

Large-Scale Diversification of Skull Shape in Domestic Dogs: Disparity and Modularity

Abby Grace Drake* and Christian Peter Klingenberg

Faculty of Life Sciences, University of Manchester, Michael Smith Building, Oxford Road, Manchester M13 9PT, United Kingdom

Submitted June 1, 2009; Accepted October 27, 2009; Electronically published January 22, 2010

ABSTRACT: The variation among domestic dog breeds offers a unique opportunity to study large-scale diversification by microevolutionary mechanisms. We use geometric morphometrics to quantify the diversity of skull shape in 106 breeds of domestic dog, in three wild canid species, and across the order Carnivora. The amount of shape variation among domestic dogs far exceeds that in wild species, and it is comparable to the disparity throughout the Carnivora. The greatest shape distances between dog breeds clearly surpass the maximum divergence between species in the Carnivora. Moreover, domestic dogs occupy a range of novel shapes outside the domain of wild carnivorans. The disparity among companion dogs substantially exceeds that of other classes of breeds, suggesting that relaxed functional demands facilitated diversification. Much of the diversity of dog skull shapes stems from variation between short and elongate skulls and from modularity of the face versus that of the neurocranium. These patterns of integration and modularity apply to variation among individuals and breeds, but they also apply to fluctuating asymmetry, indicating they have a shared developmental basis. These patterns of variation are also found for the wolf and across the Carnivora, suggesting that they existed before the domestication of dogs and are not a result of selective breeding.

Keywords: *Canis familiaris*, Carnivora, geometric morphometrics, morphological integration, novelty, selection.

Introduction

Evolutionary change in morphological traits can be very rapid, as has been documented by a range of studies (Reznick et al. 1997; Hendry and Kinnison 1999; Huey et al. 2000; Grant and Grant 2006). Most of the changes found in natural populations are at a relatively small scale, however, and therefore the question is raised as to whether there are inherent limits to the amounts of change that can occur by microevolutionary mechanisms or whether special macroevolutionary processes are required to

achieve large-scale change (Stanley 1998; Gould 2002). Similarly, studies of adaptive radiation face difficulties in extrapolating from microevolutionary data recorded in extant species to the larger scale of the entire radiation (e.g., Gavrillets and Losos 2009). These problems can be addressed directly in domesticated organisms, where sustained selection by breeders has long been known to cause large-scale phenotypic change (e.g., Darwin 1868).

Although large-scale variation has been indicated for other domesticated species such as pigeons (Darwin 1868; Helms and Brugmann 2007), and the morphological variation of these species has been studied quantitatively (e.g., Johnston 1992), the variation among the breeds of the domestic dog (*Canis familiaris*) is particularly suitable for examining large morphological changes that originated exclusively from microevolutionary processes (Darwin 1868; Stockard 1941; Wayne 1986a, 1986b; Clutton-Brock 1995; Coppinger and Coppinger 2001; Chase et al. 2002; Fondon and Garner 2004; Parker et al. 2004; Lindblad-Toh et al. 2005; Wayne and Ostrander 2007). Many dog breeds were established by selecting limited numbers of individuals for breeding from larger populations (such as a regional pool of farm dogs) or from one or more existing breeds; therefore, these breeds are equivalent to new lineages resulting from founder events and hybridization (Parker et al. 2004; Lindblad-Toh et al. 2005; Sampson and Binns 2006; Räber 2008). The reproductive separation and limited effective population sizes of established breeds provide extensive opportunity for divergence by genetic drift (Parker et al. 2004; Wayne and Ostrander 2007; Björnerfeldt et al. 2008; Calboli et al. 2008). Moreover, breeds are under selection for a variety of morphological and behavioral traits (Coppinger and Coppinger 2001; Parker et al. 2004; Ostrander et al. 2006; Räber 2008). For instance, selection by breeders for specific traits of the head has been shown to yield sustained and substantial change in skull shape (Drake and Klingenberg 2008). As a result, domestic dogs have a vast spectrum of cranial variation (Darwin 1868; Stockard 1941; Nussbaumer 1982; Wayne 1986a; Young and Banasch 2006), which has clear functional consequences, for

* Corresponding author. Present address: Department of Biology, College of the Holy Cross, P.O. Box B, Worcester, Massachusetts 01610; e-mail: abbygracedrake@googlemail.com.

instance, on bite forces (Ellis et al. 2009) or breathing (Koch et al. 2003). In many ways, this situation corresponds to an adaptive radiation (Schluter 2000; Gavrillets and Losos 2009), but at the intraspecific level.

To what extent morphological variation is modular or integrated throughout an entire structure is widely considered to be a key determinant of evolutionary flexibility (Cheverud 1984; Wagner and Altenberg 1996; Klingenberg 2005). Because strong integration among parts may act as a constraint if they are under opposing selection regimes, modularity may enhance the capacity of morphological traits to evolve. Moreover, the patterns of integration can influence the direction of evolution and therefore may have long-term consequences, for instance, if there are multiple fitness peaks (Schluter 1996; Arthur 2001). In turn, the patterns of morphological integration are also expected to evolve under the influence of selection and, as a consequence, to reflect functional associations among traits (Cheverud 1984; Wagner and Altenberg 1996). Both integration and modularity can vary in strength and are not all-or-nothing phenomena (Klingenberg et al. 2003). Integration and modularity can be studied by analyzing the covariation among traits. Covariation of traits among individuals reflects all differences, including evolutionary divergence of taxa or breeds, whereas the covariation of fluctuating asymmetry can reveal integration and modularity of the developmental processes that are generating the traits of interest (Klingenberg 2003, 2005).

Domestic dogs show abundant variation in the arrangement of the nasomaxillary complex in relation to the neurocranium (Stockard 1941; Nussbaumer 1982; Fondon and Garner 2004; Drake and Klingenberg 2008), suggesting that the two cranial complexes may be separate modules. Moreover, there is integrated shape variation along a spectrum, from dolichocephalic breeds, which have slender and elongate skulls, to brachycephalic breeds, which have short and broad skull shapes (Wayne 1986a; Haworth et al. 2001; Young and Bannasch 2006). Although parts of the skull can be involved to different degrees, this type of variation tends to have effects on most of the parts and suggests integration throughout the whole skull. Similar patterns of variation were also reported in domestic cats (Künzel et al. 2003), in interspecific comparisons in Carnivora, and even in marsupials (Sears et al. 2007; Wroe and Milne 2007), which raises the question as to whether the process of domestication and divergence of breeds disrupted ancestral constraints or exploited pre-existing patterns of modular and integrated variation.

Here we use geometric morphometrics to characterize and quantify shape variation in the skulls of domestic dogs, and we compare this variation to variation in the three most closely related wild species (Lindblad-Toh et al. 2005), the gray wolf (*Canis lupus*), the coyote (*Canis la-*

trans), and the golden jackal (*Canis aureus*). Because cranial variation in domestic dogs is known to exceed that in the family Canidae (Wayne 1986a), we use representatives from the entire order Carnivora as the basis for comparison. In addition to quantifying the shape disparity in these taxa, we also examine the patterns of integration in the skull. Integration in the average shapes of the left and right sides of the skull provides information about variation among individuals in the samples, including the differentiation of breeds or species. Cranial asymmetries, however, arise from perturbations in the development of each individual and can thus provide information about the inherent tendency of skull development to produce new morphological variation (Klingenberg 2005, 2008b). By comparing integration in domestic dogs, in the wolf, and across the Carnivora, we investigate whether domestication changed the patterns of integration and modularity, thereby disrupting ancestral evolutionary constraints, or whether the diversification of domestic dogs used conserved patterns of cranial covariation.

Material and Methods

Data Set

Our study includes 677 adult dogs from 106 breeds (numbers of individuals per breed range from one to 62). The sample of Carnivora includes one species each from 122 genera representing all major groups within the order (Flynn et al. 2005), and care was taken to include the full range of disparity. In addition, we examined samples of adult gray wolves ($n = 288$), coyotes ($n = 57$), and golden jackals ($n = 49$). Skulls were obtained from the following collections: the Smithsonian Institution's National Museum of Natural History (Washington, DC); the private collection of Bonnie Dazell; the University of Alaska Museum in Fairbanks, Alaska; the Museum of Vertebrate Zoology at the University of California in Berkeley, California; the Natural History Museum (London); the Natural History Museum in Bern, Switzerland; the Powell-Cotton Museum (Birchington, United Kingdom); and the Oxford University Museum of Natural History (Oxford, United Kingdom).

