



Age dimorphism in the wild boar (*Sus scrofa* L., 1758) mandible is centred on the condylar ramus

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(Received: 10/02/15)

(Accepted: 21/03/15)

ABSTRACT

We report here a geometric morphometric analysis based on 16 homologous landmarks by which the expression and magnitude of mandibular age dimorphism during late growth in 37 European wild boars (*Sus scrofa* L., 1758) were captured. These samples were subgrouped into two age clusters according to eruption of the third molar: "subadults" (erupting or not yet erupted third upper molar, $n = 22$) and "adults" (complete dentition, $n = 15$). Multivariate statistics were applied to visualize the pattern, and assess the significance, of shape variation between ages. All samples demonstrated highly significant size and shape dimorphism, with the condyle consistently being the most dimorphic region of the mandible between ages.

Keywords: age assessment, jaw, geometric morphometrics, morphological variation, pigs

INTRODUCTION

Alternative analytical techniques, such as those drawn from the discipline of geometric morphometrics (GM), can be used in physical zoometry. Geometric morphometric methods (GMMs) use anatomical landmark data for the quantitative analysis of biological form. They are statistically powerful and offer great potential for visualization of results in terms of anatomy. Thus, the objective of this paper is to explore the nature of age dimorphism in the Wild Boar (*Sus scrofa* L., 1758) mandible in relation to both of its form components (size and shape). To better appreciate the range of variation in the expression and magnitude of age dimorphism in this population, the material was initially examined according to third molar eruption, as an indicator of age [1].

The Wild Boar is one of the most common and widespread large mammals of the Old World. Its distribution covers most of Eurasia, where it is relatively common in substantial woodland and reed bed areas. Not only has the wild boar been hunted by people for millennia – thereby providing an important protein source to the human diet – but also it has given rise to the domestic pig (*Sus domesticus*), one of the most important farm animals. The large geographic range occupied by wild boar populations is reflected in the great morphological and size variability that characterizes this species. This has been intensively investigated from quite different points of view (see [2]). However, much of this morphological and biometrical work has focused on lineal morphological characters, with only marginal attention paid to the geometrical (size and form) study, and none to a particular region, such as the mandible.

MATERIALS AND METHODS

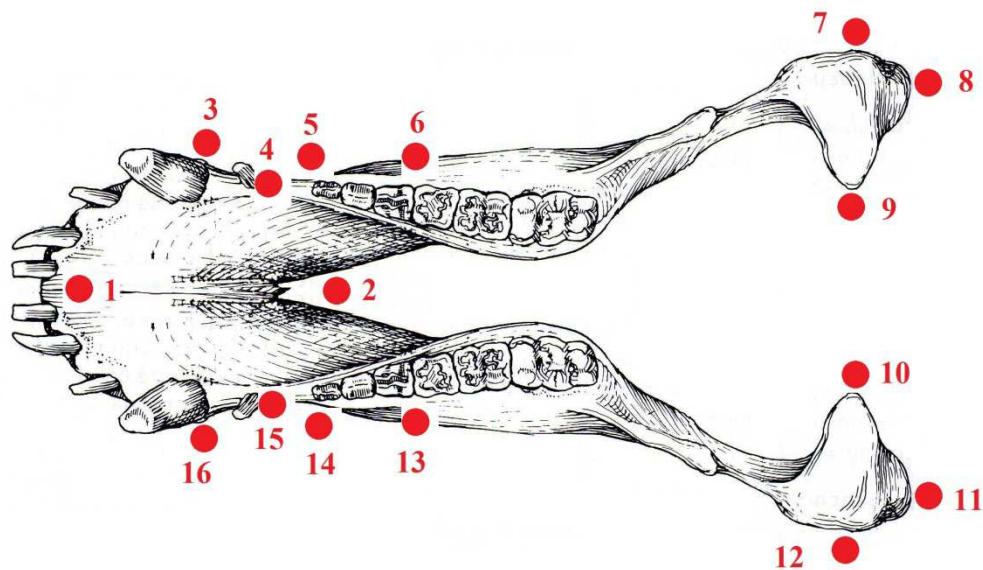
A sample of 37 dentulous dry mandibles (*os dentale*) from European wild boar (*Sus scrofa*), fully preserved and collected from a vulture feeding point in Catalonia (NE Spain), was studied. The animals had been hunted and their entire corpses deposited there, so the sex of these samples was unknown. When collecting specimens, the mandibles were disarticulated and the skulls were not studied. Whole specimens are necessary for GMM, and therefore only complete, undamaged, and non-pathological mandibles (as assessed on the basis of macroscopic examination) were chosen. These samples were posteriorly subgrouped into two age clusters employing the third molar (M_3) eruption

as an age criterion [3]: not yet erupted or erupting M_3 ("subadults", $n = 22$) and fully erupted M_3 (complete dentition, "adults", $n = 15$).

