

Allometric shape variation in *Ovis aries* mandibles: a digital morphometric analysis

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Abstract

Morphological differences among 75 specimens of domestic sheep were investigated using landmark-based geometric morphometrics of the lateral aspect of the left hemimandible. The set was grouped at different ages according to tooth eruption: first molar (M) erupting (n=28), only first molar erupted (n=18), only second molar erupted (n=4), and all three molars erupted (n=25). The link between centroid size and shape was significant. This showed that the differences in mandible shape were due to allometry, which can be explained by changes in elongating molar length (expanding rostro-nuchally with age) and the corresponding *pars molaris* of the *corpus mandibulae* (*margo ventralis*). These changes could be also related to a certain morphofunctional change, as they correspond to insertion points of important masticatory muscles: *mylohyoideus*, *digastricus*, *masseter* and *pterygoideus medialis*.

Keywords: allometry, jaw, landmark, sheep.

1 Introduction

A useful way of monitoring the relative growth trajectories of biological structures is by allometry. In general allometric growth, there is a variation in shape related to a variation in size (LLEONART, SALAT and TORRES, 2000). Since 1924, it has been established that morphological adaptation can proceed via allometry, the change in relative dimensions of body parts that are correlated with changes in overall size. Changing size often means changing shape (GOULD, 1966). In practice, such allometric relations can be studied during the growth of a single individual, between different individuals within one breed or between different breeds. In this study, digital morphometric analysis was performed in order to relate structural and functional growth trajectories in the sheep mandible.

2 Materials and Methods

2.1 Specimens

Seventy-five hemimandibles from domestic sheep (different European breeds, mainly *Xisqueta*, *Rípollesa*, *Aranesa* and *Berberina*) were studied. The set was grouped at different ages according to tooth eruption: first molar (M) erupting (“young 1”, n=28), only first molar erupted (“young 2”, n=18), only second molar erupted (“subadults”, n=4), and all three molars erupted (“adults”, n=25). The sex of each specimen was not available. All pieces showed no gross pathological appearance that might lead to errors in measurement. Specimens comprised only left hemimandibles.

2.2 Geometric morphometrics

The GM technique (see BOOKSTEIN, 1991; ROHLF and MARCUS, 1993; MONTEIRO and REIS, 1999) was used to analyse mandible variation. This technique has been

shown to be objective and efficient compared to traditional methods (ROHLF, 1998). Geometric and morphometric analyses were performed separately using two-dimensional projection of the mandible.

2.3 Image acquisition

Image capture was performed with a Nikon® D70 digital camera (image resolution of 2,240 × 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 lateral aspect of each hemimandible. A ruler was used in this process (interval 50 mm) in order to determine the real size of each specimen. Fourteen homologous and topologically equivalent landmarks were plotted on the skull in order to describe size and shape variations (Figure 1). Shape variables were obtained as linear combinations of the original landmark coordinates after standardising for size and removing artefactual variation due to different positions of the specimens in the process of data collection (generalised procrustes analysis). Shape differences were visualised with deformation grids, where an object (reference) is deformed into another (target); shape features can be described in terms of deformation grids depicting the differences between objects (ADAMS, SLICE and ROHLF, 2004). The thin plate spline algorithm was used to compute the deformation grid with the least bending energy between the reference and target landmark configurations. Landmarks were digitised using tpsDig 2.16 (ROHLF, <http://life.bio.sunysb.edu/morph/index.html>). Landmark positions were converted to scaled x and y coordinates using CoordGen6f (www.canisius.edu/sheets). In order to compare shape, the coordinates for each specimen in this study were scaled, aligned and transformed by General Procrustes Alignment (GPA). The GPA method computes a consensus configuration (least-squares procrustes average configuration) based on the landmark coordinates of

all specimens (see BOOKSTEIN, 1991 for methodological details). The consensus plot was obtained with tpsRel 1.49 (<http://life.bio.sunysb.edu/morph/index.html>). Principal Coordinate Analysis (also known as Metric Multidimensional Scaling) was performed with a transformation exponent $c=2$. The algorithm was from DAVIS (1986). Size information was retained as centroid size (CS), which corresponds to the sum of the squared distances from the landmarks to the centroid of configuration (BOOKSTEIN, 1991). CS was extracted using CoordGen6f. Differences calculated for each age group (shape and CS) were finally tested by a one-way non-parametric multivariate analysis of variance (MANOVA, also known as PERMANOVA). Significance was computed by permutation of group membership, with 9,999 replicates.

