



Copy-cat evolution: Divergence and convergence within and between cat and dog breeds

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Many domesticated species exhibit remarkable phenotypic diversity. In nature, selection produces not only divergence but also convergence when organisms experience similar selective pressures. Whether artificial selection during domestication also produces convergence has received little attention. Three-dimensional shape analysis of domestic cat and dog skulls demonstrated convergence at multiple levels. Most broadly, cats and dogs have both diversified greatly: equaling or exceeding the morphological disparity among all modern-day species of their respective families. Moreover, as a result of artificial selection, some breeds of these two phenotypically distinct species, evolutionarily separated for 50 My, have converged to such an extreme extent that they are more similar to each other than they are to many members of their own species or their ancestors, a phenomenon never previously observed in domesticated species. Remarkably, this convergence evolved not only between dogs and cats but also multiple times within each taxon.

domestication | evolution | convergent evolution | dog | cat

Selective breeding was central to Darwin's formulation of the theory of evolution by natural selection (1), culminating in *The Variation of Animals and Plants under Domestication* (2). Darwin recognized that artificial selection had greatly transformed many domesticates from their ancestral phenotypes (1, 2), a trend that has continued and accelerated since Darwin's day (3). It is well documented that natural selection can produce not only divergence but also convergence (4, 5). However, in comparison to the considerable discussion of variation within domesticated species, relatively little attention has been directed toward the extent to which artificial selection has led to phenotypic convergence among such species.

Domestic cats (*Felis catus*) and dogs (*C. familiaris*) are two of our most beloved animal companions, each with global populations estimated to be approaching one billion. Selective breeding has produced scores of named breeds of both species, most of which have been developed over the last 150 y (6, 7). The extraordinary diversity of dog breeds—from Pugs to Labrador Retrievers to Collies—is well known (8, 9). Previous work has shown that the diversity of skull shapes among dog breeds is vastly greater than that of the ancestral wolf (*Canis lupus*) and, indeed, of all members of the Canidae (8, 9). Notably, the variation of extant wild canids is a subset of the variation seen among dog breeds, with the latter exhibiting many phenotypes outside the range of wild canid diversity (Figs. 1 and 2 and *SI Appendix*, Fig. S1). Whether domestication of cats has produced similar variation relative to their ancestors has never been investigated, nor has the extent to which phenotypic convergence, as well as divergence, has been involved.

Results

We used three-dimensional geometric morphometrics to explore skull shape variation in domestic cats, dogs, wildcats (*Felis silvestris*, the ancestor of the domestic cat), wolves (*C. lupus*, the ancestor of the dog), and other extant members of the Felidae, Canidae, and Carnivora. Forty-seven three-dimensional landmarks (*SI Appendix*, Fig. S2 and Table S1) were captured on 1,810 skulls allowing us to comprehensively measure shape variation in these taxa. In the principal components analysis (PCA) of the covariance matrix of the shape coordinates, the first three principal components (PCs) accounted for 73.9% of the skull shape variation (Fig. 1), with all other PCs describing <5% each. We calculated two main measures of variability (disparity) for each group, Procrustes shape variance (PV) and maximum Procrustes shape distance (Tables 1 and 2). Morphological variation correlated with size differences (allometry) is a major

Significance

Domestication underscores the extensive phenotypic diversity that can result from artificial selection. Investigating the evolution of domesticated species has enhanced our understanding of the mechanisms of natural selection. Observations of convergent evolution in nature can provide valuable insight into how natural selection drives morphological change; however, the phenomenon of convergence in domesticated species has been largely overlooked. This study documents convergent evolution of skull shape not only between cats and dogs but also multiple times within each species, demonstrating that similar selection pressures can lead to highly convergent morphologies within and between domesticated species. Unexpectedly, we found that skull shape variation among felids is substantial, indicating that—despite the great variety of dog breeds—canids are not more inherently evolvable than felids.

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The authors declare no competing interest.

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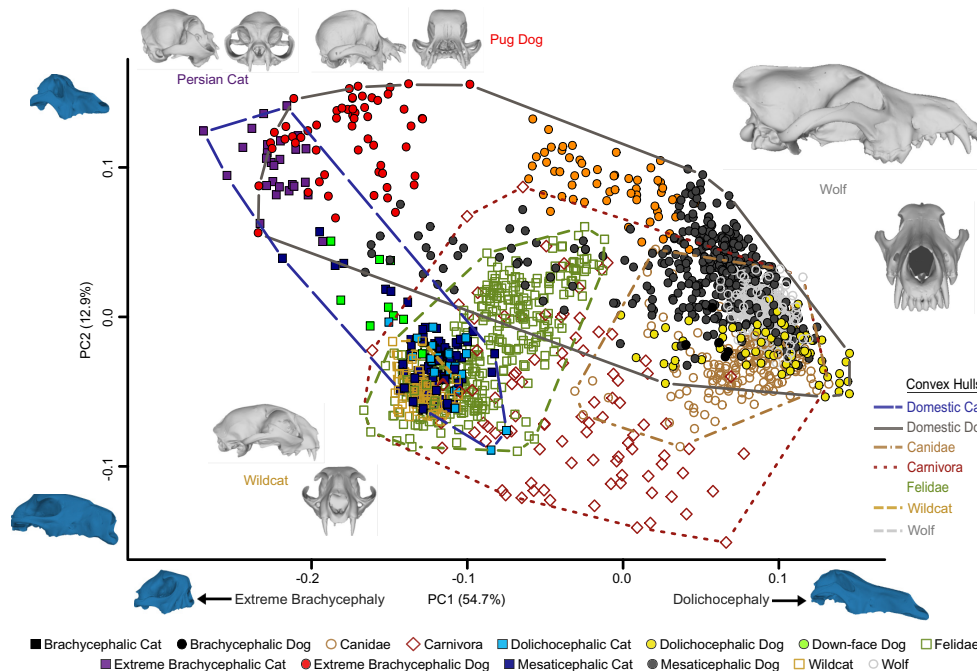