A set of 50 landmarks (12 median landmarks and 19 pairs on the left and right sides; fig. 1; table 1) was digitized in three dimensions on the dorsal and the ventral aspects of each skull using a MicroScribe digitizer. The landmarks of the dorsal and the ventral aspects were combined by a least squares fit (translation and rotation only) using four landmarks that were digitized from both the dorsal and the ventral views. Every skull was digitized twice.

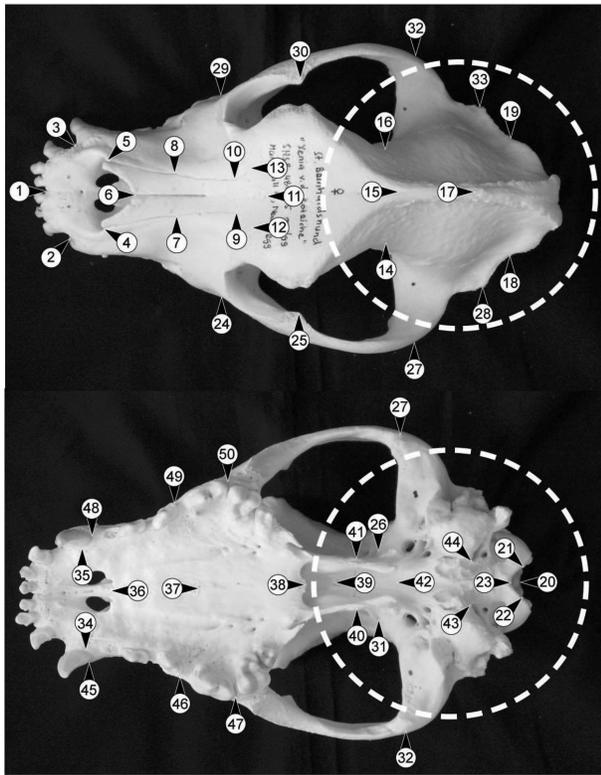


Figure 1: Landmarks on the dorsal and ventral sides of the skull that were digitized (for anatomical definitions, see table 1). The dashed circles indicate the hypothesis of modularity; the landmarks inside these circles belong to the neurocranial module, whereas the landmarks outside the circles are included in the facial module.

Shape Analysis

We quantify shape variation in the skulls of dogs by using the methods of geometric morphometrics as implemented in the MorphoJ software (Klingenberg 2008a). Shape variation was extracted from the coordinate data by a full Procrustes fit and projection to the shape-tangent space (Dryden and Mardia 1998), using a procedure that takes into account the object symmetry of the skull (Klingenberg et al. 2002). An initial Procrustes ANOVA (Klingenberg et al. 2002) confirmed that the Procrustes mean squares for individual variation and fluctuating asymmetry substantially exceeded measurement error, such that measurement error is negligible (particularly for the analyses of variation among individuals). For the remaining analyses, we averaged the shape data from the replicate measurements of each specimen. To explore the shape variation in the total data set, we used a multivariate ordination of skull shapes by a principal component (PC) analysis based on the covariance matrix of the symmetric component of shape variation (Klingenberg et al. 2002). Visualizations of

shapes at the extremes of the PC axes were performed by warping the scanned surface of a wolf skull, using the Landmark software (Wiley et al. 2005).

Comparisons of Disparity

As a direct measure of the differences in shape, we computed Procrustes distances between all possible pairs of specimens in the dog sample and in the carnivoran sample. Procrustes distances between specimens were computed as Euclidean distances in tangent space (Dryden and Mardia 1998). Even the greatest pairwise distances between specimens were within the range of distances where the tangent-space approximation performs well (Marcus et al. 2000).

Two measures of shape disparity were computed. The first is the Procrustes variance of observations in each group, which is the mean squared Procrustes distance of each specimen or breed average from the mean shape of the respective group or, equivalently, the sum of the sample variances of all Procrustes coordinates (Klingenberg and McIntyre 1998; Zelditch et al. 2003). Procrustes variance quantifies the average dispersion of data points around the mean shape. The second measure is the volume of the convex hull (de Berg et al. 2000) enclosing the data points of each group, which quantifies the portion of shape space occupied by the group. This is a measure of the degree of difference among opposite extremes in each group, and therefore it does not consider observations located near the center of the scatter of data points. Convex hulls were computed from the first three PCs because they contained most of the variation in the sample and because computation of higher-dimensional volumes presented computational difficulties (dimensions with small amounts of variation produce volumes near 0 for all samples, which led to problems with numerical precision). The statistical significance for pairwise comparisons of samples was established with permutation tests (Good 2000) that simulated the null hypothesis of equal dispersion within groups by randomly exchanging the deviations of data points from the respective sample mean.

Allometry is a major factor in the diversification of dogs (e.g., Wayne 1986a). To correct for the effects of allometry on shape disparity, we computed the same disparity measures for the residuals from pooled within-group regression of shape on size. Because of the large amount of variation in and the sample size of the dogs, this common estimate of allometry is likely to be a better fit for dogs than for the other groups in this study. It is therefore expected to eliminate the allometric component of shape variation more effectively from dogs than from the other groups and, thus, to reduce the total shape disparity for the dogs to a greater degree than for the other samples.

Analyses of disparity were conducted to compare dogs,

Table 1: Osteometric landmarks collected on each skull, and their definitions

Landmark	Definition
1	Midline point on the premaxilla at the inferior tip of the bony septum between the upper central incisors (F)
2	Premaxillary-maxillary suture, anterior, left side (F)
3	Premaxillary-maxillary suture, anterior, right side (F)
4	Nasal, anterior tip, left side (F)
5	Nasal, anterior tip, right side (F)
6	Nasale, nasal, anterior, midline (F)
7	Premaxillary-maxillary suture, posterior end in dorsal view, left side (F)
8	Premaxillary-maxillary suture, posterior end in dorsal view, right side (F)
9	Frontal-maxillary-nasal suture, left side (F)
10	Frontal-maxillary-nasal suture, right side (F)
11	Nasion, nasal-frontal suture, midline (F)
12	Frontal-maxillary suture, posterior, left side (F)
13	Frontal-maxillary suture, posterior, right side (F)
14	Frontal-parietal-sphenoid suture, left side (N)
15	Bregma, frontal-parietal suture, midline (N)
16	Frontal-parietal-sphenoid suture, right side (N)
17	Lambda, parietal-occipital suture, midline (N)
18	Asterion, posterior at occipital-parietal-temporal suture, left side (N)
19	Asterion, posterior at occipital-parietal-temporal suture, right side (N)
20	Opisthion, dorsal lip of foramen magnum, midline (N)
21	Occipital condyle (widest point of foramen magnum), left side (N)
22	Occipital condyle (widest point of foramen magnum), right side (N)
23	Basion, ventral lip of foramen magnum, midline (N)
24	Zygo-maxillare inferior, left side (F)
25	Squamosal-jugal suture, anterior projection of zygomatic process of temporal bone, left side (F)
26	Optic canal (ventral lip), left side (N)
27	Squamosal-jugal suture, posterior projection of jugal, ventral, left side (F)
28	External auditory meatus, posterior, left side (N)
29	Zygo-maxillare inferior, right side (F)
30	Squamosal-jugal suture, anterior projection of zygomatic process of temporal bone, right side (F)
31	Optic canal (ventral lip), right side (N)
32	Squamosal-jugal suture, posterior projection of jugal, ventral, right side (F)
33	External auditory meatus, posterior, right side (N)
34	Premaxillary-maxillary suture, lateral end in ventral view, left side (F)
35	Premaxillary-maxillary suture, lateral end in ventral view, right side (F)
36	Premaxillary-maxillary suture, posterior at midline (F)
37	Maxillary-palatine suture, anterior at midline (F)
38	Palatine, posterior at midline (F)
39	Presphenoid, anterior tip at midline (F)
40	Palatine-pterygoid suture posterior, right side (N)
41	Palatine-pterygoid suture posterior, left side (N)
42	Presphenoid-basisphenoid suture, midline (N)
43	Tympanooccipital fissure, anterior lip, right side (N)
44	Tympanooccipital fissure, anterior lip, left side (N)
45	Canine (posterior buccal corner), right side (F)
46	Premolar 3 (posterior buccal corner), right side (F)
47	Premolar 4 (posterior buccal corner), right side (F)
48	Canine (posterior buccal corner), left side (F)
49	Premolar 3 (posterior buccal corner), left side (F)
50	Premolar 4 (posterior buccal corner), left side (F)