2.4 Numerical statistical analysis

Data were analysed using the MorphoJ (KLINGENBERG, 2011) and PAST (Paleontological Statistics Software Package for Education and Data Analysis) (HAMMER, HARPER and RYAN, 2001) software. Nomenclature was according to *Nomina Anatomica Veterinaria* (2005).

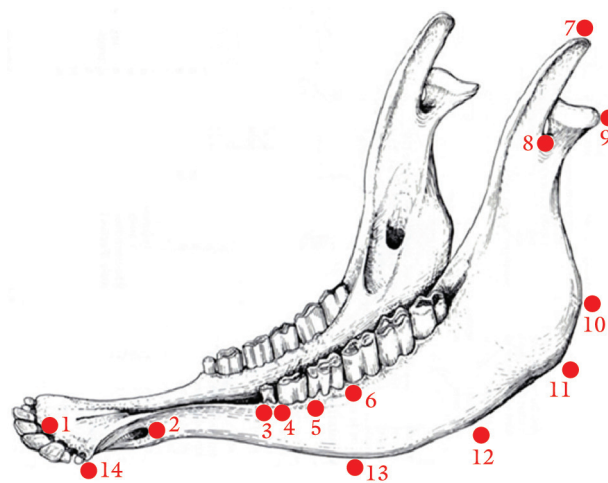


Figure 1. Mandibular landmarks used (dots).

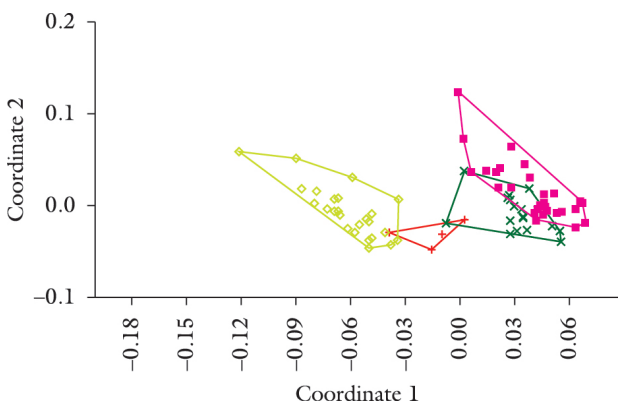


Figure 2. Principal Coordinate Analysis for Axis 1 (51.0%) and Axis 2 (18.6%). Age groups are identified by symbol shape: filled squares represent “young 1” (first molar erupting), X-shaped figures represent “young 2” (only first molar erupted), crosses represent “subadults” (only second molar erupted) and diamonds represent “adults” (all three molars erupted).

3 Results and Discussion

The first three principal shape axes accounted for 77.5% of total mandible shape variance. Axis 1 (51.0%) separated all groups. Projection of the specimens onto axes 1 and 2 is shown in Figure 2. NPMANOVA indicated that all ages were recognizable by shape ($F=23.26$, $p=0.0001$). Differences in CS were highly significant among groups ($F=634.5$, $p=0.0001$). A box plot graph of group CS (Figure 3) showed that adults had the largest mandible, while young sheep had the smallest. The link between CS and shape was significant ($R^2=0.09$, $p=0.006$) (Figure 4). This showed that the differences in mandible shape were due to allometry, which can be explained by changes in expanding molar length (as M_2 and M_3 erupt rostro-nuchally with age) and the corresponding *pars molaris* of *corpus mandibulae* (*margo ventralis*) (Figure 5). These changes could also