Fig. 1. Principal components analysis (PCA) of three-dimensional geometric morphometric data illustrating skull shape variation across domestic cats and dogs, wildcats, wolves, and broader representatives of Canidae, Felidae, and Carnivora. The morphospace occupied by each group quantifies the amount of skull shape diversity in that group and is outlined by a convex hull; the key to the convex hull lines is shown at the right. The broader groups and skull types within domestic dogs (circles) and cats (squares) are color-coded as indicated in the key. Skull shapes associated with the extreme positive and negative ends of PC1 and PC2 are illustrated by the blue skull models found along each axis.

component of skull shape diversification (8). We therefore used residuals from a pooled within-group regression of shape on log centroid size to compute the nonallometric portion of shape variation and performed the same analyses on this aspect of shape variation as well. The results of the analyses of nonallometric shape were similar to those from the main analysis and can be found in supplemental materials (*SI Appendix, Tables S2 and S3*).

Patterns of Skull Shape Variation in Canidae and Felidae. All wild members of the Canidae (i.e., all extant members of the family included in this study except *C. familiaris*) tend to have similar skull shapes with a neurocranium that is slightly taller dorso-ventrally than the muzzle, which tends to be elongated (Fig. 3 and *SI Appendix, Fig. S4*). There is little cranial flexion among wild canids—the muzzle and neurocranium tend to be on the same horizontal plane. In contrast, wild Felidae species (i.e., all extant members of the family included in this study except *F. catus*) exhibit substantial variability. For example, cheetahs (*Acinonyx jubatus*) display a great amount of cranial flexion—the muzzle is angled downward from the neurocranium (klinorhynch)—whereas other felids, such as those in the genus *Panthera*, have longer muzzles and wider zygomatic arches, and the Pampas cat (*Leopardus colocola*) is distinguished by its bulging nasal region (Fig. 3 and *SI Appendix, Fig. S4*).

Although the maximum Procrustes shape distances between specimens in wild Felidae and Canidae are about equal (Table 1 and *SI Appendix, Table S2*), wild Felidae exhibits substantially greater overall disparity (variance) in skull shape than wild Canidae (Felidae PV = 0.007, Canidae PV = 0.003, $P < 0.0001$, Table 1 and Fig. 3 and *SI Appendix, Fig. S4*); these findings agree with previous studies that have found great variability in wild felids (10–13) that exceeds that of wild canids (13).

Skull Shape Diversity in Domestic Cats and Dogs. As with dogs (PV = 0.013), domestic cats are extremely variable, ranging from highly dolichocephalic (long muzzles and narrow skulls) breeds like Siamese and Oriental Shorthairs to greatly brachycephalic (short faces and wide, rounded skulls) breeds like Persians and Burmese (PV = 0.01). Domestic cat and dog diversification are similar in a macroevolutionary context in that both are substantially more variable than their wild ancestors, wildcats (*F. silvestris*) (PV = 0.002, $P < 0.0001$, Table 1) and wolves (*C. lupus*) (PV = 0.002, $P < 0.0001$, Table 1); Figs. 1 and 2 and Table 1). Dogs are more variable than domestic cats ($P < 0.043$, Table 1); this result, however, does not parallel the ancestral condition as wolves are no more variable than wildcats ($P < 0.66$, Fig. 1 and Table 1). Cat and dog diversification are also similar in that both are more diverse than the broader clades to which they belong. Domestic cats are more variable than the entire wild Felidae ($P < 0.0001$, Table 1 and Fig. 1 and *SI Appendix, Fig. S5*), and the comparison is more extreme in dogs, which exhibit four times more variability than all of wild Canidae ($P < 0.0001$, Table 1 and Fig. 1 and *SI Appendix, Fig. S1*); indeed, the disparity of dogs is nearly as great as that exhibited by the entire order Carnivora (Carnivora PV: 0.015, $P < 0.0004$, Fig. 1 and Table 1) (8).

