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CRANIAL MORPHOLOGY OF DOMESTIC AND WILD CANIDS: THE INFLUENCE OF DEVELOPMENT ON MORPHOLOGICAL CHANGE

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Abstract.—The domestic dog varies remarkably in cranial morphology. In fact, the differences in size and proportion between some dog breeds are as great as those between many genera of wild canids. In this study, I compare patterns of intracranial allometry and morphologic diversity between the domestic dog and wild canid species. The results demonstrate that the domestic dog is morphologically distinct from all other canids except its close relatives, the wolf-like canids. Following this, I compare patterns of static and ontogenetic scaling. Data on growth of domestic dogs are presented and used to investigate the developmental mechanisms underlying breed evolution. Apparently, most small breeds are paedomorphic with respect to certain morphologic characters. In dogs and other domestic animals, morphologic diversity among adults seems to depend on that expressed during development.

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In what ways can morphology change in the absence of appreciable genetic change? Evolutionary biologists often make the implicit assumption that some morphological alterations, such as the evolution of a bird's wing from the leg of a reptile progenitor, require extensive developmental and presumably, genetic changes. Other morphological alterations, such as the paedomorphic evolution of plethodontid salamanders, are said to be due to less extensive developmental and genetic rearrangements, such as changes in the time of maturation or in growth rate (Wake, 1966; Larson, 1980; Alberch and Alberch, 1981).

The limits to morphological change, in the absence of appreciable genetic alteration, are best studied in a group which is morphologically diverse, but genetically very homogeneous, such as the domestic dog, *Canis familiaris.* The differences in size and proportion between some breeds are as great as those between any wild canid genera, but all dogs are clearly members of the same species. No case of infertility between breeds has been reported, and, relative to most wild species, dog breeds have been genetically isolated for a very short time (less than 15,000 years) (Zeuner, 1963; Lawrence, 1967; Scott, 1968; Epstein, 1971; Olsen and Olsen, 1977; Davis and Valla, 1978). Moreover, chromosomal and isozyme studies of dog breeds have shown that no significant amount of genetic differentiation has occurred (Borgaonkar et al., 1968; Clark et al., 1975; Shaughnessy et al., 1975; Fisher et al., 1976; Simonsen, 1976).

In this study, I investigate the extent to which the shared developmental and genetic architecture of dog breeds may have limited their morphological evolution under domestication. I first compare bivariate allometries of dogs and wild canids to uncover similarities in scaling. Bivariate allometry has proved to be a very effective approach for delineating phylogenetic or functional groupings (e.g., Huxley, 1932; Rensch, 1959; Kurtén, 1954; Cock, 1966; Gould, 1966, 1975, 1977; McMahon, 1975; Harvey and Mace, 1980; Jungers, 1985). Thus, one might expect scaling differences to exist between dogs under artificial selection and distantly-related wild canids under natural selection. Next, I use discriminant analysis to determine the extent of multivariate similarity between dogs and wild canids. In the discriminant analysis, interspecific variation is maximized in the derivation of canonical axes, and thus positional differences among taxa on these axes should reflect evolutionary distance (Sokal and Sneath, 1973). Finally, allometric scal-

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ing of adult dogs is compared to that of an ontogenetic series of juvenile dogs. An idealized growth model is used to explain the similarities between these two levels of morphologic variation.

MATERIAL AND METHODS

Measurements.—Twenty-one dental and cranial measurements were taken, when possible, on skulls of 202 domestic dogs and 95 wild canids (see Appendices 1 and 2). A reduced subset of measurements was made on skulls of juvenile domestic dogs in museum collections and on radiographs of skulls, in dorsal-ventral view, from four growing puppies, each from a different breed (Wayne, 1984). The measurements were selected to correspond with those used in other studies of dog morphology and to represent observed differences in cranial morphology between domestic and wild canids (Becker, 1923; Wagner, 1930; Lumer, 1940; Stockhaus, 1962; Lawrence and Bossert, 1967; Wortmann, 1971; Epstein, 1971; Lups, 1974; Clutton-Brock et al., 1976; Evans and Christensen, 1979).

Bivariate Analysis.—The objective of the bivariate analysis is to uncover differences between domestic dogs and species of wild canids in the scaling of cranial and dental lengths and widths. Total skull length (TSL) was chosen as the independent variable because this allows differences in the scaling of cranial measurements to be readily interpreted as changes in skull shape as seen in skull outlines (Fig. 9). Multivariate approaches to allometry exist (e.g., Jolicoeur, 1963; Strauss and Bookstein, 1982), but I have chosen a bivariate approach because bivariate coefficients are more easily interpretable in terms of size-dependent changes in proportion (Jungers and German, 1981) and because such coefficients can be derived from simple growth models of each measurement (Laird, 1965). In bivariate studies, the scaling behavior of any individual measurement may be strongly affected by the choice of an independent variable (Humphries et al., 1981; Smith, 1981), but since most measurements are highly correlated (Table 1), the relative scaling behavior of variables (e.g., differences in scaling between dental and cranial measurements) will not change appreciably with the choice of independent variable. Thus, the relative scaling of variables is emphasized in my discussion.