Note: The letters F and N indicate whether a landmark belongs to the face or to the neurocranium, respectively.

the three wild canid species, and the Carnivora (see “Data Set” for sample sizes). Moreover, we also compared the disparity of dogs according to the following functional groups (as defined by the United Kennel Club): Companion Dog ($n = 138$, 20 breeds), Guardian Dog ($n = 246$, 23 breeds), Gun Dog ($n = 42$, nine breeds), Herding Dog ($n = 44$, 10 breeds), Northern Breed ($n = 51$, 12 breeds comprising various sledge, hunting, and guard dogs), Scenthound ($n = 19$, six breeds), Sighthound and Pariah ($n = 68$, 13 breeds, including the dingo and the New Guinea singing dog), and Terrier ($n = 69$, 13 breeds).

Integration and Modularity

Because differences in the arrangement of the snout relative to the braincase—for instance, the variation between klinorhynch and airohynch (Nussbaumer 1982; Fondon and Garner 2004)—are an important component of cranial variation in domestic dogs, we examine the hypothesis that the face and the neurocranium are separate modules (fig. 1; table 1). Modules are regions that are integrated internally but that are relatively independent of each other. The hypothesis of modularity therefore implies that the covariation between the landmarks of the face and those of the neurocranium should be weaker than the covariation for other partitions of the landmarks into subsets of the corresponding sizes (Klingenberg et al. 2003; Klingenberg 2008b, 2009).

To assess the strength of modularity, we compared the strength of covariation between subsets of landmarks for the hypothesized modules with that of alternative partitions of the total set of landmarks into subsets (Klingenberg 2009). To quantify the strength of covariation between subsets of landmarks, we used the RV coefficient (Escoufier 1973), which can be interpreted as a multivariate generalization of the bivariate R^2 value (for detailed explanations, see Klingenberg 2009; Laffont et al. 2009). The RV coefficient for the subdivision of landmarks into facial and neurocranial regions was compared with the distribution of RV coefficients for randomly generated subdivisions. Random subdivisions were formed from the paired landmarks of one side and the median landmarks such that the numbers of landmarks matched those in the facial and neurocranial regions (Klingenberg 2009). We limited this comparison to those subdivisions where both subsets of landmarks were spatially contiguous (i.e., connected by the edges of a graph indicating landmarks that are anatomically adjacent; fig. 2; for details, see Klingenberg 2009).

For the analysis of modularity in the symmetric component of shape variation in the Carnivora, we used independent contrasts (Felsenstein 1985) to take into account the phylogenetic structure of the data, using the supertree of Bininda-Emonds et al. (2007). This adjust-

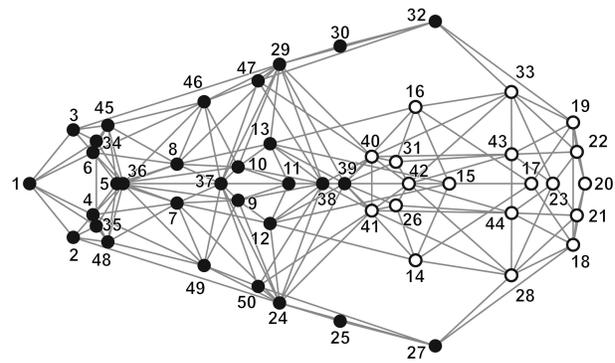


Figure 2: Hypothesis of modularity and adjacency graph for the landmarks. The filled circles denote the landmarks of the facial module; the open circles denote the landmarks of the neurocranial module (see also fig. 1 and table 1). The lines connect landmarks that are deemed to be anatomically adjacent to one other, and they are used to define spatial contiguity of partitions of landmarks (Klingenberg 2009). A subset of landmarks is spatially contiguous if all of its landmarks are connected by the edges of the adjacency graph. A partition of the configuration is contiguous if all subsets of landmarks are contiguous themselves (Klingenberg 2009).

ment was not required for the asymmetric component, because the left-right differences are computed within individuals and are therefore independent with respect to phylogeny.

For quantifying overall similarity of covariance matrices, we computed matrix correlations and the associated permutation tests, using procedures adapted for geometric morphometrics and object symmetry (Klingenberg and McIntyre 1998; Klingenberg et al. 2002; Klingenberg 2008a).

Results

Patterns of Morphological Diversification and Novelty

The first three PCs account for 71.8% of the total shape variation, and therefore, they provide a reasonable approximation of the total variation (no other PC accounts for more than 5%). PC1 primarily contrasts brachycephalic and dolichocephalic skulls; PC2 opposes elongate skulls, where the braincase is aligned posterior to the muzzle, to broader and higher skulls, where the braincase is raised above the rostrum; and, finally, PC3 sets skulls with enlarged faces and broad and high rostra against others with relatively larger braincases and muzzles that taper markedly toward the front (fig. 3D). The scatter of PC scores (fig. 3A–3C) shows that the amount of variation is much greater in dogs than it is in wolves, coyotes, and golden jackals and that the dispersion of data points for dogs is comparable to that across the Carnivora.

