CRANIAL SHAPE VARIATION IN *CANIS*: A COMPARISON BETWEEN WILD CANIDS AND DOMESTICATED BREEDS

Introduction

Humans have engineered an extraordinary variety of dog breeds differing in shapes and sizes (Selba et al 2019). In particular, brachycephaly (drastic snout shortening; Selba et al 2020), offers an extreme example of domestication-induced skull modifications. This project aims to quantify differences in cranial shape and examines the effect of evolutionary constraints on how modularity (covariation between skull regions) inhibits or promotes domestication-induced changes (Drake and Klingenberg 2010). Wild canid species and a selection of brachycephalic and normocephalic breeds, are used as case-studies.

Project aims

Hypothesis 1: Modularity is observed to a greater degree in domesticated breeds than in wild canids
Hypothesis 2: Snout shortening in brachycephalic dogs is accompanied by decreasing orbit depth

Methodology

Skull images were sourced from Skull Base (skullbase.info) and the Dog Skull Database (https://dogskulls.tumblr.com/). Both side and dorsal skull views were used in all analyses and statistical tests.

Specimens were assigned to three categories:

1) wild canid species (N = 8)
2) normocephalic dog breeds (N = 52)
3) brachycephalic dog breeds (N = 8)

Image J (Schneider et al 2012) was used to open each of the images and rotate them to a consistent orientation in which the furthest point of the snout was horizontally aligned with the lowermost point of the exoccipital bone. Placing the skulls in consistent orientations ensured that there were no discrepancies between landmarks – for example those used to define the 'highest point' on the skull

Landmarks (Figs 1-2) sought to capture aspects of shape variation relevant to the main aims

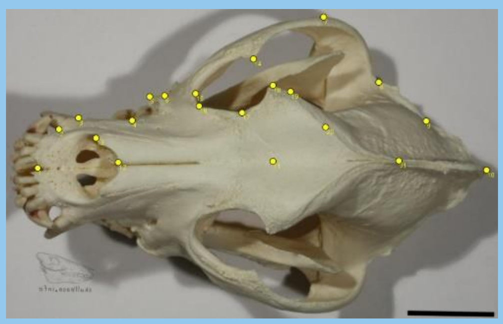


Fig. 1. Dorsal view landmarks on American Bulldog (http://skullbase.info/skulls/dogs.php)

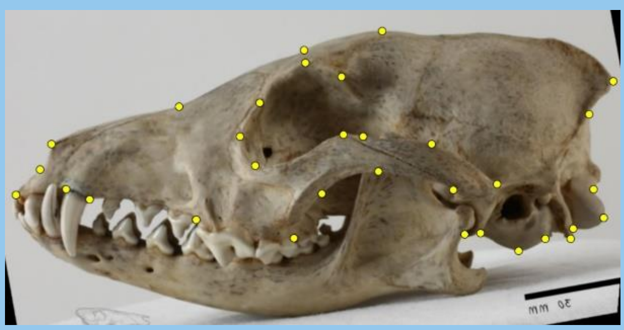


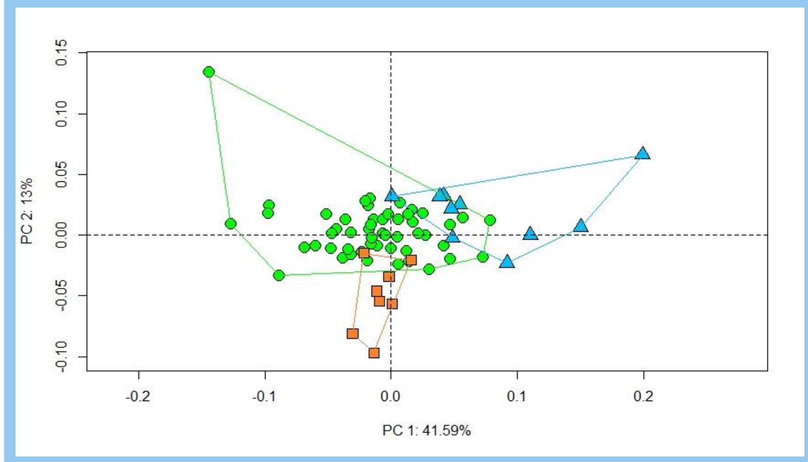
Fig. 2. Side view landmark on Black-backed Jackal (http://skullbase.info/skulls/dogs.php)

For each view, the combined landmark coordinates were imported into MorphoJ (Klingenberg 2011) to carry out morphometric analyses; a Procrustes fit was performed to remove the effects of scale, translation, and rotation; the Procrustes-adjusted coordinates were used to build a covariance matrix to which Principal Component Analysis was applied.