Least squares regression was used to calculate bivariate coefficients (a and b of the equation $y = a + bx$ where x = logarithm of the independent variable, TSL; a = y-intercept; b = slope; and y = logarithm of the dependent variable). Separate regressions were derived for wild canid species (interspecific), for domestic dogs (dog-intraspecific), and for juvenile dogs of different ages (dog-ontogenetic). Specific growth rates were also calculated for developing domestic dogs and plotted against age (Brody, 1945; Laird, 1965). In this study, the specific growth rate (SGR) was estimated as $\text{SGR} = [\ln(s_2) - \ln(s_1)]/(t_2 - t_1)$ where s_1 and s_2 are the sizes of the same measurement at age t_1 and a later age t_2. The units for SGR can be expressed either as a rate per unit size (cm/day/cm) or by letting the size units cancel out, as a percentage increase per day (day^{-1}). Two properties of the specific growth rate make it a desirable measure of growth. First, since it expresses the proportional increment of growth with an increase in age, animals of different sizes can be compared on an equivalent basis. Second, since the ratio of specific growth rates for two measurements at any point in time equals their bivariate slope, specific growth rates are useful in explaining patterns of bivariate allometry (Laird, 1965; Atchley and Rutledge, 1981).

Multivariate Analysis.—Discriminant analysis is used to assess whether the morphological differences that separate canid taxa also vary among dog breeds. In other words, is the pattern of morphological differences among wild canid species similar to that among domestic dogs? One might expect that the morphological and developmental differences separating most canid genera are more profound than those separating dog breeds. If so, then dogs are likely to share morphological characteristics which distinguish them as a group from distantly-related wild canids. Discriminant analysis is an excellent multivariate technique for testing these ideas because morphological differences among, rather than within, predefined groups (species) are maximized. In discriminant analysis, morphological differences among breeds and species can be effectively summarized on a few discriminant axes. Moreover, some indication of

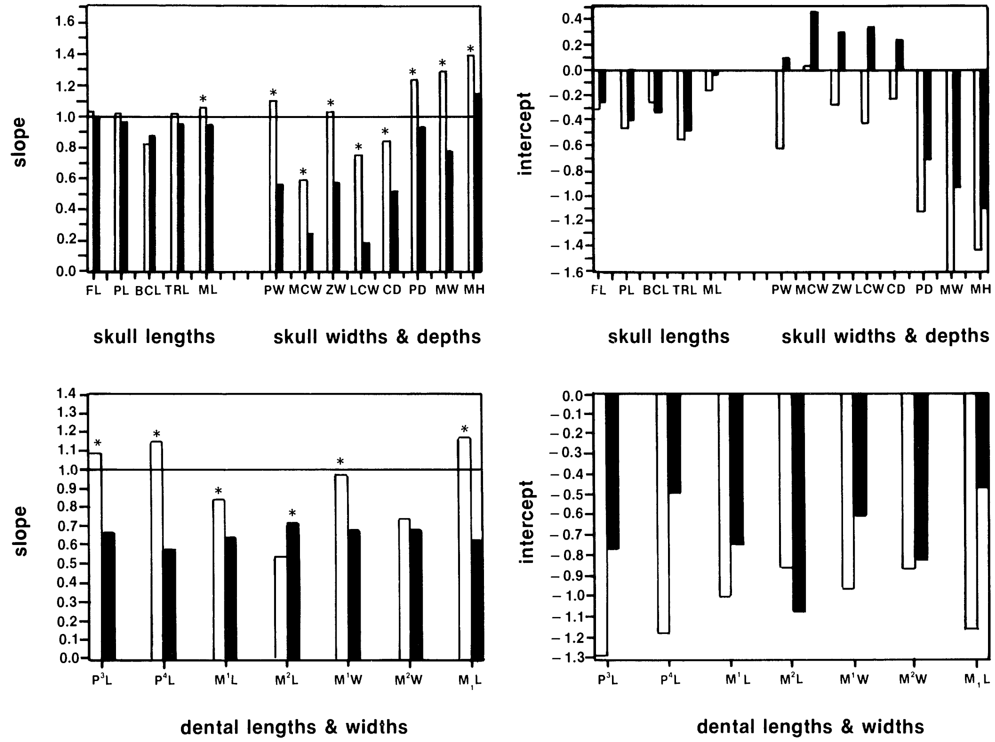


FIG. 1. Histogram of slopes and intercepts of interspecific (left bar, clear) and dog-intraspecific regressions (right bar, solid) for the indicated measurements against total skull length. Asterisks indicate variables having inter- and intraspecific regression lines that can be statistically distinguished at the 0.05 level (two-tailed *t*-test; Zar, 1984).

which variables are important to species discrimination is suggested by their weights on these axes. The overall similarity of breeds and species can be assessed by determining the classification of breeds within wild canid species (Tatsuoka, 1970; Sokal and Sneath, 1973; Nei et al., 1975).

All analyses were done using SPSS subprogram DISCRIMINANT (Nei et al., 1975). Raw data on only wild species were used in the derivation of the discriminant functions. Each wild species defined a separate discriminant group. To check for the effects of differences in sample sizes of wild species the discriminant analysis was also performed with groupings by genus. Both analyses yielded a very similar separation of groups.

Data on domestic dogs were entered into the analysis as if their species memberships were unknown. The multi-dimensional position of each breed was then calculated and compared with that of wild species. Similarly, dogs were entered into the classification analysis as if they were of unknown species membership and then assigned to the morphologically nearest wild species. This provided an estimate of the similarity between domestic dogs and wild canid species.