The pattern of diversification of domestic cats and dogs is not similar in all respects; one difference is the extent to which their diversity resembles that of their wild relatives. The skulls of many wild canid species are similar to the skulls of at least one recognized breed of domestic dog, and more than half (51.2%) of wild Canidae disparity overlaps with that of the dogs on PCs 1 and 2 (Fig. 1 and *SI Appendix, Fig. S1*). In contrast, for the most part, domestic cat skull shapes are different from the skull shape diversity of wild felid species: The disparity of domestic cat skull shape overlaps with only 19.3% of the space occupied by wild Felidae (Fig. 1 and *SI Appendix, Fig. S5*). Indeed, many wild felid species are quite different from all domestic cats, and some are actually

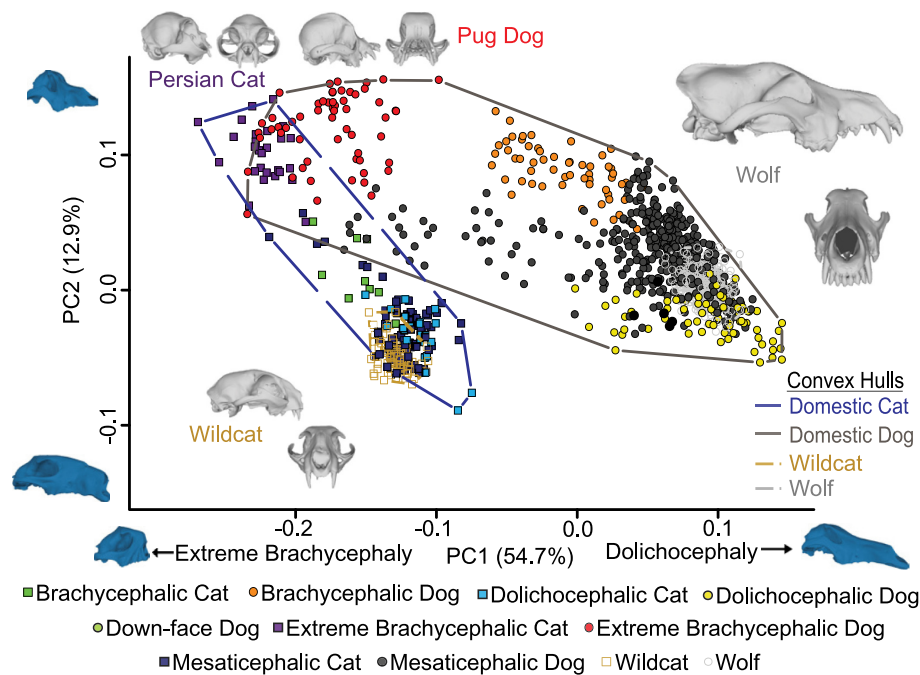


Fig. 2. Morphospace as in Fig. 1 but displaying only domestic cats and dogs, wildcats, and wolves to allow examination of the skull variation in each of these groups in more detail. The morphospace occupied by each group, delineated by convex hulls, quantifies skull shape diversity; line styles for convex hulls are keyed at the right. Within domestic dogs (circles) and domestic cats (squares), the skull types are color-coded as indicated. Skull shapes associated with the extreme positive and negative ends of PC1 and PC2 are illustrated by the blue skull models found along each axis.

more similar in skull shape to some breeds of dogs than they are to any breed of domestic cat. Lions (*Panthera leo*), for example, are more similar to many dog breeds—including Chow Chow, Neapolitan Mastiff, Shar-Pei, and Newfoundland—than they are to any domestic cat.

To highlight the morphological diversification of domestic cats and dogs compared to wildcats and wolves, Fig. 2 shows the position of only these groups in the morphological space defined by the PC analysis. PC1 contrasts elongated or dolichocephalic skulls associated with the positive end of PC1 with the extremely shortened and rounded brachycephalic skulls on the negative end of PC1 (see blue shape models on the x-axis of Fig. 1). Wolves and dolichocephalic dog breeds have long, narrow skulls and are found at the positive end of PC1. Wildcats, with their rounded skulls and shorter muzzles, are found midway along PC1 while brachycephalic domestic cat and dog breeds are found at the negative end of PC1. PC2 primarily reflects cranial flexion: The positive end of PC2 is associated with skulls where the muzzle is angled up relative to the neurocranium and the angle between the muzzle and forehead is concave, while the negative end of PC2 is associated with skulls in which the muzzle is angled down relative to the neurocranium and the nasal and the forehead region is convex (see blue shape models on the y-axis of Fig. 1). Brachycephalic cats and dogs have shorter faces in part because their muzzles are angled up relative to the neurocranium and are found at the positive end of PC2, whereas the more extreme skull elongation of dolichocephalic dogs and Siamese cats results from the muzzle being angled ventrally; these breeds are found at the negative end of PC2. An extreme case of ventral cranial flexion occurs in klinorhynchic “down-face” dogs like the Bull Terrier. Evolutionarily, dogs have diverged to become both more dolichocephalic (e.g., Borzois and Collies) and more brachycephalic (e.g., Bulldogs and Pekingese) than their wolf ancestors. In contrast, domestic cat divergence has been mostly unidirectional: Although Siamese cats have evolved to become

dolichocephalic, most of the divergence in cat breeds has been in the direction of brachycephaly (Fig. 2).

Multilevel Skull Shape Convergence in Domestic Cats and Dogs.