Data acquisition

Image capture was performed with a Nikon® D70 digital camera (image resolution of $2,240 \times 1,488$ pixels) equipped with a Nikon AF Nikkor® 28–200 mm telephoto lens. The focal axis of the camera was parallel to the horizontal plane of reference and centred on the dorsal aspect of each mandible. Images always included a scale (interval 50 mm). Sixteen landmarks were plotted on the mandible in order to describe the size and shape variations, producing a set of 32 raw coordinates for each specimen. Fourteen of these landmarks were topologically equivalent. Figure 1 shows the location of the anatomical landmarks, together with specimen orientation, which represented the form of each mandible. *Nomina Anatomica Veterinaria* [4] and von Driesch [5] were used to guide the spelling of the anatomical and zoological terms in this investigation.

Figure 1. Designated landmarks for geometric morphometric analysis of the wild boar mandible (dorsal aspect)



Shape analysis

All images were saved in JPEG format and stored on a personal computer. The software TpsUtility v. 1.50[6] was used to prepare and organize the images. Landmarks were digitized using TpsDig v. 2.04 software [7]. Data were analysed using geometric morphometric methods [8, 9]. TpsSmall v. 1.20 software [10] was used to assess the correlation between Procrustes and the Kendall tangent space distances to ensure that the amount of shape variation in a data set was small enough to allow subsequent statistical analyses. As the correlation between Procrustes and the Kendall shape spaces was very high ($r = 1.0000$), we proceeded with the morphometric analyses. Landmark positions were converted to scaled x and y coordinates using CoordGen6f [11], which was also used to translate and rotate images. Centroid size (CS), which was computed as the square root of the sum of squared distances of all landmarks from the centroid [12], was used as a measurement independent of shape [8]. The new Cartesian coordinates obtained after the superimposition were the shape coordinates used for statistical comparisons of individuals and they can be summarized using a standard principal components analysis (PCA) on the covariance matrix; mean "adult" and "subadult" configurations were then visualized. Statistical analyses were carried out using MorphoJ [13] and PAST software [14].

Statistical comparisons

Differences in size (CS) between ages were explored using analysis of variance (ANOVA). To assess the significance of age dimorphism in mandibular shape, a cross-validated discriminant function analysis (DFA) was used, in which the true difference between means (Procrustes distance) was compared with the distribution of differences between means obtained by randomly permuting group membership 1,000 times.

Intra-observer error

To estimate the amount of measurement error due to digitization, duplicated measurements were taken for all samples, and a Procrustes ANOVA was carried out. No differences appeared between replicas ($P = 0.999$) and so individually averaged samples were studied.

RESULTS

Size, represented by CS, showed significant differences between ages ($P < 0.0001$, $F = 58.25$). This indicates strong size age dimorphism in the mandibles of wild boar. The DFA test indicated that the Procrustes distance between age groups' means was also significantly different ($P = 0.0009$, $T^2 = 99.50$), and thus adults and subadults present different mandibular shape. DFA for age resulted in a 2.7% correct classification. Multivariate regressions of shape against age (performed using PC1, which accounted for 40.5% of the total variance) indicated a significant age dimorphism. PC2 accounted for 23.6%.

The main shape differences visualized by warping between the adults' and subadults' configurations evidenced that mandibles have relatively distinctive condylar structure according to age; there is a progressive expansion of the condylar points. On viewing the adult mandible, an increase in relative condylar breadth is also observed and it is apparent that the heads of the condyles are relatively more medially relocated than in subadults. The opposite configuration is evident in the subadults' mandible. This could be associated with the strengthening of attachment points for masticatory muscles during the animals' growth.

DISCUSSION

In this study we have used a documented skeletal collection to investigate mandibular age dimorphism in wild boars. The techniques applied were drawn from the discipline of geometric morphometrics, by which highly significant size and shape dimorphism was shown in the pooled population. The following discussion considers the age-based variation in mandibular morphology in relation to developmental and functional requirements. The age classification accuracy achieved using the GM technique was also considered. Aspects of age variation in the mandibular morphology of the individual local populations are also discussed.

Our data show distinct shape changes in the mandible of wild boar during late growth. In considering shape variation between the adults and subadults, it was evident that the most dimorphic region of the mandible was the condyle. From a more general swine-like shape, the mandible shape changes to become more slender with a more posteriorly positioned angular process. These shape changes appear to coincide with ontogenetic changes in muscle development, with jaw adductor muscles (notably the masseter complex) becoming heavier and disproportionately stronger in adults. In fact, the major muscles used in chewing (e.g. *masseter* and *pterygoid*) are attached to the coronoid process, which is a large expansion of the lower jaw or mandible. In piglets, the media pterygoid and temporal muscles grow intensively, and during development, their mass increases [15].

