relationship between bony labyrinth, skull size and body

mass in ruminants. (October) *36*, 36. https://doi.org/10.1117/12.2530702

Cucchi, T., Hulme-Beaman, A., Yuan, J., & Dobney, K. (2011). Early Neolithic pig domestication at Jiahu, Henan Province, China: Clues from molar shape analyses using geometric morphometric approaches. *Journal of Archaeological Science*, *38*(1), 11–22. https://doi.org/10.1016/j.jas.2010.07.024

Evin, A., Cucchi, T., Cardini, A., Strand Vidarsdottir, U., Larson, G., & Dobney, K. (2013). The long and winding road: Identifying pig domestication through molar size and shape. *Journal of Archaeological Science*, *40*(1), 735–743. https://doi.org/10.1016/j.jas.2012.08.005

Evin, A., Dobney, K., Schafberg, R., Owen, J., Strand Vidarsdottir, U., Larson, G., & Cucchi, T. (2015). Phenotype and animal domestication: A study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. *BMC Evolutionary Biology*, *15*(1), 6. https://doi.org/10.1186/s12862-014-0269-x

Evin, A., Lebrun, R., Durocher, M., Ameen, C., Larson, G., & Sykes, N. (2020). Building three-dimensional models before destructive sampling of bioarchaeological remains: A comment to Pálsdóttir et al. (2019). *Royal Society Open Science*, *7*(3), 192034. https://doi.org/10.1098/rsos.192034

Evin, A., Owen, J., Larson, G., Debiais-Thibaud, M., Cucchi, T., Vidarsdottir, U. S., & Dobney, K. (2017). A test for paedomorphism in domestic pig cranial morphology. *Biology Letters*, *13*(8), 20170321. https://doi.org/10.1098/rsbl.2017.0321

Frantz, L., Haile, J., Lin, A. T., Scheu, A., Geörg, C., Benecke, N., Alexander, M., Linderholm, A., Mullin, V. E., Daly, K. G., Battista, V. M., Price, M., Gron, K. J., Alexandri, P., Arbogast, R. M., Arbuckle, B., Bălăşescu, A., Barnett, R., Bartosiewicz, L.,, ... Larson, G. (2019). Ancient pigs reveal a near-complete genomic turnover following their introduction to Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(35), 17231–17238. https://doi.org/10.1073/pnas.1901169116

Harbers, H., Neaux, D., Ortiz, K., Blanc, B., Laurens, F., Baly, I., Callou, C., Schafberg, R., Haruda, A., Lecompte, F., Casabianca, F., Studer, J., Renaud, S., Cornette, R., Locatelli, Y., Vigne, J. D., Herrel, A., & Cucchi, T. (2020). The mark of captivity: Plastic responses in the ankle bone of a wild ungulate (*Sus scrofa*). *Royal Society Open Science*, *7*(3), 192039. https://doi.org/10.1098/rsos.192039

Harbers, H., Zanolli, C., Cazenave, M., Theil, J. C., Ortiz, K., Blanc, B., Locatelli, Y., Schafberg, R., Lecompte, F., Baly, I., Laurens, F., Callou, C., Herrel, A., Puymerail, L., & Cucchi, T. (2020). Investigating the impact of captivity and domestication on limb bone cortical morphology: An experimental approach using a wild boar model. *Scientific Reports*, *10*(1), 1–13. https://doi.org/10.1038/s41598-020-75496-6

Janssens, L. A., Gunz, P., Stenger, T. E., Fischer, M. S., Boone, M., & Stoessel, A. (2019). Bony labyrinth shape differs distinctively between modern wolves and dogs. *Zoomorphology*, *138*(3), 409–417. https://doi.org/10.1007/s00435-019-00445-5

Jeffery, N., & Spoor, F. (2004). Prenatal growth and development of the modern human labyrinth. *Journal of Anatomy*, *204*(2), 71–92. https://doi.org/10.1111/j.1469-7580.2004.00250.x

Lebrun, R. (2018). MorphoDig, an Open-Source 3D Freeware Dedicated to Biology. Paris.