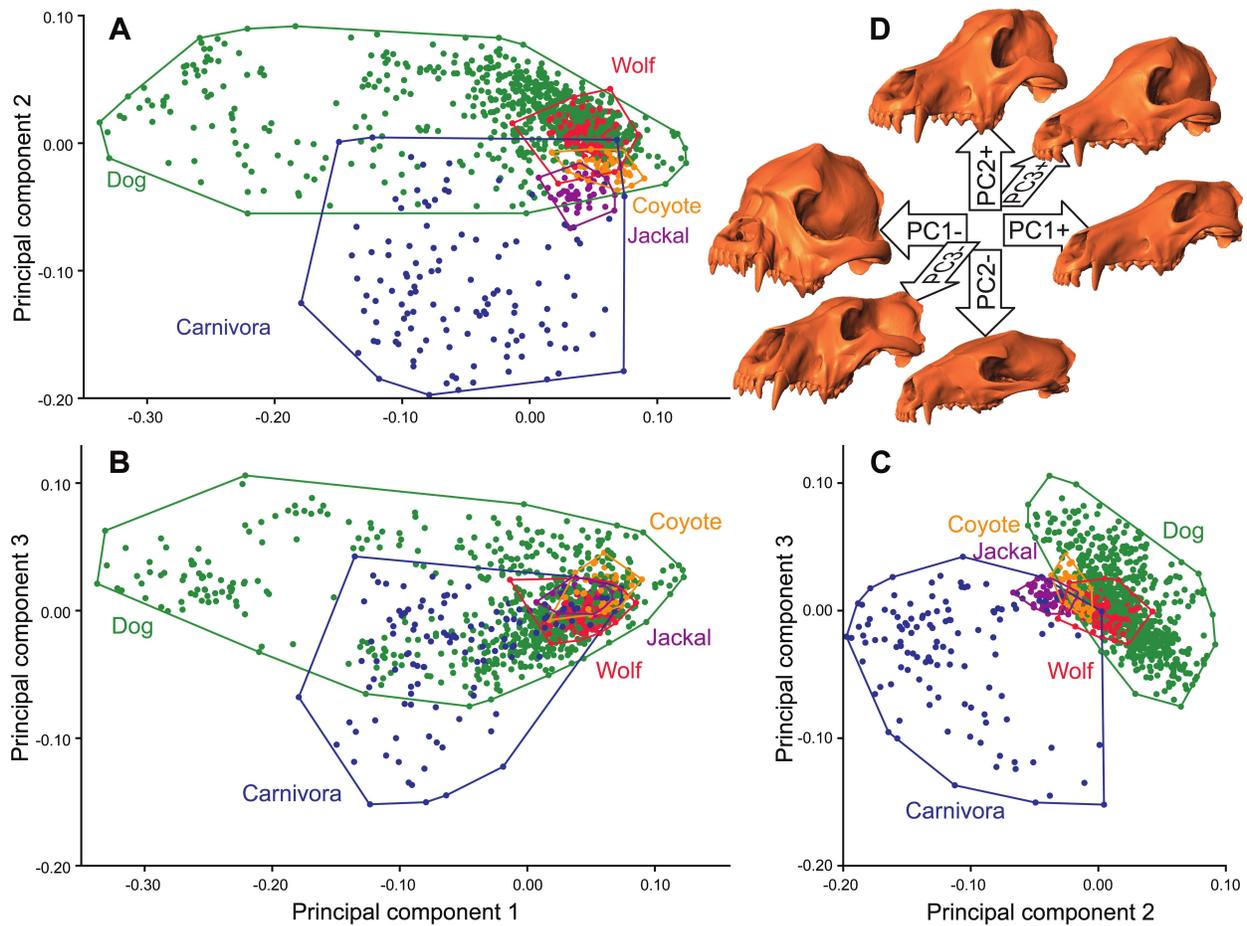


Figure 3: Principal component (PC) analysis for skull shape in the complete data set. A–C, Plots of the PC scores. D, Shape changes associated with the PC axes. For each PC, the shapes corresponding to the observed extremes in the positive and negative directions are shown as a warped surface of a wolf skull (Wiley et al. 2005).

Closer inspection of the PC plots for shape variation (fig. 3) clearly shows that domestic dogs have only limited overlap with the other carnivores (see particularly fig. 3C). The samples of wolves, coyotes, and golden jackals are located in the region of the intersection between dogs and the other carnivores. It is clear from this analysis not only that domestic dogs occupy a large region of shape space that is outside of the range of the ancestral species, the wolf, and the other members of the family Canidae (Wayne 1986a) but also that much of the shape variation in domestic dogs is novel relative to the range of skull shapes in the order Carnivora as a whole.

Quantifying Disparity

The greatest Procrustes distance between specimens in the dog sample is 0.477 (between a Collie and a Pekingese),

which exceeds the distance of 0.424 between the most divergent specimens in the Carnivora sample (walrus *Odobenus rosmarus* and falanouc *Eupleres goudotii*). Among domestic dogs, pairwise distances greater than 0.45 involve other pairings of breeds (Borzoi–Pekingese, Collie–Japanese Chin, Borzoi–Japanese Chin, Borzoi–Pug, Airedale Terrier–Pekingese, Scottish Deerhound–Pekingese, Collie–Pug). All of these contrasts are between dolichocephalic and brachycephalic breeds. In the sample of the Carnivora, all other Procrustes distances greater than 0.4 also involve the walrus, in combination with the mountain coati (*Nasuella olivacea*, 0.405), the Malagasy civet (*Fossa fossana*, 0.404), Owston’s palm civet (*Chrotogale owstoni*, 0.404), and the servaline genet (*Genetta servalina*, 0.401).

To compare the amounts of shape variation in the entire sample of domestic dogs, the three wild species, and the Carnivora, we used two measures of disparity that capture

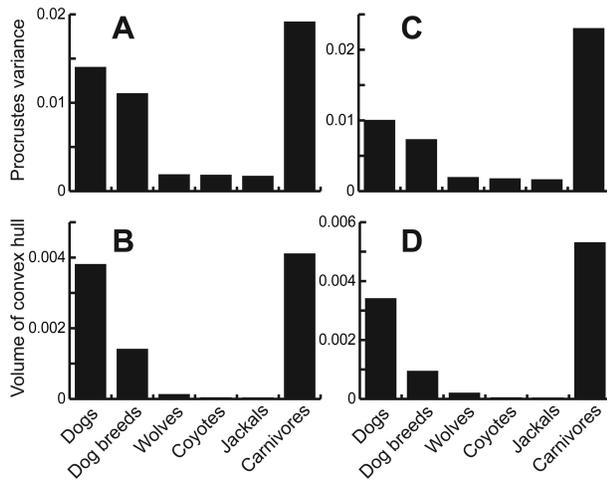


Figure 4: Skull shape disparity in the different samples. *A*, Total shape disparity, quantified by Procrustes variance. *B*, Total shape disparity, quantified by the volumes of the convex hulls for the first three dimensions. *C*, Shape disparity corrected for the effects of size, quantified by Procrustes variance. *D*, Shape disparity corrected for the effects of size, quantified by the volumes of convex hulls for the first three dimensions.

different aspects of shape diversification within samples: Procrustes variance and the volume of the convex hull enclosing the data points. Both measures of shape disparity give similar results (fig. 4A, 4B). The variation among average shapes of dog breeds is less than that among individual dogs (significantly so for the volume of convex hulls, $P = .0004$; nonsignificantly so for Procrustes variance, $P = .12$). The disparity within dogs, both among individuals and among breed means, is consistently much greater than the disparity within wolves, coyotes, and golden jackals (for both measures of disparity; all $P \leq .002$). Finally, the variation among individual dogs is of a magnitude similar to that in the carnivore sample (significant difference for Procrustes variance, $P = .0028$; no significant difference for the volume of convex hulls, $P = .99$). The fact that this match between dogs and carnivores is closer for the volumes of the convex hulls (fig. 4B) than for the Procrustes variances (fig. 4A) reflects the fact that the disparity among dogs is dominated particularly by some breeds that are highly divergent, whereas many breeds retain a skull shape that is closer to the ancestral shape (fig. 3).

Because allometry is a major factor in the diversification of dog breeds, we repeated these comparisons with data that were corrected for the effects of allometry. The estimates of disparity based on the residuals from allometric regression (fig. 4C, 4D) are similar to the uncorrected values, with substantially greater disparity for domestic dogs than for the wild canid species. Because the estimate

of allometry is dominated by domestic dogs, the amounts of variation are reduced more for the dogs than for the other groups (fig. 4C, 4D; the slight increase for the carnivore sample is due to differences in allometries). Nevertheless, this analysis shows conclusively that the disproportionate amount of shape variation in domestic dogs is not simply due to allometric scaling.

Among the groups of dog breeds as defined by the United Kennel Club, the Companion Dog group has a far greater disparity than do any of the other groups, regardless of which of the two disparity measures is used or whether a correction for allometric effects is made (fig. 5; all $P \leq .0001$). If the Companion Dog group is contrasted to all other groups jointly (rightmost columns in the panels of fig. 5), it still has a much greater Procrustes variance ($P < .0001$), but it has a comparable volume of the convex hull ($P = .99$ and $.82$ for analyses without and with the correction for allometric effects, respectively). The difference in the results reflects the manner in which the two measures of disparity consider the average versus the extreme deviations from the shape averages in the groups under comparison.

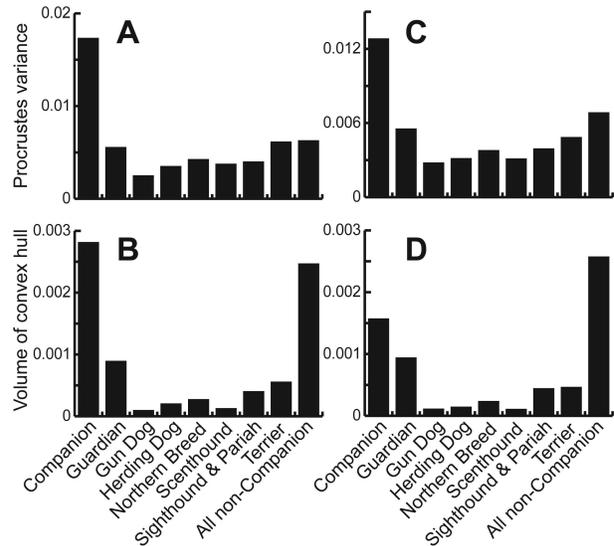


Figure 5: Skull shape disparity in the different groups of dogs, according to the breed classification of the United Kennel Club. *A*, Total shape disparity, quantified by Procrustes variance. *B*, Total shape disparity, quantified by the volumes of the convex hulls for the first three dimensions. *C*, Shape disparity corrected for the effects of size, quantified by Procrustes variance. *D*, Shape disparity corrected for the effects of size, quantified by the volumes of convex hulls for the first three dimensions. The last column in each panel (“All non-Companion”) includes all groups other than Companion Dog. The size correction for *C* and *D* was computed for dogs separately, and therefore it differs from the one used in figure 4; *A* and *B* are directly comparable to figure 4A and 4B, respectively.