From a functional perspective, the elongation of posterior insertion of the masseter and pterygoid muscles likely provides a greater horizontal force component upon contraction, which will result in a more extensive displacement of the lower jaw during jaw closure. Moreover, the strong development of the masseter complex indicates an optimal functioning of the jaw system at very low gape angles, which would accord well with the omnivorous and versatile feeding habit of the Wild Boar [16]. The relatively strong development of the masseter also assures a uniform force generation across the entire cheek tooth row, which may be beneficial in reducing hard material. Adaptive hypotheses regarding the specialization of the masticatory system in the function of an omnivorous diet could be tested by careful biomechanical modelling of representative rodents with different feeding ecologies.

These observations suggest that the aetiology of such variation is likely attributable to differential growth trajectories and functional adaptations, with the usual anatomy of wild boar likely being related to aspects of the use of the feeding system. In this respect, the results of the present study appear to support previous research, showing in particular that age dimorphism in this bone is differentially expressed across its functional units and mostly apparent in the condyle. No information has been obtained from the ramus as this study was focused on the dorsal plane, not the lateral one.

The results could also express an origin of a change in diet according to age. It would thus appear plausible to suggest that age-specific mechanical forces involving the masticatory apparatus could directly influence the development of the muscles of the lower jaw and in consequence their underlying skeletal structures. Our results, however, offer anatomically informative visualizations of age dimorphism as well as statistical findings. The above

statistics, in addition to the lack of similar studies available in the literature, suggest that a higher upper limit of age classification accuracy is possible for the pooled sample, seemingly changing the studied dorsal aspect.

CONCLUSION

This study demonstrates that GMMs are a valuable tool for elucidating morphological differences related to age dimorphism, in this case in mandibles. The analyses presented here showed highly significant size and shape dimorphism according to age, with the condyle and ramus being consistently the most dimorphic regions of the mandible between subadults and adults. Also we can confidently assert that the condyle and ramus of the mandible are equally suitable elements for age classification when no complete mandible is available (especially when the bony part for cheek teeth is lost).

Acknowledgements

Thanks to Marta Caballero-Sala who provided me with all the facilities to visit the feeding point and helped to collect and landmark them.

REFERENCES

- [1] Magnell, O. and Carter, R., *Veterinarija Ir Zootechnika*, **2007**, 40, 43-48.
- [2] Albarella, U., Dobney, K. and Rowley-Conwy, P., *Environmental Archaeology*, **2009**, 14, 2.
- [3] Dyce, K.M., Sack, W.O. and Wensing, C.J.G., *Veterinary Anatomy*, 2nd ed., W. B. Saunders Company. Philadelphia, London, New York, St. Luis, Sydney, Toronto, **1996**.
- [4] *Nomina Anatomica Veterinaria*. International Committee on Veterinary Gross Anatomical Nomenclature. 5th ed. Pub. by the Ed. Com., USA, **2005**.
- [5] Driesch, A. Von, *Peabody Museum Bulletin*, **1976**, 1, 1-137.
- [6] Rohlf, F.J. *TpsUtility Program*, ver. 1.50. Department of Ecology and Evolution, State University of New York at Stony Brook, **2012**.
- [7] Rohlf, F.J. *TpsDig*, ver. 2.04. Department of Ecology and Evolution, State University of New York at Stony Brook, **2005**.
- [9] Rohlf, F.J., Marcus, L.F., *Trends in Ecology and Evolution*, **1993**, 8, 129-132.
- [8] Bookstein, F.L., *Morphometric Tools for Landmark Data: Geometry and biology*. Cambridge University Press, Cambridge, **1991**.
- [10] Rohlf, F.J. *TpsSmall*, ver. 1.20. Department of Ecology and Evolution, State University of New York at Stony Brook, **2003**.
- [11] Sheets, H.D. *IMP-integrated morphometrics package*. Department of Physics, Canisius College, Buffalo, New York, **2003**.
- [12] Dryden, I.L. and Mardia, K.V., Multivariate shape analysis. *Sankhya*, **1993** 55(A), 460-480.
- [13] Klingenberg, C.P. *MorphoJ*. Faculty of Life Sciences, University of Manchester, UK, http://www.flywings.org.uk/MorphoJ_page.htm, **2011**.
- [14] Hammer, Ø., Harper, D.A.T. and Ryan, P.D., PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontology Electronica* 4, 1, <http://folk.uio.no/ohammer/past/>, **2001**.
- [15] Kushkhov, K.T. [Masticatory muscles of domestic sheep and swine in ontogenesis]. *Arkhivanatomii, gistologiiiémbriologii*, **1991**, 100, 1, 88-93.
- [16] Hafez, S., Ashfaq, M., Hafeez, T., Ahsan, M. and Tiwana, U., *Turkish Journal of Zoology* **2012**, 36, 5, 676-681.