Despite their greatly different evolutionary origins, extremely brachycephalic dogs and cats have evolved to be remarkably similar in skull shape (Figs. 1, 2, and 4 and *SI Appendix, Fig. S3*). Brachycephalic cats like Persians have evolved short, broad skulls with an upward-angled palate that closely resembles the brachycephalic skulls of dog breeds like Pugs and Shih Tzus (Figs. 1, 2, and 4 and *SI Appendix, Fig. S3*). Strikingly, some Persians are more brachycephalic than any of the dogs, as indicated by their extreme position on PC1 (Fig. 2). Indeed, in some flat-faced Persians, the nasal bones are entirely absent (14, 15). Extremely brachycephalic cats and dogs are substantially closer to each other in morphological space (Procrustes shape distance: 0.13) than either group is to their respective ancestors, or than their ancestors are to each other (Procrustes shape distance from extremely brachycephalic cats to wildcats: 0.20; extremely brachycephalic dogs to wolves: 0.29; wildcats to wolves: 0.23; Table 2 and *Dataset S1*). A resampling procedure comprising 10,000 rounds confirmed a significant difference in the Procrustes distances. Specifically, the Procrustes distance of 0.13 between extremely brachycephalic cats and dogs is significantly smaller ($P < 0.0001$, Table 2 and *Dataset S1*) than the distance (0.20) between extremely brachycephalic cats and wild cats. Moreover, it is also significantly smaller than the distance between extremely brachycephalic dogs and wolves ($P < 0.0001$, Table 2 and *Dataset S1*), as well as the distance between wildcats and wolves ($P < 0.0001$, Table 2 and *Dataset S1*). In other words, selection for brachycephaly has eliminated much of the ancestral difference in skull shape between cats and dogs.

Given the differences between wildcats and wolves, this convergence required different evolutionary trajectories. The morphological differences between extremely brachycephalic dogs at one

Table 1. Comparisons of disparity among groups, comparing Procrustes shape variance (PV) ratios and absolute differences

Comparisons of disparity (Procrustes variance)		Ratio	Two-tailed <i>P</i> -value	Difference	Two-tailed <i>P</i> -value
Domestic dogs (0.013, 0.45)	Domestic cats (0.010, 0.32)	1.3	<0.0034	0.003	<0.0431
Wild felid species (0.007, 0.23)	Wild canid species (0.003, 0.22)	2.33	<0.0003	0.004	<0.0001
Domestic cats (0.010, 0.32)	Wild felid species (0.007, 0.23)	1.43	<0.0003	0.003	<0.0002
Domestic dogs (0.013, 0.45)	Wild canid species (0.003, 0.22)	4.33	<0.0001	0.01	<0.0001
Carnivora (0.015, 0.40)	Domestic cats (0.010, 0.32)	1.5	<0.0001	0.005	<0.0001
Carnivora (0.015, 0.40)	Domestic Dogs (0.013, 0.45)	1.15	<0.0004	0.002	<0.0015
Domestic cats (0.010, 0.32)	Wildcats (0.0025, 0.13)	5.00	<0.0001	0.008	<0.0001
Domestic dogs (0.013, 0.45)	Wolves (0.0017, 0.12)	6.50	<0.0001	0.011	<0.0001
Wildcats (0.0025, 0.13)	Wolves (0.0017, 0.12)	1.46	<0.0438	0.0008	<0.6506

Procrustes variance and maximum pair-wise Procrustes distance in parentheses. For the same analysis of the nonallometric data, see [SI Appendix, Table S2](#).

end of PC1 and wolves near the other end highlight the great amount of morphological modification required for these short-faced dogs to evolve from their long-muzzled ancestor. Domestic cats, with ancestrally shorter muzzles, changed less along PC1. Conversely, domestic cats have changed more than dogs along PC2: As the muzzle has angled upward relative to the neurocranium, the rounded, convex profile of the ancestral wildcat has been transformed into a “stop” or concave angle between the forehead and the muzzle. Brachycephalic dogs have changed in the same manner, but not as dramatically, because the ancestral wolf muzzle is not convex (Figs. 1, 2, and 4).

When we remove allometric effects, we find the same general disparity patterns ([SI Appendix, Tables S2 and S3](#)) demonstrating that brachycephaly is not primarily an allometric phenomenon. Brachycephaly in cats is restricted to small breeds in the bottom half of the feline size distribution (Fig. 5). In contrast, brachycephalic dogs come in all sizes, from Pekingese (4.5 kg) to Mastiffs (89 kg), though extreme brachycephaly is limited to breeds in the bottom third of the size distribution (<23 kg, Fig. 5) (16). For both cats and dogs, a minority of skull shape (Procrustes shape coordinates) variation is explained by size regardless of method (domestic cat: multivariate regression of skull shape on log centroid size: 35.0%; on average breed weight: 10.0%; dog: multivariate regression of skull shape on log centroid size: 39.0%; on average breed weight: 12.7%).

Indeed, many small dogs and cats are not brachycephalic, and some large dogs are. Two of the ways in which a shortened face (brachycephaly) can occur is from shortening of the muzzle relative to the neurocranium (allometric scaling) or from a dorsal rotation of the palate (airorhynchy) (16). Extremely brachycephalic cat and dog skulls have been modified by a combination of both processes. They have shortened faces because of a reduction in the length of bones on the muzzle (e.g., nasal, palate) and in addition, the palate is rotated dorsally, bringing the nasal opening closer to the eyes. Thus, in response to very similar selection pressures (see below), dogs and cats evolved extremely brachycephalic skulls via the same types of morphological modifications, though the relative contribution of muzzle shortening and rotation of the palate differed between the two.

