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Patterns of integration in the canine skull: an inside view into the relationship of the skull modules of domestic dogs and wolves

Stefan Curth[a,b,*], Martin S. Fischer[a], Kornelius Kupczik[a,b]

[a] *Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Erbertstr. 1, D-07743 Jena, Germany*
[b] *Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany*

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A B S T R A C T

The skull shape variation in domestic dogs exceeds that of grey wolves by far. The artificial selection of dogs has even led to breeds with mismatching upper and lower jaws and maloccluded teeth. For that reason, it has been advocated that their skulls (including the teeth) can be divided into more or less independent modules on the basis of genetics, development or function. In this study, we investigated whether the large diversity of dog skulls and the frequent occurrence of orofacial disproportions can be explained by a lower integration strength between the modules of the skull and by deviations in their covariation pattern when compared to wolves. For that purpose, we employed geometric morphometric methods on the basis of 99 3D-landmarks representing the cranium (subdivided into rostrum and braincase), the mandible (subdivided into ramus and corpus), and the upper and lower tooth rows. These were taken from CT images of 196 dog and wolf skulls. First, we calculated the shape disparity of the mandible and the cranium in dogs and wolves. Then we tested whether the integration strength (measured by RV coefficient) and the covariation pattern (as analysed by partial least squares analysis) of the modules subordinate to the cranium and the mandible can explain differing disparity results. We show, contrary to our expectations, that the higher skull shape diversity in dogs is not explained by less integrated skull modules. Also, the pattern of their covariation in the dog skull can be traced back to similar patterns in the wolf. This shows that existing differences between wolves and dogs are at the utmost a matter of degree and not absolute.

1. Introduction

Domestic dog skulls (*Canis lupus f. familiaris*, Linnaeus 1758) are much more diverse than those of grey wolves and even approximate the variation found in all wild carnivores (Drake and Klingenberg, 2010). By domesticating the wolf and by breeding dogs according to breeding standards, humans created over 350 dog breeds (http://www.fci.be), each with uniquely formed heads. As a result, dog skulls vary greatly in size, relative rostrum length (from brachycephalic to dolichocephalic), skull flexion (from klinorhynch to airorhynch) and gracility/robustness (Fig. 1) (Klatt, 1949; Rosenberg, 1966; Nussbaumer, 1982; Brehm et al., 1985; Drake and Klingenberg, 2010). Moreover, some dog skulls show disproportions between the mandible and the cranium and between the teeth and the jaw (e.g., bulldogs with undershot bite and crowded teeth (Colyer, 1990), implying a reduced integration of those skull parts when compared to the wolf.

Parts of the skull which are strongly integrated internally but only weakly integrated with other skull parts have been coined ‘modules’ (Klingenberg, 2008, 2009, 2013). For example, some authors have suggested that the rostrum and the braincase are modules of the dog cranium (Drake and Klingenberg, 2010; Cardini and Polly, 2013). A modular structure like this could allow single modules to vary more independently without any negative consequences for other parts of the skull. This would then, in theory, increase the evolvability of the skull as a whole (Goswami, 2007; Zelditch et al., 2008; Kuratani, 2009; Marroig et al., 2009; Porto et al., 2009, 2013). Modularity in the skull is suggested to be caused by ‘local factors’. These are influences, such as specific genes or developmental factors, which affect only restricted areas of the skull rather than the skull as a whole (Mitteroecker and Bookstein, 2008). For example, certain genes influence tooth formation without any direct effects on the surrounding bone (Hall, 2003).

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* Corresponding author at: Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Erbertstr. 1, D-07743 Jena, Germany.
E-mail address: stefan_curth@hotmail.com (S. Curth).

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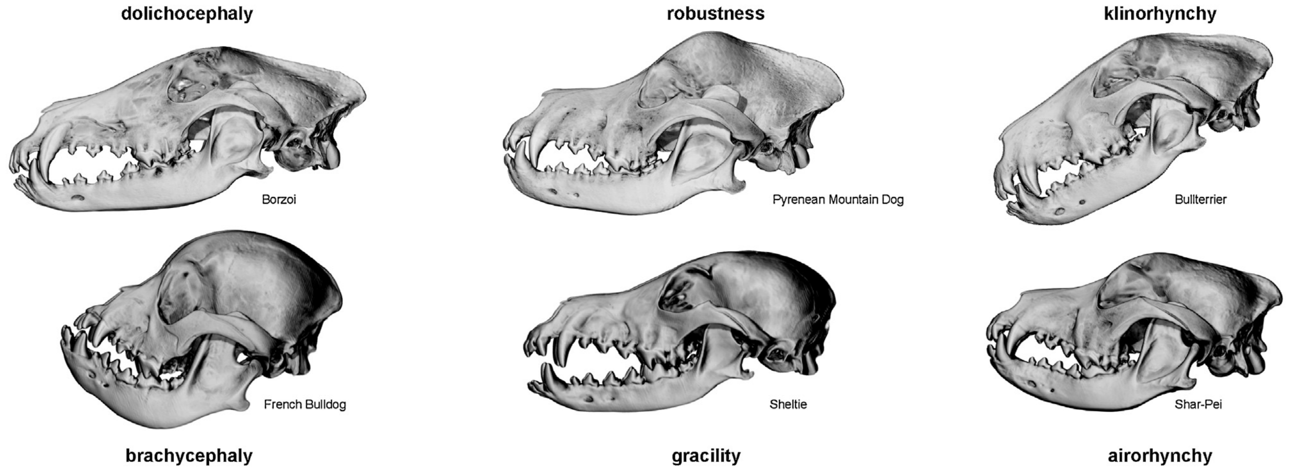