Integration and Modularity of the Skull

In the sample of domestic dogs, the RV coefficient between facial and neurocranial landmarks is 0.87 for the symmetric component of variation, which indicates a very strong association. This value shows the tight integration of the entire skull in dogs (PC1, which represents a contrast between dolichocephalic and brachycephalic breeds, alone accounts for more than 63% of the symmetric variance in the sample). Nevertheless, the RV coefficient between the facial and neurocranial subsets is lower than those for most other subdivisions of the landmarks ($P = .0475$; fig. 6A). Analyses with a correction for allometric variation yield very similar results. Overall, therefore, the face and the neurocranium possess a degree of modular separation despite the strong integration, particularly in the differences between breeds (e.g., breeds with short skulls vs. those with long skulls).

For asymmetry in dogs, integration is generally lower than it is for the symmetric component (fig. 6B), and the RV coefficient between facial and neurocranial regions is 0.32. This RV coefficient is lower than those for most alternative partitions ($P = .0052$). The matrix correlation between the covariance matrices for the symmetric and the asymmetric components of variation in dogs is 0.20 ($P = .044$), indicating a weak but statistically discernible relationship between the diversification of skull shapes across breeds and the intrinsic pattern of cranial variation.

Integration in the symmetric component of shape variation in the wolf is substantially weaker than it is for the domestic dogs (fig. 6C). The RV coefficient between facial and neurocranial landmarks is 0.32, which is lower than the RV coefficients for most alternative partitions ($P = .0538$). For asymmetry in wolves, the RV coefficient for the subdivision into facial and neurocranial sets is 0.21, and only 26 of 10,000 random subdivisions yield a lower covariation. The range of RV coefficients is fairly limited for both symmetric and asymmetric components (fig. 6C, 6D), because all partitions have a similar, low-to-moderate covariation. Whereas this result is consistent with the hypothesis of facial and neurocranial modules, the limited range of RV coefficients indicates a fairly weak modularity. The matrix correlation between the covariance matrices for the symmetric and asymmetric components of variation in the wolf sample is 0.63 ($P < .0001$). The asymmetric components of the dog and the wolf samples have a matrix correlation of 0.77 ($P < .0001$) and are thus quite similar, suggesting shared patterns of developmental variation in wolves and dogs. The patterns of variation in the symmetric component are less similar (matrix correlation: 0.47; $P < .0001$).

In the analysis of the symmetric component of shape variation in the Carnivora, the RV coefficient for the sub-

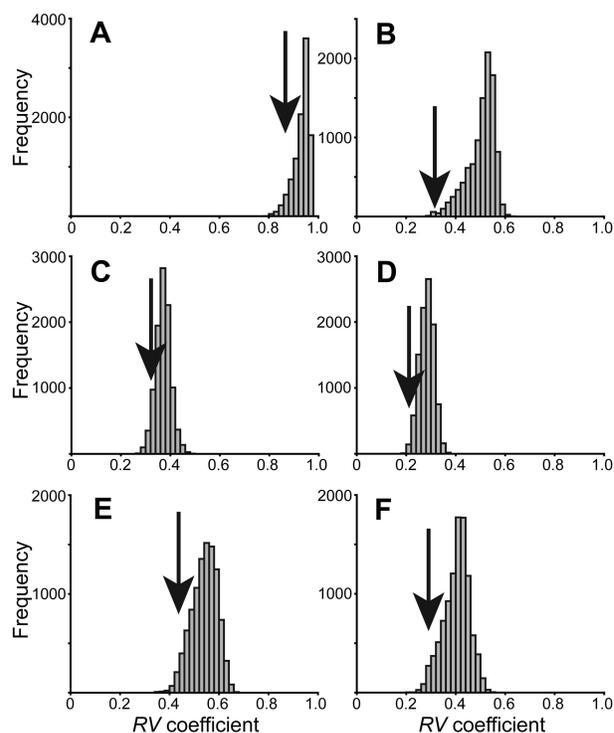


Figure 6: Analysis of modularity in the skull. Graphs show the RV coefficients (interpreted as multivariate generalizations of the bivariate R^2 values; Escoufier 1973) for the subdivision of landmarks into facial and neurocranial regions (arrows) and the distribution of RV coefficients for 10,000 alternative partitions of landmarks into anatomically contiguous subsets (histograms). A, Domestic dogs, symmetric component of variation. This includes the shape variation among breeds. B, Domestic dogs, asymmetric component. This is the component of fluctuating asymmetry, and it provides a measure of the tendency of cranial development to produce new variation. C, Wolves, symmetric component of variation. D, Wolves, asymmetric component. E, Carnivora, independent contrasts (Felsenstein 1985) for the symmetric component of variation. F, Carnivora, asymmetric component.

division into facial and neurocranial sets is 0.44, and it is less than the values for most random partitions ($P = .0293$; fig. 6E). For fluctuating asymmetry in the Carnivora, the RV coefficient between the hypothesized modules is 0.29, which is lower than the RV coefficients for most random partitions ($P = .0231$; fig. 6F). These results are consistent with the hypothesis of modularity. The patterns of variation of the symmetric and asymmetric components are moderately similar (matrix correlation: 0.45; $P = .0016$). The correspondence between the asymmetric component in the Carnivora and those in dogs and wolves is considerably better (matrix correlation: 0.73 and 0.72, respectively; both $P < .0001$). Moreover, there is a significant similarity between the covariance matrix of independent contrasts in the Carnivora and that for the symmetric

component of variation in domestic dogs (matrix correlation: 0.54; $P < .0001$), indicating that the patterns of diversification in domestic dogs are moderately similar to those in the Carnivora.

Discussion

The breeds of domestic dogs have long been known for their great variety of skull shapes (Darwin 1868; Stockard 1941; Nussbaumer 1982; Wayne 1986a; Clutton-Brock 1995; Young and Bannasch 2006). Our analyses show that the variation of cranial shape in dogs is comparable to that across the entire order Carnivora (figs. 3, 4) and that differences in skull shape between extreme dog breeds even exceed the maximal distances we found among the species of Carnivora.

This massive disparity among dogs has evolved in a few hundred to several thousand years (Clutton-Brock 1995; Lindblad-Toh et al. 2005), a very brief time span by comparison with the evolution of natural clades with comparable disparity, which raises the question as to whether the diversification in dogs can be representative of large-scale evolution in nature. Studies in natural populations have documented rapid change due to selection (Reznick et al. 1997; Hendry and Kinnison 1999; Huey et al. 2000) and, in some cases, also hybridization (Grant and Grant 2002), but the changes observed in these populations were much smaller than the differences among dog breeds. At a larger scale, bursts of relatively rapid increase in disparity have been inferred for clades of species (e.g., Harmon et al. 2003; Ricklefs 2004), and speciation itself may be a factor in this process (Ricklefs 2004; Mattila and Bokma 2008). Because dogs are a single species, however, with separation of breeds maintained only by human intervention, it is not speciation per se that is the driving force producing morphological disparity, although population bottlenecks and founder effects during establishment of breeds might cause genetic conditions similar to those in new species or island populations (Meffert 2006; Millien 2006; Losos and Ricklefs 2009). As a consequence of these effects, nonsynonymous mutations have accumulated in the dog genome (Cruz et al. 2008), which may facilitate morphological divergence. Some of the divergence between dog breeds has been linked to single mutational steps with large effects (Sutter et al. 2007; Parker et al. 2009), but there are also reports of mechanisms producing incremental change in dog breeds as well as among carnivoran species (Fondon and Garner 2004; Sears et al. 2007). There is little information on the dynamics of change in dog breeds, but a detailed study of the historical change of skull shape in St. Bernard dogs found that the features that were described as desirable in the breed standard gradually became more accentuated (Drake and Klin-

genberg 2008). Overall, it appears that the processes of morphological diversification in dog breeds are broadly comparable to those in natural lineages. Dogs are therefore an excellent model system for the study of evolutionary processes, including adaptive radiation and the origin of large-scale morphological disparity.