Discussion

Convergence Driven by Similar Selection Regimes. Biologists have long debated the relative importance of natural selection and constraint in directing evolutionary change. In the case of brachycephalic cats and dogs, the explanation for convergent evolution is clear: Cat and dog breeders have been selecting for the same large-eyed, round-headed, short-muzzled phenotype—Lorenz’s “baby schema” (17) (Fig. 4). Indeed, the “breed standards”

Table 2. Comparisons of procrustes distances between groups to show which groups are closer to each other in morphospace and which are more distant

Procrustes distances		Procrustes distance			Procrustes distance	Two-tailed <i>P</i> -value
Extreme brachycephalic cats	Extreme brachycephalic dogs	0.12	Wildcats	Wolves	0.23	<0.0001
Extreme brachycephalic cats	Extreme brachycephalic dogs	0.12	Extreme brachycephalic cats	Wildcats	0.20	<0.0001
Extreme brachycephalic cats	Extreme brachycephalic dogs	0.12	Extreme brachycephalic dogs	Wolves	0.29	<0.0001

For the same analysis of the nonallometric data, see [SI Appendix, Table S3](#).

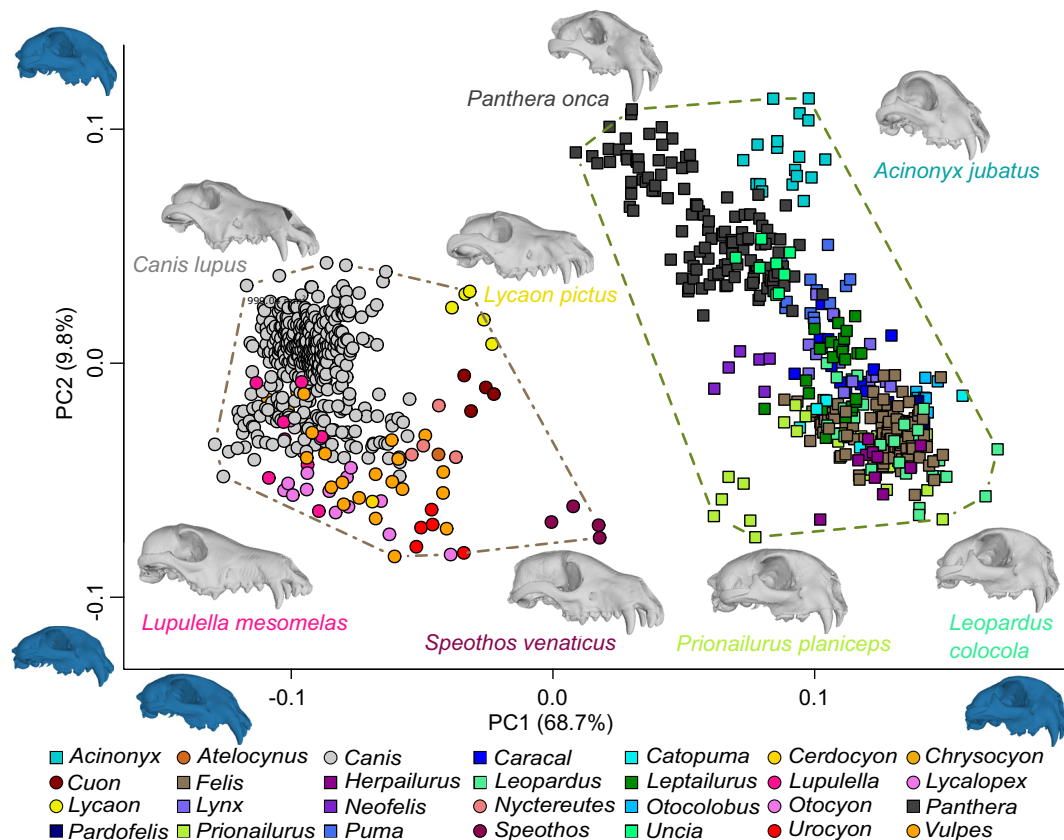


Fig. 3. Skull shape variation in wild species of Felidae is greater than shape variation in wild species of Canidae. The morphospace occupied by the specimens sampled within each family is delineated by convex hulls. Genera within Felidae (circles) and Canidae (squares) are color-coded as indicated. Skull shapes associated with the extreme positive and negative ends of PC1 and PC2 are illustrated by the blue skull models found along each axis.

for extreme brachycephalic breeds of cats and dogs are nearly identical, requiring the profile to be completely vertical with no protrusion of the muzzle and for the nose to be centered between the eyes rather than below it. For example, the Cat Fancier Association's standard for Persian cats includes "Head...round and massive...When viewed in profile, the prominence of the eyes is apparent and the forehead, nose, and chin appear to be in vertical alignment... Nose...centered between the eyes" (18). The Pekingese standard from the American Kennel Club is very similar: "The topskull is massive...When viewed from the side, the chin, nose leather and brow all lie in one plane.... A line drawn horizontally over the top of the nose intersects slightly above the center of the eyes" (19).

The broad range of phenotypes in dogs and domestic cats, and the diversity present in fossil taxa like the Borophaginae, indicates that the relatively limited modern-day diversity of wild Canidae

and Felidae is not the result of genetic or developmental constraints precluding the production of diverse phenotypes in these lineages (20). Rather, this limited variation likely is the result of natural selection preventing divergent phenotypes from becoming established in a population. Certainly, many dog and cat breeds would be unlikely to persist in the wild and, indeed, feral dog and cat populations exhibit a limited range of phenotypes that depart little from that of the ancestral wolf and wildcat (21–23).