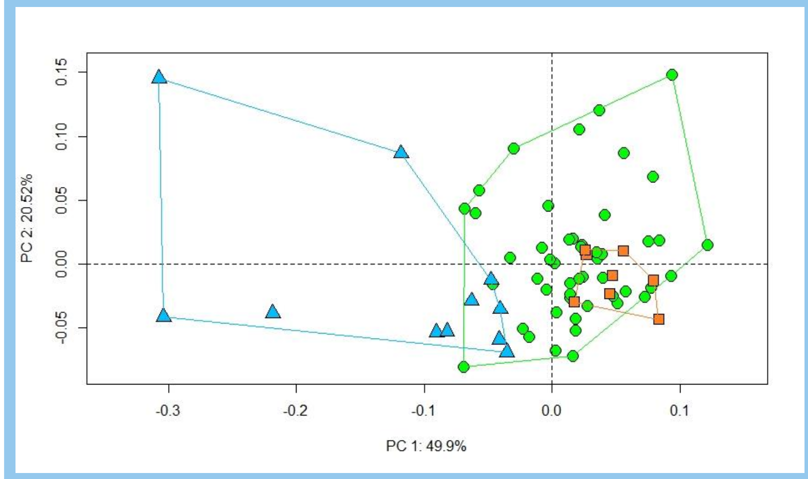
To test hypotheses of modularity, landmarks were divided into subsets pertaining to the muzzle, the back of the skull, and the orbit. Finally, differences among categories were tested. For these analyses, scripts in the R 'geomorph' package were utilized.

Results

Figure 3A shows a moderate overlap between brachycephalic and normocephalic dogs, a comparatively small amount of overlap between wild canids and normocephalic dogs, and no overlap between wild canids and brachycephalic dogs.



A



B

Figure 3. Patterns of morphological space occupation generated from PCA of lateral (A) and dorsal (B) skull views; blue triangles = brachycephalic dogs; green circles = normocephalic; dogs; orange squares = wild canids

Figure 3B reveals a conspicuous overlap between wild canids and normocephalic dogs. Brachycephalic dogs, on the other hand, show no overlap with wild canids, and only a moderate overlap with normocephalic dogs.

A randomised residual permutation procedure on PC scores from the side view data showed significant differences between normocephalic and brachycephalic dogs ($p=0.007$), and between brachycephalic dogs and wild canids ($p=0.049$); conversely, normocephalic dogs and wild canids were not significantly different ($p=0.803$); for brevity, results from dorsal data are not shown. Only brachycephalic and normocephalic dogs show a positive significant relationship between muzzle length and orbit depth ($p<0.0001$) (Fig. 4).

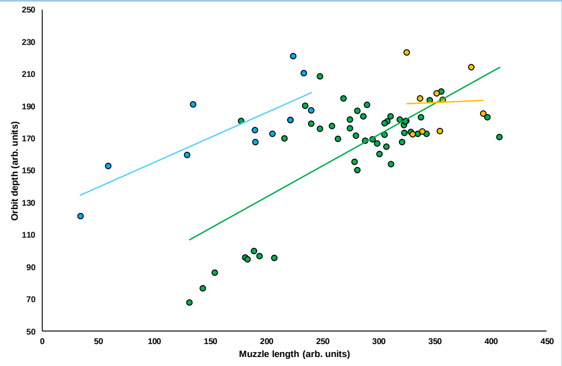


Figure 4. Simple linear regression between muzzle length and orbit depth in the three categories; colours as in Fig 3.

Discussion

One major implication of the results from this study is that, overall, the cranial shape of domesticated dogs shows greater plasticity than that of wild canids, likely brought about by domestication and the influence of artificial selection (Drake and Klingenberg 2010).

This finding was in line with the first hypothesis presented above: this corresponds to Drake and Klingenberg's (2010) findings that "domestic dogs occupy a large region of shape space … outside of the range of ancestral species".

During this study, problems with the sourcing of canine skull images were encountered. Many of those available were taken from varying angles, resulting in many images having to be rejected, thus reducing the sample size. There also appeared to be a significant lack of images of smaller dog breeds such as terriers, with a greater prevalence of large dog breeds in the study: had more breeds been available, the distribution of brachycephaly among the sample may have been different. This study also challenges traditional subdivision of breeds based upon their muzzle proportion, suggesting instead a more nuanced pattern of cranial variation that affects the cranial vault, the robustness of the cheek region, the slope of the frontal part at the vault-muzzle junction, and the shape and proportions of the basicranial region.

This work has applications in both evolutionary and veterinary fields. Domestic dog breeds provide a suitable model for understanding cranial shape changes (Smith and Laitman 2020) and offer opportunity to examine alterations to modularity brought on by artificial selection (Drake and Klingenberg 2010). Brachycephalic dogs experience a wide range of health problems, including heritable disorders affecting the head and neck – for example respiratory disorders (Packer et al 2015).

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