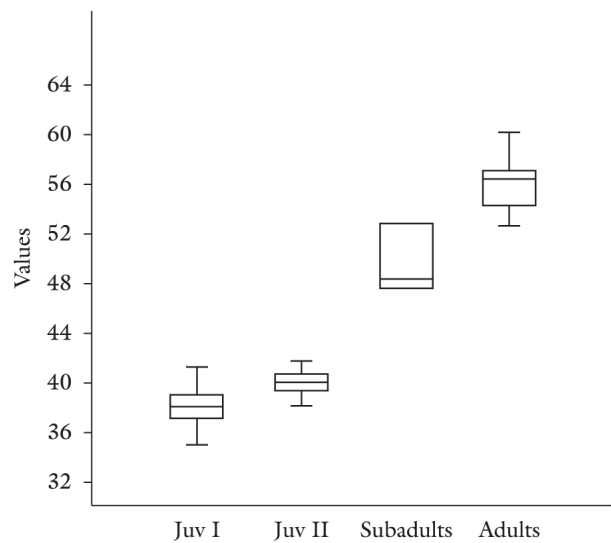


Figure 3. Box plot for centroid size of the lateral aspect of the mandibles in each age group: “young 1” (first molar erupting), “young 2” (only first molar erupted), “subadults” (only second molar erupted) and “adults” (all three molars erupted). For each group, the 25-75 percent quartiles are drawn. The median is shown with horizontal line inside the box. The minimal and maximal values are shown as short horizontal lines (“whiskers”).

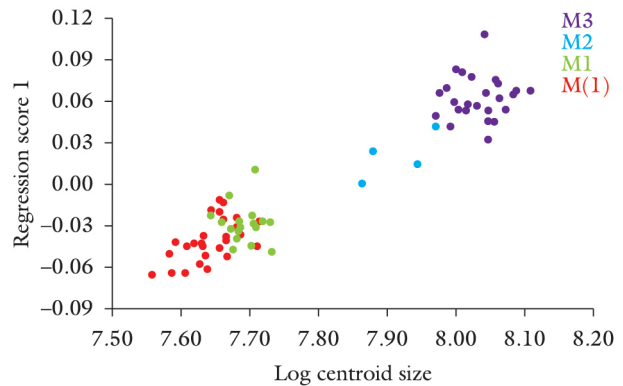


Figure 4. Shape plotted against (log) centroid size (log CS) of mandibles for each age group.

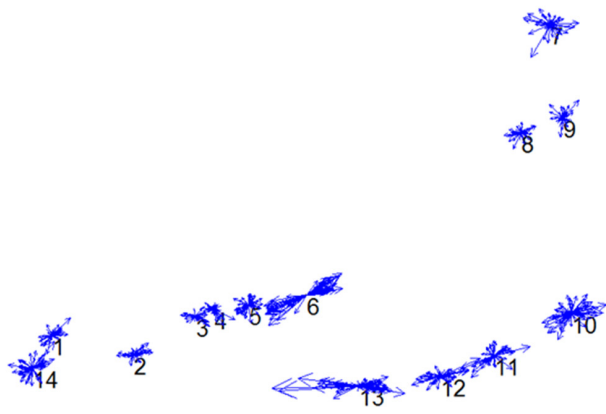


Figure 5. Consensus plot of mandibles (numbers correspond to landmarks). Note the long vectors in landmarks corresponding to the molar space (#6) and corresponding molar parts of the body of the mandible (ventral margin) (#10 to 13). The muscles that are attached to these points are: *mylohyoideus* (#3 to 6), *digastricus* (#12 and 13), *masseter* (#10 and 11) and *pterygoideus medialis* (#10).

be related to a certain morphofunctional change, as they correspond to the insertion points of important masticatory muscles: *mylohyoideus*, *digastricus*, *masseter* and *pterygoideus medialis*.

4 Conclusions

Ages are recognizable by shape. This is in agreement with the results obtained from the analysis of centroid size, which in older animals was significantly larger than in younger ones. The results of this study support the hypothesis that allometry contributes to the organization of variation in the mandible, but only for certain morphological parts, and particularly to the molar row and the corresponding molar body of the mandible. These changes could be also related to a certain morphofunctional change. Our findings have implications for our understanding of morphological growth in domestic sheep and suggest that further investigations into the nature of mandible shape variation are needed.

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