Convergent evolution of brachycephaly occurs not only between felids and canids but also within each clade. Phylogenetic analysis of dog breeds suggests that it has evolved at least twice in dogs, once in Asia [e.g. Pekingese (19)] and a second time in western breeds [e.g. English bulldog (24)], and possibly multiple times within one or both regions (25) (*SI Appendix, Fig. S6*). Similarly, among cat breeds, brachycephaly has evolved in Persians and, more recently, in distantly related American Burmese (26–31).

Phenotypic Convergence via Different Genetic Mechanisms.

This multilevel convergence provides the opportunity to examine the extent to which convergent phenotypes evolve as the result of convergent genetic changes, a topic of great current interest (32, 33). However, given the different phenotypic trajectories by which dogs and domestic cats have evolved brachycephaly, one would expect convergent genetic changes to be much more common within than between the two species. Although a number of candidate genes involved in brachycephaly have been identified in dogs and a few in cats (16, 26, 34), including *BMP3*, *DLV2*, *THB2*, and *ALX1*, the data as yet are insufficient to determine the extent to which mutations in the same genes are responsible for brachycephaly in cats and dogs. Within dogs, mutations in several genes appear to have evolved at least twice in association

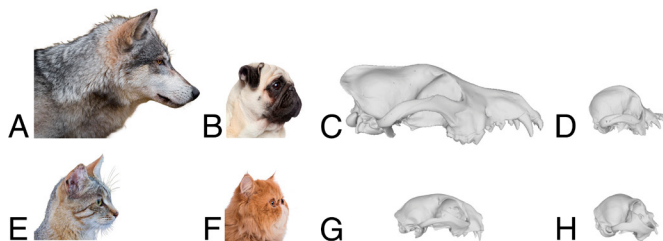


Fig. 4. Evolutionary convergence of head shape in brachycephalic domestic dogs and cats, as illustrated by photographs and CT scans of canids (A–D) and felids (E–H). Although wolves (A and C) and wildcats (E and G) have very different skull shapes, some of their domestic descendants like Pugs (B and D) and Persians (F and H) have convergently evolved similar skull shapes (D and H) as a result of selection for similar phenotypes.

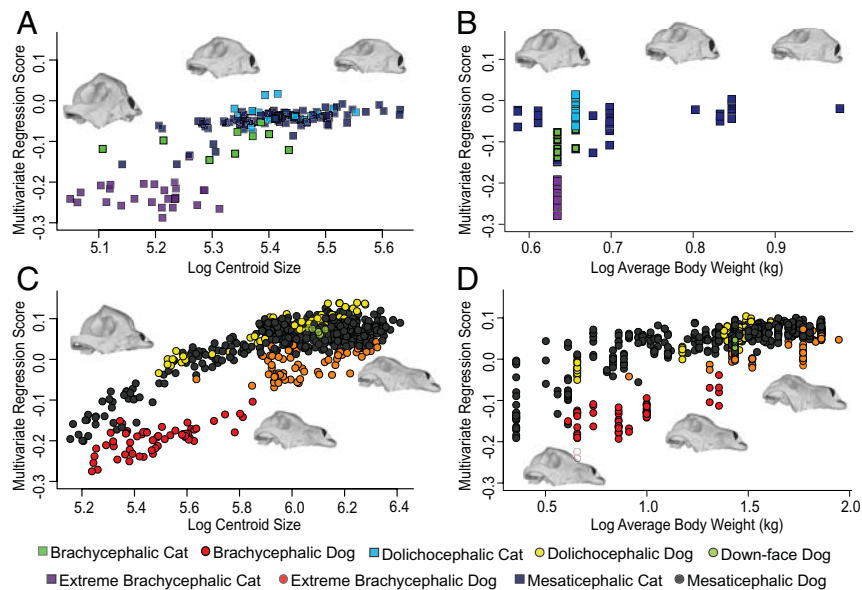


Fig. 5. Allometric influences on skull shape variation in domestic cats and dogs. (A) Multivariate regression of cat cranial shape on log centroid size and (B) log average breed weight (kg). (C) Multivariate regression of dog cranial shape on log centroid size and (D) log average breed weight (kg). Gray skull models illustrate average skull shapes associated with small, medium, and large sizes, highlighting size-related morphological trends.

with brachycephaly—different variants of these genes are found in brachycephalic Asian toy breeds and brachycephalic dogs of the bulldog clade (*SI Appendix, Fig. S6*) (35–39).

Phenotypic Convergence Is Not Linked to Phylogenetic Historical Patterns. The Feliformia and Caniformia, the larger clades to which Felidae and Canidae belong, diverged about 50 mya (40). Not surprisingly given this long evolutionary divergence, felids and canids are very different in many aspects of natural history, including, as Figs. 1 and 3 illustrate, their skull morphology, which is associated with differences in bite force and predatory behavior (41). That 50 My of divergent evolution could be substantially erased by a few hundred years of similar selective pressures testifies to the power of artificial selection (indeed, the extreme brachycephalic phenotype of modern-day Persian cats was produced over the course of a few decades in the mid-twentieth century from previously ordinary-looking domestic cats, and many brachycephalic dog breeds have a similar history).