By comparison, there is only little quantitative information about the degree of variation in other domesticated animals. Although cranial variation in domestic cats is considerable (Künzel et al. 2003), it is not clear whether it is comparable to the variation across the family Felidae (Christiansen 2008). This apparently smaller scale of variation may reflect the fact that genetic distance among cat breeds tends to be clearly less than that among dog breeds (Menotti-Raymond et al. 2007). For domestic pigeons, widely different cranial shapes have been reported (Helms and Brugmann 2007), but no quantitative studies of cranial variation have been published. Divergence of skeletal traits among pigeon breeds is much greater than the differences between rock pigeons (*Columba livia*) and feral pigeon populations (Johnston 1992). Unfortunately, the differences in measurements and methods make it difficult to compare across these studies, and none of these studies includes more than a small number of breeds. Moreover, except for those of domestic dogs (this article; Wayne 1986a, 1986b), no study directly compares the morphological variation in a domesticated species with that in the larger clade to which it belongs.

In addition to the great amount of variation in domestic dogs, a striking result is that most of the range of skull shape variation is outside the range of that for the Carnivora (fig. 3C). Even if allowance is made for intraspecific variation, for which the range of variation in the three wild canid species can serve as a basis of comparison, a substantial part of the domain of variation for the dogs is still outside the zone of overlap (fig. 3). These shapes represent novel arrangements of the skull in domestic dogs that are not found in other carnivorans.

These novel skull shapes, as well as the disparity in dog breeds and in wild species (figs. 4, 5), suggest that diversification of dog skull shapes is due, at least in part, to the radical change of the selective regime, as dog breeds were derived from wolves through domestication and the later establishment of modern breeds (Lindblad-Toh et al. 2005; Pollinger et al. 2005; Björnerfeldt et al. 2006; Wayne and Ostrander 2007). Domestication relaxed selective pressures in contexts such as foraging, and the requirement to process hard or tough foods was reduced. This new selective regime may tolerate changes in cranial morphology even if they affect aspects of performance such as bite force (Ellis et al. 2009) or breathing, which is impeded in brachycephalic dogs (Koch et al. 2003; similar problems for cats are discussed in Künzel et al. 2003). One would expect the functional

demands on skull shape to be most permissive for the Companion Dog group, intermediate for breeds selected to perform work (such as hunting, herding, or guarding), and most stringent for the wild species. In agreement with this expectation, the greatest amounts of disparity are found in the Companion Dog group, fewer are found in the other groups of breeds, and the smallest amounts are found in the three wild species (figs. 4, 5). Furthermore, this argument predicts that feral dogs should be less variable than pet dogs and other domestic breeds. This is difficult to assess, because only a few specimens were available: three dingos and two New Guinea singing dogs, which are ancient populations derived from feral dogs (Savolainen et al. 2004). The Sighthound and Pariah group, which contains both breeds, is not unusually variable by comparison with the other functional groups. Stronger support for such an argument was found for skeletal measurements in pigeons, where feral pigeons resemble wild rock pigeons, whereas domestic pigeon breeds are much more different from each other, suggesting that feral pigeons were under selection for trait values similar to those of their wild ancestor but that domestic pigeons were not (Johnston 1992; Sol 2008). No comparable evidence appears to be available for cranial shape in pigeons or for any skeletal structure in other feral animals.

Since the establishment of modern dog breeds, artificial selection for behaviors or appearance desired by breeders specifically favored divergence (Kemp et al. 2005; Drake and Klingenberg 2008). Direct selection for head shape is expected to be strongest for pet dogs, which is consistent with the large disparity of the Companion Dog group (fig. 5). In addition, the process of domestication itself may bring about a variety of changes due to selection for tameness (Trut et al. 2004) and due to changes in the selective regime (Björnerfeldt et al. 2006) and direct mechanical influence on skull growth (O'Regan and Kitchener 2005). In addition to selection, bottleneck events in the establishment of new breeds and subsequent inbreeding (Lindblad-Toh et al. 2005; Björnerfeldt et al. 2008; Calboli et al. 2008) may have further enhanced diversification through the fixation of mutations that affect cranial shape (Haworth et al. 2001; Neff et al. 2004; Pollinger et al. 2005; Björnerfeldt et al. 2006; Cruz et al. 2008).

Morphological Integration and Modularity

The large-scale divergence of dog breeds in response to selection by breeders raises the question about the developmental basis of variation. Was there any particular predisposition in the developmental system of the skull that facilitated this diversification? Or, did the processes of domestication and artificial selection themselves produce a reorganization of the patterns of integration and modu-

larity? If genetic and developmental modularity are molded by functional associations of traits and selection (Cheverud 1984; Wagner and Altenberg 1996), a drastic change of the selective regime such as domestication may be expected to affect the integration and modularity of the skull.

The results of the comparisons of RV coefficients for dogs (fig. 4) are generally consistent with the hypothesis that the face and the neurocranium are morphological modules, as the subdivision into face and neurocranium produces RV coefficients that are lower than those for most alternative partitions. Moreover, the relatively limited range of RV coefficients in each of the analyses indicates that modularity is relatively weak, that is, that the covariation within modules is not much stronger than the covariation between modules (Klingenberg et al. 2003; Klingenberg 2009). The high RV coefficients, particularly for the symmetric component in dogs, also reflect the large proportion of variation that is integrated throughout the skull, such as the spectrum between brachycephalic and dolichocephalic skull shapes (e.g., PC1 in fig. 3; Stockard 1941; Wayne 1986a; Haworth et al. 2001; Young and Bannasch 2006). For fluctuating asymmetry, which originates from random variation produced by the developmental system, integration is weaker and the range of RV coefficients tends to be greater than that for the symmetric component of variation. Particularly for the dogs, the modular structure of the skull is therefore more apparent for this spontaneous developmental variation than it is for the symmetric component of shape variation, which includes the evolved differences among breeds. A lower degree of integration of asymmetry than for the among-individual variation has also been found in similar analyses for rodents and fly wings (e.g., Klingenberg 2009; Laffont et al. 2009) and may therefore be a widespread phenomenon.

The patterns of developmental integration, as characterized by the covariance matrices for fluctuating asymmetry (Klingenberg 2003, 2008b), are similar in domestic dogs, in the wolf, and across the order Carnivora (all matrix correlations >0.7 and $P < .0001$). Accordingly, there is no indication that domestication changed the way in which new morphological variation is generated. On the contrary, the results are consistent with the possibility that the ancestral developmental system was mostly conserved throughout the evolution of the carnivores and the domestication of dogs, despite the long evolutionary time spans and the large scale of morphological diversification. We are not aware of similar comparisons of the patterns of integration for fluctuating asymmetry, except at the intraspecific level (Debat et al. 2006, 2008, 2009). At the level of intraspecific variation, where factors other than development may also influence the observed patterns, a comparison across the order Carnivora found that patterns

of cranial integration within species are mostly similar (Goswami 2006b) and that there are some shared patterns of integration even across therian mammals (Goswami 2006a; Porto et al. 2009). Despite this large-scale conservation, patterns of integration can vary at small taxonomic scales (Steppan 1997; Mitteroecker and Bookstein 2008; Jamniczky and Hallgrímsson 2009; Kulemeyer et al. 2009).

The matrix correlation between the symmetric and the asymmetric components of shape variation for the wolf (0.63) is stronger than the low-to-moderate matrix correlations for domestic dogs (0.20) or Carnivora (0.45). For both dogs and Carnivora, the symmetric component of variation is dominated by the evolved differences among breeds or species, whereas in the wolf it is mainly within-population variation. The relatively high matrix correlation between symmetric and asymmetric components of the wolf suggests that new variation generated by the developmental system is incorporated into the pool of within-population variation in a fairly equitable manner. In contrast, the lower matrix correlations for the Carnivora and for dogs suggest that patterns of diversification among taxa or breeds differ substantially from the patterns of variation spontaneously produced by the developmental system because phylogenetic divergence of Carnivora and artificial selection by dog breeders disproportionately favored some directions in shape space over others. These matrix correlations correspond to the mixed results found in similar comparisons between patterns of symmetric variation and fluctuating asymmetry for other animals (e.g., Klingenberg and McIntyre 1998; Debat et al. 2000; Klingenberg et al. 2002; Willmore et al. 2005; Breuker et al. 2006), with the difference being that all of those studies were based on intrapopulation variation.