RESULTS AND DISCUSSION

Interspecific and Intraspecific Allometry.—Two conclusions are apparent from a comparison of bivariate coefficients in Figure 1. First, interspecific and dog-intraspecific regressions of skull length components (FL, PL, BCL, TRL, and ML) against total skull length are not significantly different, except for mandible length (ML), in either slope or intercept ($P < 0.05$, two-tailed *t*-test; Zar, 1984). In contrast, significant differences are found between dogs and wild species in all but one (M^2W) of the regressions of cranial width and depth and dental length and width. Second, in all cases where interspecific and intraspecific regressions differ significantly, intraspecific slopes are

TABLE 1. Standard error of the residuals (SE) and Pearson product-moment correlations (r) for regressions discussed in text.

Dependent variable	Interspecific		Intraspecific	
	SE	r	SE	r
Skull length				
TSL	—	—	—	—
FL	0.012	0.99	0.014	0.99
PL	0.021	0.99	0.027	0.99
BCL	0.021	0.98	0.034	0.97
TRL	0.034	0.95	0.041	0.96
ML	0.012	0.99	0.022	0.99
Skull width and depth				
PW	0.033	0.98	0.060	0.82
MCW	0.027	0.95	0.026	0.81
ZW	0.028	0.98	0.050	0.87
LCW	0.050	0.90	0.059	0.44
CD	0.031	0.97	0.037	0.90
PD	0.046	0.97	0.065	0.91
MW	0.041	0.97	0.064	0.88
MH	0.047	0.97	0.052	0.96
Dental length and width				
P^3L	0.042	0.96	0.050	0.89
P^4L	0.041	0.97	0.035	0.93
M^1L	0.062	0.88	0.054	0.87
M^2L	0.072	0.73	0.082	0.82
M^1W	0.032	0.97	0.038	0.93
M^2W	0.048	0.91	0.037	0.91
M_1L	0.042	0.97	0.032	0.94

smaller and intercepts larger than the equivalent interspecific regressions, except for M^2 length.

Regressions of skull length components, except for BCL, have slopes close to 1 (FL, PL, TRL, and ML in Fig. 1). This approximate isometric scaling means that there are only small changes in proportion with a change in size among both breeds and species. For instance, the proportion of face length to skull length in a small canid, the kit fox, is 0.77 and in a large canid, the grey wolf, is 0.78. Moreover, since the standard errors are small and the correlation coefficients are large for skull length measurements (Table 1), the scatter about the regression line is small for these measurements relative to others. In contrast, the scalings of skull width, dental length, and dental width variables often depart appreciably from isometry (slopes range from 0.19 to 1.39; Fig. 1). The change in these dimensions with size, especially for dog-intraspecific regressions of skull width, is often strongly allometric. For instance, the ratio of cranial width (MCW) to total skull length (TSL) is 0.59 in the Chihuahua and 0.31 in the Great Dane.

These results are exemplified in bivariate plots. For instance, domestic dogs (dots) and wild species (open circles) overlap completely in a plot of face length against total skull length (Fig. 2a). The scatter about both regression lines is small; hence their correlation coefficients are large, and their standard errors are small (Table 1). In contrast, plots of skull width variables against skull length (Figs. 2b and 2c, ZW and PW against TSL, respectively) show an increased separation of breeds and wild species as size decreases: all small breeds have skulls that are wider than wild species of equivalent skull length. However, interspecific and dog-intraspecific regression lines do intersect at large skull lengths; hence large domestic dogs are similar in size and proportion to their close relatives, the large wolf-like canids (1 in Figs. 2b and 2c; Clutton-Brock et al., 1976; Olsen and Olsen, 1977; Nowak and Paradiso, 1983). Also, scatter about the regression lines, especially for the dog-intraspecific regressions, is larger than in Fig. 2a. Plots of dental length variables, except M^2 length, against total skull length differ from those of skull width only in that the grey wolf often has relatively longer teeth than dog breeds of equivalent skull length (e.g., Fig. 2d).

The similarity between intraspecific and interspecific regressions of skull length measurements against total skull length and the lack of scatter about their regression lines suggest that variability in the scaling of skull length components is tightly constrained. In fact, the scaling of skull length measures may be relatively constant throughout the entire order Carnivora: Radinsky (1981), in a family level study, found the scaling of skull length measurements against total skull length to be similar to that demonstrated here ($b = 1.08$ for TRL and 1.09 for ML in his study). Moreover, as has been found in this study, measures of basicranium length relative to skull length or body weight often scale with negative allometry (Krogman, 1931; Huxley, 1932; Rohrs, 1959; Freedman, 1962; Jerison, 1973; Gould, 1975; Bauchot, 1978; Radinsky, 1981, 1984; Cheverud, 1982*a*).