Lösel, P. D., van de Kamp, T., Jayme, A., Ershov, A., Faragó, T., Pichler, O., Jerome, N. T., Aadepu, N., Bremer, S., Chilingaryan, S. A., Heethoff, M., Kopmann, A., Odar, J., Schmelzle, S., Zuber, M., Wittbrodt, J., Baumbach, T., Heuveline, V., Heuveline, V. (2020). Introducing biomedisa as an open-source online platform for biomedical image segmentation. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-19303-w

Mayer, J. J., & Brisbin, I. L. (1988). Sex identification of *Sus scrofa* based on canine morphology. *Journal of Mammalogy*, *69*(2), 408–412. https://doi.org/10.2307/1381402

Mennecart, B., & Costeur, L. (2016a). A *Dorcatherium* (mammalia, ruminantia, middle miocene) petrosal bone and the tragulid ear region. *Journal of Vertebrate Paleontology*, *36*(6), e1211665. https://doi.org/10.1080/02724634.2016.1211665

Mennecart, B., & Costeur, L. (2016b). Shape variation and ontogeny of the ruminant bony labyrinth, an example in Tragulidae. *Journal of Anatomy*, *229*(3), 422–435. https://doi.org/10.1111/joa.12487

Mennecart, B., DeMiguel, D., Bibi, F., Rössner, G. E., Métais, G., Neenan, J. M., Wang, S., Schulz, G., Müller, B., & Costeur, L. (2017). Bony labyrinth morphology clarifies the origin and evolution of deer. *Scientific Reports*, *7*(1), 1–11. https://doi.org/10.1038/s41598-017-12848-9

Mennecart, B., Rössner, G. E., Métais, G., DeMiguel, D., Schulz, G., Müller, B., & Costeur, L. (2016). The petrosal bone and bony labyrinth of early to middle Miocene European deer (Mammalia, Cervidae) reveal their phylogeny. *Journal of Morphology*, *277*(10), 1329–1338. https://doi.org/10.1002/jmor.20579

Miller, J. D. (2007). Sex differences in the length of the organ of Corti in humans. *The Journal of the Acoustical Society of America*, *121*(4), EL151–EL155. https://doi.org/10.1121/1.2710746

Ministère de la transition Écologique. (2021). CORINE Land Cover (CLC) - Répartition des superficies en 15 postes d'occupation des sols (métropole). Données et études statistiques pour le changement climatique, l'énergie, l'environnement, le logement, et les transports.

O'Leary, M. A. (2010). An anatomical and phylogenetic study of the osteology of the petrosal of extant and extinct artiodactylans (mammalia) and relatives. *Bulletin of the American Museum of Natural History*, *335*(335), 1–206. https://doi.org/10.1206/335.1

Orliac, M. J. (2013). The petrosal bone of extinct Suoidea (Mammalia, Artiodactyla). *Journal of Systematic Palaeontology*, *11*(8), 925–945. https://doi.org/10.1080/14772019.2012.704409

Osipov, B., Harvati, K., Nathena, D., Spanakis, K., Karantanas, A., & Kranioti, E. F. (2013). Sexual dimorphism of the bony labyrinth: A new age-independent method. *American Journal of Physical Anthropology*, *151*(2), 290–301. https://doi.org/10.1002/ajpa.22279

Owen, J., Dobney, K., Evin, A., Cucchi, T., Larson, G., & Strand Vidarsdottir, U. (2014a). The zooarchaeological application of quantifying cranial shape differences in wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics. *Journal of Archaeological Science*, *43*(1), 159–167. https://doi.org/10.1016/j.jas.2013.12.010

Owen, J., Dobney, K., Evin, A., Cucchi, T., Larson, G., & Strand Vidarsdottir, U. (2014b). The zooarchaeological application of quantifying cranial shape differences in wild boar and domestic pigs (Sus scrofa) using 3D geometric morphometrics. *Journal of Archaeological Science*, *43*(1), 159–167. https://doi.org/10.1016/j.jas.2013.12.010

Pálsdóttir, A. H., Bläuer, A., Rannamäe, E., Boessenkool, S., & Hallsson, J. H. (2019). Not a limitless resource: Ethics and guidelines for destructive sampling of archaeofaunal remains. *Royal Society Open Science*, *6*(10), 191059. https://doi.org/10.1098/rsos.191059

Pelletier, M., Kotiaho, A., Niinimäki, S., & Salmi, A. K. (2020). Identifying early stages of reindeer domestication in the archaeological record: A 3D morphological investigation on forelimb bones of modern populations from Fennoscandia. *Archaeological and Anthropological Sciences*, *12*(8), 169. https://doi.org/10.1007/s12520-020-01123-0

Pelletier, M., Niinimäki, S., & Salmi, A. K. (2021). Influence of captivity and selection on limb long bone cross-sectional morphology of reindeer. *Journal of Morphology*, *282*(10), 1533–1556. https://doi.org/10.1002/jmor.21403

Ponce de León, M. S., Koesbardiati, T., Weissmann, J. D., Milella, M., Reyna-Blanco, C. S., Suwa, G., Kondo, O., Malaspinas, A. S., White, T. D., & Zollikofer, C. (2018). Human bony labyrinth is an indicator of population history and dispersal from Africa.