Our analyses uncovered an unexpected contrast: Whereas variation in the skulls of dog breeds far outstrips that among cat breeds, the reverse is seen when comparing the clades to which they belong: extant wild felid skull diversity is substantially greater than that of extant wild canids (Fig. 3 and *SI Appendix, Fig. S4*). Canids, in other words, are not more inherently evolvable than felids. The explanation for these divergent patterns of skull variability might relate to variation in size. Whereas dog breeds span a much greater size range than cat breeds, wild felids range from 1.5 to 300-plus kg, in contrast to wild canids, which have a much smaller size range from 1.5 to at most 100 kg. A caveat to this conclusion is that our comparison involved only extant felids and canids, which occur in the subfamilies Felinae and Caninae. Extinct clades in both families (Felidae: Machairodontinae (saber-toothed cats); Canidae: Borophaginae (bone-crushing dogs) and Hesperocyoninae include species with morphologies that are very different from any living taxon (20, 42). Incorporating fossil data could be an important next step to quantify the variability of felids versus canids. More generally, understanding the genetic, developmental, and functional mechanisms that link variation in

overall size and skull shape will be necessary to fully fathom the complete history of macroevolutionary diversification in these carnivores, the results of artificial selection, and how the two are related.

Recently, some have suggested an evolutionary rule that relative muzzle length increases with body size in mammals (12). However, the existence of numerous exceptions among wild species suggests that this allometric “rule” is more of a generality, and that variation in selection pressures is responsible for this variation (43). Here, we have shown intraspecific exceptions exist as well—extremely short muzzles have evolved multiple times in both cats and dogs but not always associated with a reduction in body size. In this case, however, it is the lack of selection that is probably the cause. Most pedigreed dogs and cats—especially ones with short muzzles—are no longer expected to hunt and kill their prey, and many are fed soft food diets. Consequently, the relaxed selection on bite force coupled with artificial selective forces for appearance has resulted in muzzle length variation not related to body size in these species.

Convergence Among Domesticated Taxa. Short faces occur in breeds of many domesticated taxa (e.g., goats, pigs, rodents), yet these breeds are not closely convergent with brachycephalic cats and dogs, even in rabbits, on which similar artificial selection pressures favor a child-like appearance (16, 44). These different evolutionary outcomes probably result from some combination of deep evolutionary divergence (even greater than that between canids and felids), different functional demands on the skull (e.g., diet) and different selective pressures (16). Given that selective pressures are often better known in domesticated than wild species, further investigation of domesticated animals may provide a useful approach to study the interplay of deterministic and contingent factors in evolution (45, 46). Along these lines, domesticated species often evolve similarity in traits such as hair color, length, and texture; tail size and shape; limb length; and many other features (e.g., illustrations in ref. 47), but rarely are these traits considered in the context of such evolutionary questions. A comprehensive consideration of the extent, form,

and circumstances of convergence among domestic animals would be valuable.

Implications for the Health of Companion Animals. The extent of convergence between brachycephalic cats and dogs is seen in an additional, unfortunate, phenotypic aspect. Brachycephalic cat and dog breeds have predispositions to many health disorders, some shared between species (48, 49). As a result of these afflictions, pressure is mounting to ban the breeding of extreme brachycephalic individuals. We can hope such measures succeed for the welfare of our household companions, even if it has the effect of reversing this remarkable case of convergent evolution.

Materials and Methods

Measuring Skull Shape. This study includes three-dimensional measurements of skull morphology from physical skulls obtained from natural history collections, and CT and micro-CT Scans obtained from veterinary institutions and from MorphoSource (see [Dataset S2](#) for details on sources) for 1,810 specimens: 148 domestic cats (*F. catus*), 677 domestic dogs (*C. familiaris*), 69 wildcats [*F. silvestris* from all recognized subspecies except *F. silvestris bieti* (i.e., *F. cafra*, *F. libyca*, *F. ornata*, and *F. silvestris*)], 287 wolves (*C. lupus*), 185 specimens from 23 other species within Canidae representing 68% of all extant species, 350 members of 33 additional species Felidae representing 85% of all extant species, and 94 specimens of 93 other species of Carnivora representing 93 out of 131 extant genera. These data were obtained from museum collections and veterinary schools. Domestic cat skull specimens span much of the variation in *F. catus*, including individuals from Abyssinian, Balinese, Bombay, Burmese, Chartreux, Himalayan, Japanese Bobtail, Maine Coon, Manx, Norwegian Forest, Persian, Ragdoll, Russian Blue, Savannah, Scottish Fold, Siamese, and Turkish Angora breeds as well as nonpedigreed individuals (note that our sampling may underestimate the disparity of cat breeds because some of the most extreme modern phenotypes are probably not represented; see [SI Appendix](#) for more details). This sample includes 28 extreme brachycephalic cats, 8 brachycephalic, and 22 dolichocephalic cats, as well as 90 cats with intermediate (i.e., mesaticephalic) skulls (skull types were classified by breed and skull shape, [Dataset S2](#)). Dog skulls represent 106 breeds ([Dataset S2](#)). This dataset includes 58 extreme brachycephalic dogs, 127 brachycephalic dogs, 57 dolichocephalic dogs, 5 down-face dogs, and 430 mesaticephalic dogs (8). Dog skull types were categorized based on consensus within the literature on dog skull morphology and the position of specimens on PC1 and PC2. Some breeds include both extreme brachycephalic and brachycephalic specimens because of selection over time for increased brachycephaly (e.g., Boston Terrier, English Bulldog, St. Bernard) (3). Additionally, some breeds such as Scottish Terriers are mostly classified as mesaticephalic, but 3 specimens were classified as dolichocephalic. For a list of specimens, collections, and data sources, see [Dataset S2](#).