Any correspondence between interspecific and intraspecific scaling might reflect similar selection pressures, a lack of developmental variation (i.e., developmental canalization), or both (Lerner, 1954; Waddington, 1962). Strong developmental canalization would seem the most likely explanation for the observed similarity between dog breeds and wild canid species in the scaling of skull-length components because this scaling similarity transcends so many different taxonomic levels and presumably different selective regimes. For instance, in selecting for some dog breeds (such as toy or fancy breeds), humans have not emphasized the dog's ability to catch, dismember, or masticate live prey. In these instances, selection on the scaling of those skull characteristics (such as FL, PL, TRL, and ML) that appear integral to mastication (Radinsky, 1981, 1984) would seem dramatically different from that experienced by wild canids. Yet, scaling of skull-length measurements is similar in both groups. Moreover, despite considerable variability in the time, place, and conditions of origination of dog breeds, the scaling of skull length components is relatively invariant. All dog breeds are exact allometric dwarfs with respect to measures of skull length. It is unlikely that such a specific morphological relationship has been the direct result of selection by breeders. Rather, a lack of developmental variation seems a better explanation for this exact allometric dwarfism and for the similarity of intra- and interspecific scaling of skull-length components.

The decreased slope and increased intercept of dog-intraspecific regressions relative to interspecific regressions is not surprising since such a difference has been found for a number of mammalian taxa (Jerison, 1973; Gould, 1975; Harvey and Mace, 1980; Radinsky, 1984). However, the magnitude of the slope differences found in this study is relatively large, and the fact that intra- and interspecific regressions almost always cross at large skull lengths is unusual. As a result, dog breeds show a morphological similarity only to the close relatives of the domestic dog, the wolf-like canids (1 in Fig. 2b, c and d). The exception to this concerns allometry of tooth length: grey wolves usually have relatively longer teeth than equivalently-sized domestic dogs (e.g., Fig. 2d). Such tooth dwarfism frequently accompanies domestication (Zeuner, 1963; Epstein, 1971; Turnbull and Reed, 1974) and may reflect differences between artificial and natural selection (see above).

The scaling of M^2 length is an apparent exception to the general pattern exhibited by other dental variables; the interspecific slope of M^2 length is less rather than greater than its intraspecific slope. Also, unlike other dental measurements, the intraspecific and interspecific regressions of M^2 width are not significantly different. In canids, the M^2 is often vestigial and shows the greatest variability in morphology of all the molars (see larger standard error in Table 1 for M^2 length and width against TSL; Gingerich and Winkler, 1979; Pengilly, 1984). This suggests that differences in scaling of M^2 width and length relative to other dental indices are due to differences in the intensity of selection for dental function in wild and domestic canids, reflecting a functional rather than a developmental difference between teeth (Gould and Garwood, 1969; Gingerich and Winkler, 1979; Gingerich and Schoeniger, 1979; Pengilly, 1984).

Discriminant Analysis.—A plot of coordinate values on the first two discriminant axes for centroids of wild species and for individual domestic dogs is shown in Figure 3. Dog breeds were not included in the derivation of the discriminant functions. Two conclusions are apparent from the plot. First, the large wolf-like canids (1 in Fig. 3) are distinct from their smaller, distantly-related cousins, the fox-like canids (2, 3, 4, 5 in Fig. 3). Second, and more significantly, the domestic dogs (dots), which are clearly separate from the fox-like canids, overlap only with their close relatives, species in the wolf-like genera, *Canis, Cuon,* and *Lycaon* (1 in Fig. 3). The apparent morphological dissimilarity between dog breeds and fox-like wild species is not due to differences in size alone, since 30% of the measured breeds are fox size or smaller. Moreover, this separation is highly significant, since these two axes together explain 86% of the variation in the data set. Clearly, as shown by the relative areas of the least convex polygons, morphological variability within the domestic dog is considerable but is, at the same time,