Proceedings of the National Academy of Sciences of the United States of America, 115(16), 4128–4133. https://doi.org/10.1073/pnas.1717873115

R Core Team. (2021). *R: a language and environment for statistical computing. The R Foundation for Statistical Computing.* Retrieved from https://www.r-project.org

Richard, C., Laroche, N., Malaval, L., Dumollard, J. M., Martin, C. h, Peoch, M., Vico, L., & Prades, J. M. (2010). New insight into the bony labyrinth: A microcomputed tomography study. *Auris, Nasus, Larynx*, 37(2), 155–161. https://doi.org/10.1016/j.anl.2009.04.014

Rohlf, F. J., & Slice, D. (1990). Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Biology*, 39(1), 40–59.

Rowley-Conwy, P., Albarella, U., & Dobney, K. (2012). Distinguishing wild boar from domestic pigs in prehistory: A review of approaches and recent results. *Journal of World Prehistory*, 25(1), 1–44. https://doi.org/10.1007/s10963-012-9055-0

Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: a developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, 3(6), 160107. https://doi.org/10.1098/rsos.160107

Sato, H., Sando, I., & Takahasi, H. (1991). Sexual dimorphism and development of the human cochlea. *Acta Otolaryngologica*, 111, 1037–1040.

Schlager, S., Jefferis, G., & Ian, D. (2018). Package 'Morpho'.

Schweizer, A. V., Lebrun, R., Wilson, L. A. B., Costeur, L., Schmelzle, T., & Sánchez-Villagra, M. R. (2017). Size variation under domestication: Conservatism in the inner ear shape of wolves, dogs and dingoes. *Scientific Reports*, 7(1), 13330. https://doi.org/10.1038/s41598-017-13523-9

Spoor, F. (2003). The semicircular canal system and locomotor behaviour, with special reference to hominin evolution. *CFS Courier Forschungsinstitut Senckenberg*, 93–104.

Spoor, F., Wood, B., & Zonneveld, F. (1994). Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature*, 369(6482), 645–648. https://doi.org/10.1038/369645a0

Spoor, F., Wood, B., & Zonneveld, F. (1996). Evidence for a link between human semicircular canal size and bipedal behaviour. *Journal of Human Evolution*, 30(2), 183–187. https://doi.org/10.1006/jhev.1996.0018

Sykes, N., Spriggs, M., & Evin, A. (2020). Beyond curse or blessing: The opportunities and challenges of aDNA analysis. *World Archaeology*, 51(4), 503–516. https://doi.org/10.1080/00438243.2019.1741970

Urciuoli, A., Zanolli, C., Almécija, S., Beaudet, A., Dumoncel, J., Morimoto, N., & Alba, D. M. (2021). Reassessment of the phylogenetic relationships of the late Miocene apes Hispanopithecus and Rudapithecus based on vestibular morphology. *Proceedings of the National Academy of Sciences of the United States of America*, 118(5), 1–12. https://doi.org/10.1073/pnas.2015215118

Vigne, J.-D., Helmer, D., & Peters, J. (2005). New archaeological approaches to trace the first steps of animal domestication: General presentation, reflections and proposals. In (Eds.) Vigne, J.-D., Peters, J. & Helmer, D., *The first steps of animal domestication: new archaeozoological approaches. Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002* (pp. 1–16). Oxbow Books.

Ward, D. L, Pomeroy, E., Schroeder, L., Viola, T. B., Silcox, M. T., & Stock, J. T. (2020). Can bony labyrinth dimensions predict biological sex in archaeological samples? *Journal of Archaeological Science: Reports*, 31(March), 102354. https://doi.org/10.1016/j.jasrep.2020.102354

Zelditch, M., Swiderski, D., & Sheets, H. (2012). Geometric morphometrics for biologists. *Geometric Morphometrics for Biologists*, 64, 419–434. https://doi.org/10.1016/C2010-0-66209-2

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.