Fig. 1. Three commonly seen types of shape variation in the dog skull: relative rostrum length, robustness and skull flexion exemplified by six representative breeds.

On the other hand, the modules of the skull can never be fully independent from one another. This is guaranteed by their integration in the skull which is generated by 'common factors', which have an effect on the whole skull rather than on separate modules (Mitteroecker and Bookstein, 2008). Such factors are pleiotropic genes, shared developmental pathways or a common function, which underlies similar environmental influences such as diet. These common factors can also account for variation in the skull, but rather than allowing individual modules to vary independently, common factors cause multiple modules or even the whole skull to vary. For example, size variation in mammals causes variation throughout the whole skull rather than in restricted areas (Cardini and Polly, 2013).

In the present study we were interested in the balance of integration and modularity in the skulls of wolves and dogs. We assumed that less integrated skull modules could provide an explanation for the enormous skull diversity and frequent occurrence of orofacial disproportions in dogs, as opposed to the highly integrated and less diverse wolf skulls. Specifically, we hypothesized (i) that the shape disparity of the mandible and cranium (both with and without the dentition) would be significantly larger in dogs than in wolves, (ii) that this larger disparity would be explained by a low integration strength of the modules subordinate to the cranium and the mandible, and (iii) that the covariation pattern of these modules would also be different in dogs and wolves, giving another explanation for the larger skull shape variation in dogs which in part lacks natural equivalents.

The balance of integration and modularity and the covariation patterns of modules can be tested and described by using statistical methods from the field of geometric morphometrics. We did this on the basis of 196 CT scans of dog and wolf skulls and a data set of 99 landmarks. These define the shapes of several exemplary modules in the dog skull, among them the rostrum and the braincase of the cranium, the corpus and ramus of the mandible and the upper and lower tooth row. We decided on those modules based on numerous findings by other authors suggesting partly separate genetic determination and inheritance of those skull parts but also diverging selective pressures (e.g., Grüneberg and Lea, 1940; Stockard, 1941; Herre, 1951; Starck, 1953; Stengel, 1958; Boughner and Hallgrímsson, 2008; Drake and Klingenberg, 2010; Cramon-Taubadel, 2011; La Croix et al., 2011; Gómez-Robles and Polly, 2012; Le Cabec et al., 2012; Asahara, 2013).

2. Materials and methods

2.1. Sample

Our sample (Table S1 in the online Appendix) comprised 140 skull CT scans of domestic dogs (adult, both sexes, 103 breeds, types or mixtures) and 56 scans of grey wolves (adult, both sexes, different subspecies originating from North America, Europe and Asia). We aimed at covering a wide spectrum of skull forms, both in wolves and dogs. We obtained the skulls from different museums and scanned them with computerized tomography (CT) at multiple locations (details are given in Tables S1 and S2). During the scans, the mandible was articulated to the cranium.

2.2. 3D-reconstructions and landmarks

We volume-rendered the skulls in 3D in Avizo v. 7 (FEI Visualization Sciences Group, Mérignac, France) and placed a set of 99 landmarks (LM) on the renderings or directly on the CT slices (Fig. 2 and Table S3). We chose the landmarks to sufficiently reflect the external shape of the cranium and the mandible and to capture the spatial position and orientation of the teeth (including the tooth roots). We solely obtained the landmarks for the left half of the skull to reduce the total number of landmarks. In the case of missing landmarks on this side, we obtained all landmarks from the right side of the skull and mirrored them for the analysis. The procedure of digitizing only one half of a bilateral structure is applicable to dogs and wolves because their skull shape variation approaches macroevolutionary levels (Drake and Klingenberg, 2010; Cardini, 2016). Only one researcher (S.C.) digitized the landmarks in order to eliminate interobserver errors. Moreover, we performed a Procrustes ANOVA on a subset of the sample (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002) to calculate the intraobserver error during the landmark digitization. For each specimen the landmarks were digitized three times on the same CT scan. The results reflected that the error of the landmark digitization is very low compared to the skull shape variation in the sample (for the results see Table S4).

2.3. Geometric morphometric analysis

We imported the landmark set into MorphoJ (Klingenberg, 2011) and divided it into four different sets of landmarks: the mandible (13 LM), the mandible including teeth (42 LM), the cra-

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