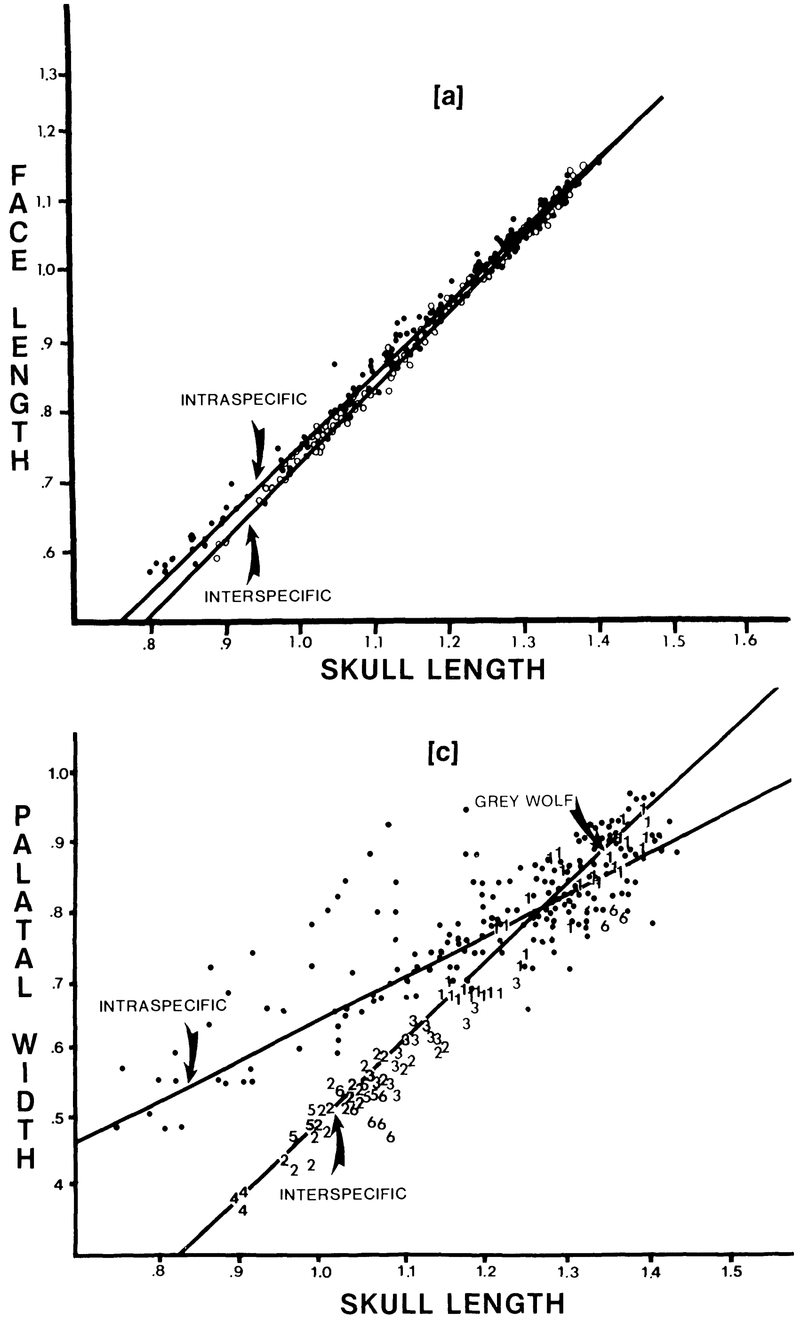
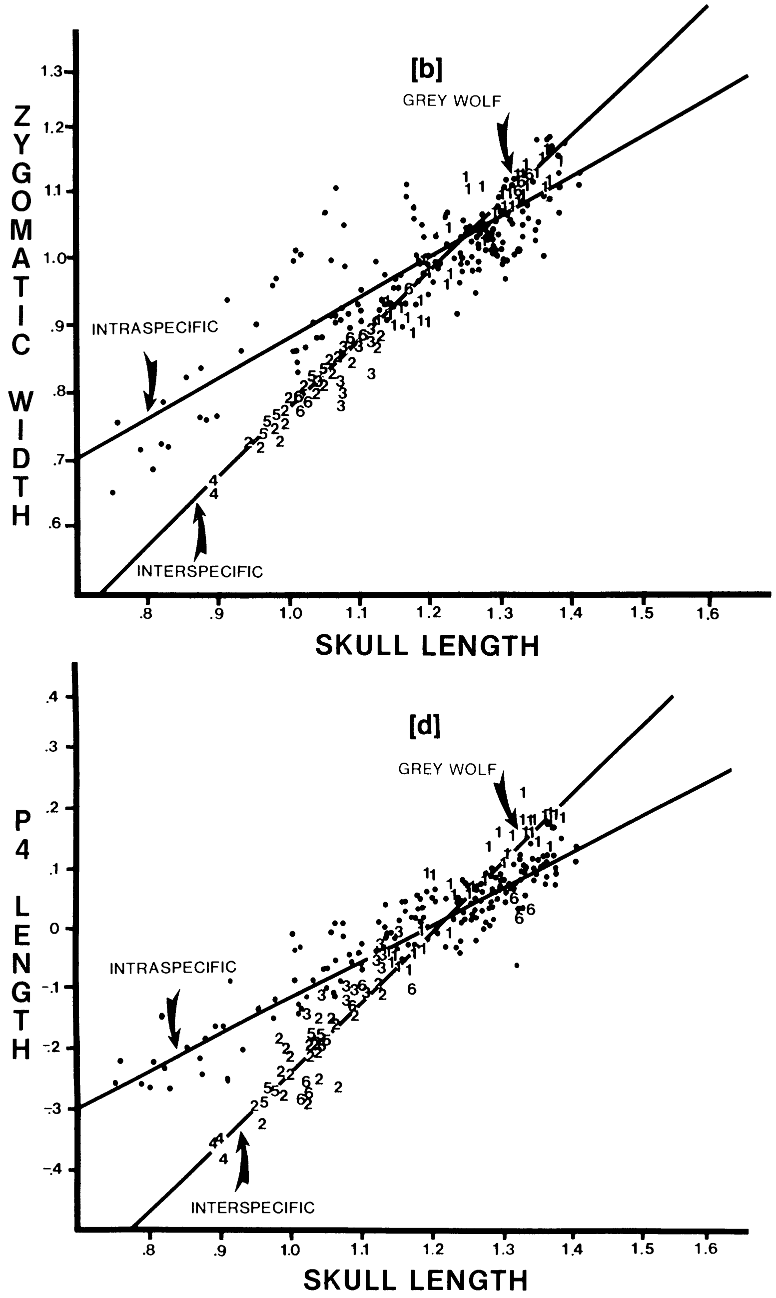


FIG. 2. a) Log/log plot of face length (FL) against total skull length (TSL) for individuals from domestic dogs (hollow circles) and wild canid species (solid circles); b, c, and d) Log/log plot of palatal width (PW), zygomatic width (ZW) and P^4 length (P^4L) against total skull length, respectively, for individuals from domestic dogs and

non-overlapping with that of the fox-like canids.