Digitization of the Three-Dimensional Anatomical Landmarks. CT and micro-CT scans were converted into Polygon files with 3D Slicer (50) and digitized with Meshlab (51). Physical specimens were digitized with a MicroScribe (52) digitizer. Three-dimensional coordinates for 47 osteological landmarks (11 median and 36 paired, [SI Appendix, Fig. S2 and Table S1](#)) were measured on the dorsal and ventral surfaces of physical specimens and CT scans. The dorsal and ventral coordinate configurations from physical specimens were combined into one set of coordinates using a least-squares fit (rotation and translation only) of four matching landmarks.

Shape Analysis. We used geometric morphometric analysis of the three-dimensional landmark-based coordinates to investigate shape variation (53). We utilized the MorphoJ software package and the R scientific computing environment (54, 55) to perform multivariate statistical analyses and visualizations, the details of which are given in SI. The coordinate data were converted to shape coordinates in MorphoJ by generalized least-squares Procrustes superimposition using a procedure that accounts for the object symmetry of the specimens (56).

Quantifying Disparity. We used a PCA based on the covariance matrix of the Procrustes shape coordinates to investigate patterns of shape variation. Phylogenetic comparative analyses are inappropriate for the data and questions presented here; nonetheless, we did conduct such analyses and the results were qualitatively unaltered (see SI for details on both points).

We then quantified the amount of phenotypic disparity in domestic cats, dogs, wildcats (*F. silvestris*, the ancestor of the domestic cat), wolves (*C. lupus*, the ancestor of the dog), wild Felidae species (all extant members of the family except *F. catus*), wild members of the Canidae (all extant members of the family except *C. familiaris*), and Carnivora included in this study in two main ways.

First, we quantified the shape disparity of each group by calculating the Procrustes variance of each using the morphol.disparity function in the R package geomorph (57). The Procrustes variance is the mean squared Procrustes distance of each specimen from the mean group shape (58, 59).

Second, to measure the maximum phenotypic difference in shape within each group, we computed Procrustes distances between all possible pairs of specimens within each group as the Euclidean distances in tangent space using the procdist function in the R package shapes (60). We used this measurement to quantify the amount of convergence between extremely brachycephalic cats and dogs (see Convergence between Brachycephalic Cats and Dogs below).

To test whether two groups (e.g., cats and dogs) differ in the extent of shape variation, we calculated both the ratio and absolute difference in Procrustes variance between the groups. To assess the statistical significance of these comparisons, we conducted a randomization test in which we first combined the coordinates from the specimens in the two groups. Then, to create a null distribution, we resampled with replacement from this pool to create groups with the same sample size as the focal groups. For each new sample, we then computed the Procrustes variance. The resampling procedures were run 10,000 times. We then compared the ratio and absolute differences between the resampled groups and recorded how many times these values exceeded the observed differences between the real groups and divided this by 10,000 to generate a *P*-value for the difference. A Bonferroni correction was applied to all *P*-values generated when multiple tests were run. We indicated when observed *P*-values are no longer significant after correction.

Convergence Between Brachycephalic Cats and Dogs. Noticing that extremely brachycephalic domestic cats and dogs are nearly coincident on PC 1 and 2, we investigated whether these breeds have evolved to be more similar [we note that the resemblance between brachycephalic breeds of cats and dogs was suggested more than three decades ago in a popular book, but this idea has received no further attention (61)]. To investigate this putative convergence, we calculated the Procrustes shape distance between extremely brachycephalic domestic cats and dogs. We then compared this distance to the Procrustes shape distance between *F. silvestris* and *C. lupus*. In addition, we also computed the Procrustes shape distance between extremely brachycephalic domestic cats and *F. silvestris* and between extremely brachycephalic dogs and *C. lupus*. To test whether the distances between these pairs were statistically significant, we bootstrapped the differences between groups. First, we resampled with replacement to generate new samples of each group (using the original sample size of each group): extremely brachycephalic cats, extremely brachycephalic dogs, wildcats, and wolves. For each new sample, we then generated the mean shape. We then computed the Procrustes distances between the mean shapes for each pair using resampling with replacement. The resampling procedures were run 10,000 times. Each time we measured whether the Procrustes distance between extremely brachycephalic cats and dogs was smaller than the Procrustes distance between extremely brachycephalic cats and wildcats, between extremely brachycephalic dogs and wolves, and between wildcats and wolves.

Allometric Shape. Centroid size (CS) is the square root of the sum of squared distances of all the landmarks of an object from their centroid and is a measure of the size of each skull. We computed the allometric vectors for dogs and cats separately using a multivariate regression of the Procrustes shape coordinates against log centroid size for each group (8). We then computed the angle between the dog and cat allometric vectors. A *P*-value was generated using a bootstrap analysis under the null hypothesis that the vectors are random vectors drawn from a uniform distribution (62). The residuals from a pooled-within group (using group category 2,

Dataset S2) regression of shape on log centroid size were used to compute the nonallometric portion of shape variation. As a secondary measure of quantifying size and investigating the amount of allometric variation in skull shape, we used the log average body weight in kg for each breed of cat (18) and dog (19).

Data, Materials, and Software Availability. Morphometric measurements data have been deposited in Dryad (<https://doi.org/10.5061/dryad.t1g1jw7r>) (63).

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