The diversification of both the Carnivora and the domestic dogs relies on a combination of the input of new variation, which retains a mostly conserved pattern, and selection that can favor particular aspects of shape. As a result, diversification in skull shape is responsive to specific selective inputs, but it follows general patterns concerning the relative length of the skull (brachycephalic vs. dolichocephalic skulls) and the relative arrangement of the facial and neurocranial parts of the skull (airorhynch vs. klinorhynch, but possibly other rearrangements as well). Investigating the contributions of the developmental system and specific selective events, in dogs and other domesticated species as well as in naturally evolved clades, will be a promising approach for understanding the processes responsible for morphological diversification.

Acknowledgments

We are grateful to the curators of the various collections (see “Material and Methods”) for access to skulls in their

care. We thank E. Sherratt for crucial technical help with visualizing three-dimensional surfaces and M. Nussbaumer and two anonymous reviewers for helpful comments on drafts of this article. This research was supported by grants from the Leverhulme Trust and the Royal Society.

Literature Cited

- Arthur, W. 2001. Developmental drive: an important determinant of the direction of phenotypic evolution. *Evolution and Development* 3:271–278.
- Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. *Nature* 446:507–512.
- Björnerfeldt, S., M. T. Webster, and C. Vilà. 2006. Relaxation of selective constraint on dog mitochondrial DNA following domestication. *Genome Research* 16:990–994.
- Björnerfeldt, S., F. Hailer, M. Nord, and C. Vilà. 2008. Assortative mating and fragmentation within dog breeds. *BMC Evolutionary Biology* 8:28.
- Breuker, C. J., J. S. Patterson, and C. P. Klingenberg. 2006. A single basis for developmental buffering of *Drosophila* wing shape. *PLoS ONE* 1:e7.
- Calboli, F. C. F., J. Sampson, N. Fretwell, and D. J. Balding. 2008. Population structure and inbreeding from pedigree analysis of purebred dogs. *Genetics* 179:593–601.
- Chase, K., D. R. Carrier, F. R. Adler, T. Jarvik, E. A. Ostrander, T. D. Lorentzen, and K. G. Lark. 2002. Genetic basis for systems of skeletal quantitative traits: principal component analysis of the canid skeleton. *Proceedings of the National Academy of Sciences of the USA* 99:9930–9935.
- Cheverud, J. M. 1984. Quantitative genetics and developmental constraints on evolution by selection. *Journal of Theoretical Biology* 110:155–171.
- Christiansen, P. 2008. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PLoS ONE* 3:e2807.
- Clutton-Brock, J. 1995. Origins of the dog: domestication and early history. Pages 7–20 in J. Serpell, ed. *The domestic dog: its evolution, behaviour and interactions with people*. Cambridge University Press, Cambridge.
- Copping, R., and L. Copping. 2001. *Dogs: a startling new understanding of canine origin, behavior, and evolution*. Scribner, New York.
- Cruz, F., C. Vilà, and M. T. Webster. 2008. The legacy of domestication: accumulation of deleterious mutations in the dog genome. *Molecular Biology and Evolution* 25:2331–2336.
- Darwin, C. 1868. *Animals and plants under domestication*. Vol. 1. J. Murray, London.
- Debat, V., P. Alibert, P. David, E. Paradis, and J.-C. Auffray. 2000. Independence between developmental stability and canalization in the skull of the house mouse. *Proceedings of the Royal Society B: Biological Sciences* 267:423–430.
- Debat, V., C. C. Milton, S. Rutherford, C. P. Klingenberg, and A. A. Hoffmann. 2006. Hsp90 and the quantitative variation of wing shape in *Drosophila melanogaster*. *Evolution* 60:2529–2538.
- Debat, V., R. Cornette, A. B. Korol, E. Nevo, D. Soulet, and J. R. David. 2008. Multidimensional analysis of *Drosophila* wing variation in Evolution Canyon. *Journal of Genetics* 87:407–419.
- Debat, V., A. Debelle, and I. Dworkin. 2009. Plasticity, canalization,

- and developmental stability of the *Drosophila* wing: joint effects of mutations and developmental temperature. *Evolution* 63:2864–2876.
- de Berg, M., M. van Krefeld, M. Overmars, and O. Schwarzkopf. 2000. *Computational geometry: algorithms and applications*. Springer, Berlin.
- Drake, A. G., and C. P. Klingenberg. 2008. The pace of morphological change: historical transformation of skull shape in St. Bernard dogs. *Proceedings of the Royal Society B: Biological Sciences* 275: 71–76.
- Dryden, I. L., and K. V. Mardia. 1998. *Statistical shape analysis*. Wiley, Chichester.
- Ellis, J. L., J. Thomason, E. Kebreab, K. Zubair, and J. France. 2009. Cranial dimensions and forces of biting in the domestic dog. *Journal of Anatomy* 214:362–373.
- Escoufier, Y. 1973. Le traitement des variables vectorielles. *Biometrics* 29:751–760.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Flynn, J. J., J. A. Finarelli, S. Zehr, J. Hsu, and M. A. Nedbal. 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology* 54:317–337.
- Fondon, J. W., III, and H. R. Garner. 2004. Molecular origins of rapid and continuous morphological evolution. *Proceedings of the National Academy of Sciences of the USA* 101:18058–18063.
- Gavrilets, S., and J. B. Losos. 2009. Adaptive radiation: contrasting theory with data. *Science* 323:732–737.
- Good, P. 2000. *Permutation tests: a practical guide to resampling methods for testing hypotheses*. Springer, New York.
- Goswami, A. 2006a. Cranial modularity shifts during mammalian evolution. *American Naturalist* 168:270–280.
- . 2006b. Morphological integration in the carnivore skull. *Evolution* 60:169–183.
- Gould, S. J. 2002. *The structure of evolutionary theory*. Harvard University Press, Cambridge, MA.
- Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- . 2006. Evolution of character displacement in Darwin's finches. *Science* 313:224–226.
- Harmon, L. J., J. A. Schulte II, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301:961–964.
- Haworth, K. E., I. Islam, M. Breen, W. Putt, E. Makrinou, M. Binns, D. Hopkinson, and Y. Edwards. 2001. Canine *TCOF1*: cloning, chromosome alignment and genetic analysis in dogs with different head types. *Mammalian Genome* 12:622–629.
- Helms, J. A., and S. A. Brugmann. 2007. The origins of species-specific facial morphology: the proof is in the pigeon. *Integrative and Comparative Biology* 47:338–342.
- Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53: 1637–1653.
- Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287:308–309.
- Jamniczky, H. A., and B. Hallgrímsson. 2009. A comparison of covariance structure in wild and laboratory murine crania. *Evolution* 63:1540–1556.
- Johnston, R. F. 1992. Evolution in the rock dove: skeletal morphology. *Auk* 109:530–542.
- Kemp, T. J., K. N. Bachus, J. A. Nairn, and D. R. Carrier. 2005. Functional trade-offs in the limb bones of dogs selected for running versus fighting. *Journal of Experimental Biology* 208:3475–3482.
- Klingenberg, C. P. 2003. Developmental instability as a research tool: using patterns of fluctuating asymmetry to infer the developmental origins of morphological integration. Pages 427–442 in M. Polak, ed. *Developmental instability: causes and consequences*. Oxford University Press, New York.
- . 2005. Developmental constraints, modules and evolvability. Pages 219–247 in B. Hallgrímsson and B. K. Hall, eds. *Variation: a central concept in biology*. Elsevier, Burlington, MA.
- . 2008a. MorphoJ. Faculty of Life Sciences, University of Manchester, Manchester. http://www.flywings.org.uk/MorphoJ_page.htm.
- . 2008b. Morphological integration and developmental modularity. *Annual Review of Ecology, Evolution, and Systematics* 39: 115–132.
- . 2009. Morphometric integration and modularity in configurations of landmarks: tools for evaluating a-priori hypotheses. *Evolution and Development* 11:405–421.
- Klingenberg, C. P., and G. S. McIntyre. 1998. Geometric morphometrics of developmental instability: analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution* 52:1363–1375.
- Klingenberg, C. P., M. Barluenga, and A. Meyer. 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution* 56:1909–1920.
- Klingenberg, C. P., K. Mebus, and J.-C. Auffray. 2003. Developmental integration in a complex morphological structure: how distinct are the modules in the mouse mandible? *Evolution and Development* 5:522–531.
- Koch, D. A., S. Arnold, M. Hubler, and P. M. Montavon. 2003. Brachycephalic syndrome in dogs. *Compendium Continuing Education for Veterinarians* 25:48–55.
- Kulemeyer, C., K. Asbahr, P. Gunz, S. Frahnert, and F. Bairlein. 2009. Functional morphology and integration of corvid skulls: a 3D geometric morphometric approach. *Frontiers in Zoology* 6:2.
- Künzel, W., S. Breit, and M. Oppel. 2003. Morphometric investigations of breed-specific features in feline skulls and considerations on their functional implications. *Anatomia Histologia Embryologia* 32:218–223.
- Laffont, R., E. Renvoisé, N. Navarro, P. Alibert, and S. Montuire. 2009. Morphological modularity and assessment of developmental processes within the vole dental row (*Microtus arvalis*, Arvicolinae, Rodentia). *Evolution and Development* 11:302–311.
- Lindblad-Toh, K., C. M. Wade, T. S. Mikkelsen, E. K. Karlsson, D. B. Jaffe, M. Kamal, M. Clamp, et al. 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* 438:803–819.
- Losos, J. B., and R. E. Ricklefs. 2009. Adaptation and diversification on islands. *Nature* 457:830–836.
- Marcus, L. F., E. Hingst-Zaher, and H. Zaher. 2000. Application of landmark morphometrics to skulls representing the orders of living mammals. *Hystrix* 11:27–47.
- Mattila, T., and F. Bokma. 2008. Extant mammal body masses suggest punctuated equilibrium. *Proceedings of the Royal Society B: Biological Sciences* 275:2195–2199.