Some understanding of the morphological features important to discrimination of wild species from each other, and of wild species from domestic dogs, can be gained by examining variable weights on the first discriminant axis. This axis accounts for



wild canid species. Dots = domestic dogs; 1 = *Canis, Cuon* or *Lycaon* (Wolf-like Canids); 2 = *Vulpes, Alopex* (Holartic foxes); 3 = *Cerdocyon, Dusicyon* (South American foxes); 4 = *Fennecus* (fennec); 5 = *Urocyon* (grey fox); 6 = aberrant genera (see Appendix 2). Inter- and intraspecific regression lines are shown. Measurements in centimeters. Statistics in Table 1 and Figure 1.

75% of the variation in the data set and is thus responsible for most of the separation among the wild canids. On the first canonical axis, the highest weights are for total skull length, TSL (1.04), zygomatic width, ZW (1.02), and maximum cranial width MCW (0.76), suggesting that species with large values on axis one have long and wide

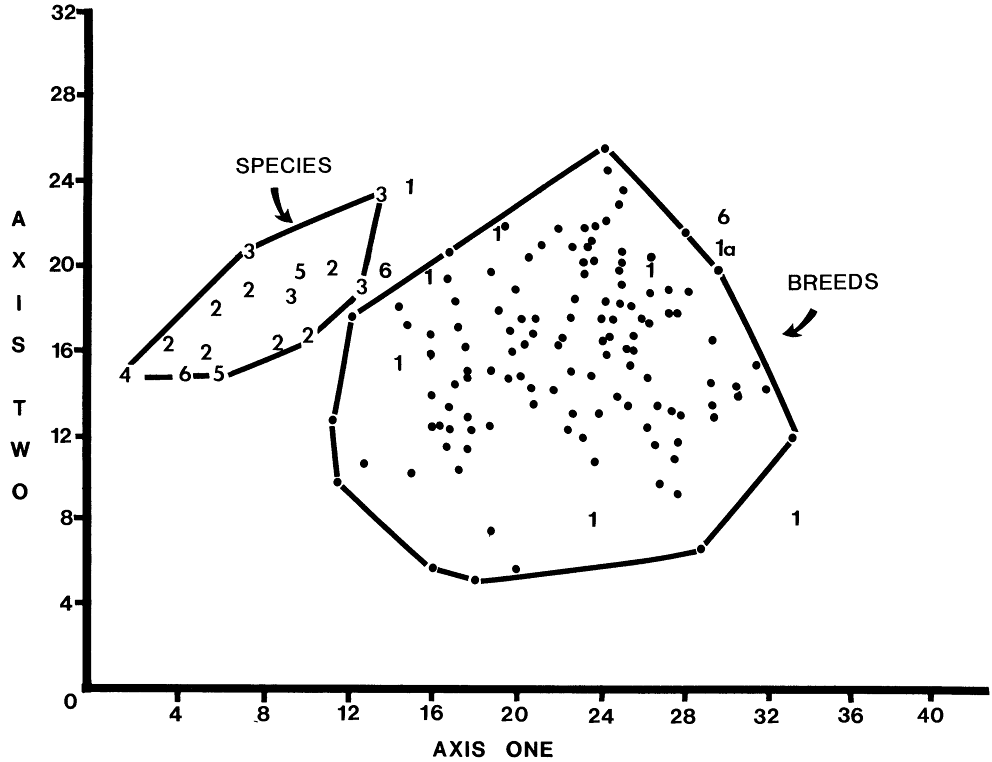


Fig. 3. Coordinate positions of individual domestic dogs and wild species centroids on the first two axes of the discriminant analysis. Units are in standardized discriminant scores, converted to positive values. Separate least-convex polygons are drawn around centroids of fox-sized species (numbers 2 through 5) and around all domestic dogs (dots). Species labeled as in Figure 2, except 1a = *Canis lupus,* the grey wolf.

skulls. As might be expected, separation on the first axis is in part due to differences in skull size, but many of the measured dog breeds (30%) have skulls equivalent in length to those of fox-size wild species. Thus, the separation of dog breeds and wild canids also reflects differences in other cranial and dental measurements, especially measurements of relative skull width. This conclusion follows directly from the bivariate analysis, in which it was shown that all small breeds have skulls that are relatively wider than equivalently-sized wild canids. However, discriminant analysis shows that this difference between dogs and wild canids is also important to discrimination of wild species from each other.

Discriminant analysis is frequently used to classify individuals of unknown group membership (Nei et al., 1975). Classification analysis utilizes the total variability inherent in the data set and is thus a more robust test of the above conclusions. The results support the notion that the tremendous range of cranial size and shape in the domestic dog has surprisingly few natural analogs among wild species. Ninety-four percent of the domestic dogs are classified within the wolf-like genera *Canis, Cuon,* and *Lycaon.* No other canid genus has more than two dogs classified within it. This important result suggests that morphological evolution within the domestic dog has produced breeds that are as different, by the same morphological criteria, as some wild canid species, but in general, morphological change within the domestic dog has not transcended ancient phylogenetic boundaries.