- Meffert, L. M. 2006. Population bottlenecks and founder effects. Pages 414–425 in C. W. Fox and J. B. Wolf, eds. *Evolutionary genetics: concepts and case studies*. Oxford University Press, New York.
- Menotti-Raymond, M., V. A. David, S. M. Pflueger, K. Lindblad-Toh, C. M. Wade, S. J. O'Brien, and W. E. Johnson. 2007. Patterns of molecular genetic variation among cat breeds. *Genomics* 91:1–11.
- Millien, V. 2006. Morphological evolution is accelerated among island mammals. *PLoS Biology* 4:e321.
- Mitteroecker, P., and F. L. Bookstein. 2008. The evolutionary role of modularity and integration in the hominoid cranium. *Evolution* 62:943–958.
- Neff, M. W., K. R. Robertson, A. K. Wong, N. Safra, K. W. Broman, M. Slatkin, K. L. Mealey, and N. C. Perderson. 2004. Breed distribution and history of canine *mdr1-1Δ*, a pharmacogenetic mutation that marks the emergence of breeds from the collie lineage. *Proceedings of the National Academy of Sciences of the USA* 101:11725–11730.
- Nussbaumer, M. 1982. Über die Variabilität der dorso-basalen Schädelknickungen bei Haushunden. *Zoologischer Anzeiger* 209:1–32.
- O'Regan, H. J., and A. C. Kitchener. 2005. The effects of captivity on the morphology of captive, domesticated feral mammals. *Mammal Review* 35:215–230.
- Ostrander, E. A., U. Giger, and K. Lindblad-Toh, eds. 2006. *The dog and its genome*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.
- Parker, H. G., L. V. Kim, N. B. Sutter, S. Carlson, T. D. Lorentzen, T. B. Malek, G. S. Johnson, H. B. De France, E. A. Ostrander, and L. Kruglyak. 2004. Genetic structure of the purebred domestic dog. *Science* 304:1160–1164.
- Parker, H. G., B. M. VonHoldt, P. Quignon, E. H. Margulies, S. Shao, D. S. Mosher, T. C. Spady, et al. 2009. An expressed *Fgf4* retrogene is associated with breed-defining chondrodysplasia in domestic dogs. *Science* 325:995–998.
- Pollinger, J. P., C. D. Bustamante, A. Fledel-Alon, S. Schmutz, M. M. Gray, and R. K. Wayne. 2005. Selective sweep mapping of genes with large phenotypic effects. *Genome Research* 15:1809–1819.
- Porto, A., F. B. De Oliveira, L. T. Shirai, V. De Conto, and G. Marroig. 2009. The evolution of modularity in the mammalian skull. I. Morphological integration patterns and magnitudes. *Evolutionary Biology* 36:118–135.
- Räber, H. 2008. *Die Schweizer Hunderassen*. Schweizerische Kynologische Gesellschaft, Bern.
- Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1937.
- Ricklefs, R. E. 2004. Cladogenesis and morphological diversification in passerine birds. *Nature* 430:338–341.
- Sampson, J., and M. M. Binns. 2006. The Kennel Club and the early history of dog shows and breed clubs. Pages 19–30 in E. A. Ostrander, U. Giger, and K. Lindblad-Toh, eds. *The dog and its genome*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.
- Savolainen, P., T. Leitner, A. N. Wilton, E. Matisoo-Smith, and J. Lundeberg. 2004. A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences of the USA* 101:12387–12390.
- Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–1774.
- . 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Sears, K. E., A. Goswami, J. J. Flynn, and L. A. Niswander. 2007. The correlated evolution of Runx2 tandem repeats, transcriptional activity, and facial length in Carnivora. *Evolution and Development* 9:550–565.
- Sol, D. 2008. Artificial selection, naturalization, and fitness: Darwin's pigeons revisited. *Biological Journal of the Linnean Society* 93:657–665.
- Stanley, S. M. 1998. *Macroevolution: pattern and process*. Johns Hopkins University Press, Baltimore.
- Steppan, S. J. 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. *Evolution* 51:571–586.
- Stockard, C. R. 1941. The genetic and endocrinic basis for differences in form and behavior as elucidated by studies of contrasted pure-line dog breeds and their hybrids. Wistar Institute, Philadelphia.
- Sutter, N. B., C. D. Bustamante, K. Chase, M. M. Gray, K. Zhao, L. Zhu, B. Padhukasahasram, et al. 2007. A single *IGF1* allele is a major determinant of small size in dogs. *Science* 316:112–115.
- Trut, L. N., I. Z. Plyusnina, and I. N. Oskina. 2004. An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics* 40:644–655.
- Wagner, G. P., and L. Altenberg. 1996. Complex adaptations and the evolution of evolvability. *Evolution* 50:967–976.
- Wayne, R. K. 1986a. Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution* 40:243–261.
- . 1986b. Limb morphology of domestic and wild canids: the influence of development on morphological change. *Journal of Morphology* 187:301–319.
- Wayne, R. K., and E. A. Ostrander. 2007. Lessons learned from the dog genome. *Trends in Genetics* 23:557–567.
- Wiley, D. E., N. Amenta, D. A. Alcantara, D. Ghosh, Y. J. Kil, E. Delson, W. Harcourt-Smith, F. J. Rohlf, K. St. John, and B. Hamann. 2005. Evolutionary morphing. Pages 431–438 in *Proceedings of the IEEE Visualization 2005 (VIS '05)*, Minneapolis.
- Willmore, K. E., C. P. Klingenberg, and B. Hallgrímsson. 2005. The relationship between fluctuating asymmetry and environmental variance in rhesus macaque skulls. *Evolution* 59:898–909.
- Wroe, S., and N. Milne. 2007. Convergence and remarkably consistent constraint in the evolution of carnivore skull shape. *Evolution* 61:1251–1260.
- Young, A., and D. Bannasch. 2006. Morphological variation in the dog. Pages 47–65 in E. A. Ostrander, U. Giger, and K. Lindblad-Toh, eds. *The dog and its genome*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.
- Zelditch, M. L., H. D. Sheets, and W. L. Fink. 2003. The ontogenetic dynamics of shape disparity. *Paleobiology* 29:139–156.

Associate Editor: Stephen B. Heard
 Editor: Mark A. McPeck