The pattern of morphological similarity between breeds and wolf-like canids does show a phylogenetic inconsistency. The progenitor of the domestic dog, the grey wolf (*Canis lupus*) does not appear as morphologically similar to most dog breeds as do other less closely related wolf-like canids: the grey wolf centroid (1a) is slightly outside the domestic dog polygon in Figure 3. Similarly, if classification assignments are examined for each species, fewer than five percent of the domestic dogs are classified with the gray wolf. Previous workers have also observed that wolves can be distinguished from domestic dogs using cranial characters but have not questioned their ancestor-descendent relationship, which is suggested by several independent lines of evidence (Lawrence and Bossert, 1967; Gipson et al., 1974; Elder and Hayden, 1977; Nowak, 1979; Newsome et al., 1980). In this study, the disparity between dog breeds and wolves follows from the latter being much larger than most domestic dogs and, more significantly, from wolves having relatively longer teeth (see Fig. 2d).

In sum, both the bivariate and discriminant analyses demonstrate that the domestic dog is extremely diverse in skull shape and that a component of this diversity has a morphological counterpart in the three wolf-like genera *Canis, Cuon,* and *Lycaon.* However, despite an overlap in size, domestic dog breeds can be completely distinguished from fox-like wild canids. This discrimination is primarily due to differences in relative cranial width and depth and in dental length and width.

Ontogenetic Allometry.—The pattern of scaling among juveniles of different ages is similar to that among adults of different sizes (Fig. 4). As before, the scaling of skull length components is not strongly allometric, since slopes are close to one. Relative to ontogenetic regressions of other variables, the standard error is small, and the correlation coefficient high, indicating minimal scatter about the regression line (see Table 2, Figs. 4 and 5). In contrast, the scaling of skull width and depth is in general strongly allometric, and hence puppies change dramatically in relative skull width as they grow (Fig. 9a and b).

Except for BCL, there is a close correspondence of interspecific, dog-intraspecific and dog-ontogenetic regressions for measures of skull length (Fig. 4). In contrast, for measurements of skull width and depth, ontogenetic scaling seems more similar to intraspecific scaling than to interspecific scaling (Fig. 4). In three of the eight skull width and depth regressions, the difference between intraspecific and ontogenetic allometry is not significant (CD, PD, MW). In every case, ontogenetic regressions of skull-width variables can be statistically distinguished from the equivalent interspecific regression.

TABLE 2. Standard error of the residuals (SE) and Pearson product-moment correlation coefficients (*r*) for regressions discussed in text. Data are from measurements on museum skulls of juvenile domestic dogs. Starred variables are from measurements on radiographs of four developing puppies of different breeds.

Dependent variable	SE	*r*
Skull length		
FL	0.017	0.99
PL	0.011	0.99
BCL	0.031	0.98
ML	0.017	0.99
Skull width and depth		
PW	0.029	0.98
MCW*	0.025	0.90
ZW*	0.030	0.99
LCW*	0.013	0.74
CD*	0.023	0.96
PD*	0.041	0.96
MW	0.041	0.94
MH	0.069	0.88

In instances where ontogenetic and intraspecific allometry differ significantly from each other (e.g., skull-width regressions: PW, MCW, ZW, LCW), the bivariate plots of these variables against total skull length show a distinct pattern (Fig. 6). Adults from small breeds (less than 15 cm total skull length, approximately 1.2 in Fig. 6) are positioned above or very near to the ontogenetic regression line. Therefore, adults of small breeds have skull proportions like those of juvenile dogs of the same or smaller skull size. That is, all small breeds are to some extent juvenilized or paedomorphic (sensu Gould, 1977). In the extreme, some adult dogs have proportions similar to neonate German Shepherds (breeds on isometric line in Fig. 6a). Large breeds fall to either side of the ontogenetic regression line and hence may be either paedomorphic or hypermorphic (equivalent in proportion to a dog that exceeds the ancestral ontogeny; Gould, 1977). Plots of the other skull mea-

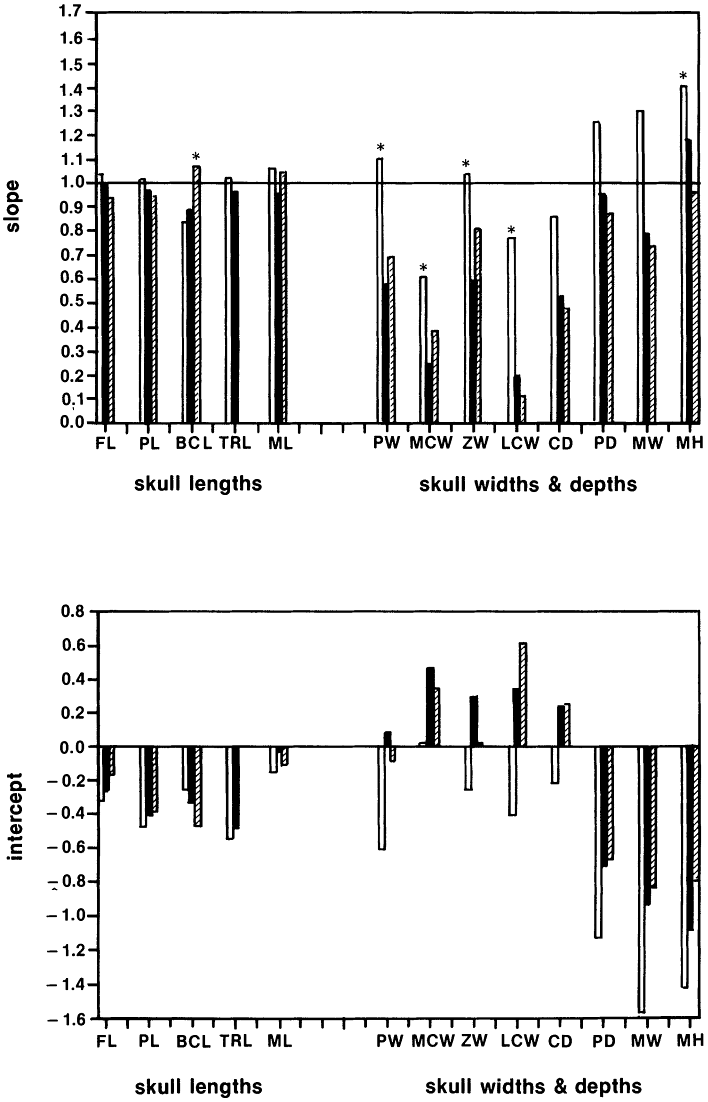


FIG. 4. Histogram of slopes and intercepts of interspecific (left bar, clear), dog-intraspecific (middle bar, solid) and dog-ontogenetic regressions (right bar, hatched) for the indicated measurements against total skull length. Asterisks indicate intraspecific and ontogenetic regression lines that can be statistically distinguished at the 0.05 level (two-tailed *t*-test; Zar, 1984).

surements (MCW, LCW, MH) show a similar relationship between adults from small breeds and juvenile domestic dogs; hence, with respect to measurements of skull shape used in this study, small dog breeds are juvenilized.

Some previous studies of dog domestication have recognized the qualitative similarity of adults of small breeds and juveniles of large dogs (Sommer, 1931; Lumer, 1940; Weidenreich, 1941; Klatt, 1948; Déchambre, 1949; Zeuner, 1963; Epstein, 1971). Other research appears to contradict these studies by demonstrating that puppies of large breeds are never identical in both size and proportion to adults of some dwarf breeds (Stark, 1962; Rosenberg, 1965). This study of many more dog breeds confirms both results. Adults of a few small breeds do fall on the ontogenetic line and are therefore identical in some respects to juveniles of the same size from large breeds, but most

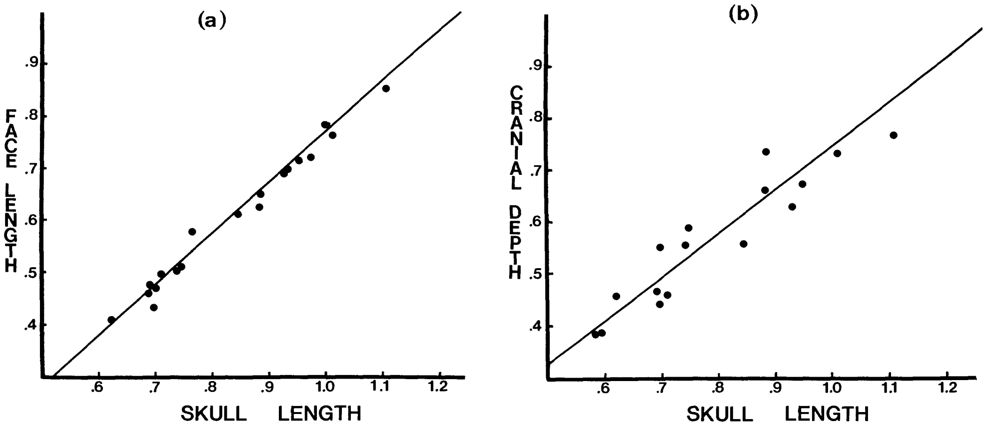


FIG. 5. Log/log plot of a) face length (FL) and b) cranial depth (CD) against total skull length for domestic dog puppies of different sizes. Data are from measurements of puppy skulls in museum collections. Ontogenetic regression line is shown. Measurements in centimeters. Statistics in Table 2 and Figure 4.

adults from small breeds fall above the ontogenetic line and hence are similar in proportion to smaller, rather than equivalently-sized juveniles of large breeds.

Why Are All Small Dog Breeds Paedomorphic?—The morphological differences among dog breeds are conceivably due to differences in shape evident at birth, in postnatal growth rates, or in time of growth cessation (for discussion see Alberch et al., 1979; Katz, 1980; Larson, 1980; Cheverud, 1982*b*). Size differences at birth would seem less important in dog evolution since, as observed by Darwin, most dog breeds are more similar at birth and diverge morphologically as they grow (Darwin, 1859, p. 445). Also, weights of breeds of vastly different adult size are much more similar at birth (e.g., the weight at birth of a Fox Terrier and German Shepherd are in a ratio of 0.43, whereas in the adult this ratio is 0.20 [Altman and Ditter, 1962 p. 211; Hubbard, 1964]).

Paedomorphic or hypermorphic adults may be produced from neonates of similar size and proportion simply by changing the specific growth rate of linear dimensions by the same proportion. Such an alteration maintains the same ratio of specific growth rates, and consequently the same bivariate slope, at corresponding points in development (Figs. 6b and 7). As long as the relationship between growth curves remains the same and the growth period is approximately equivalent, ontogenetic and intraspecific allometry will resemble one another. In fact, coincident timing of growth cessation is not necessary for this model to be valid, since specific growth rates are very low late in development (Figs. 7 and 8), and thus the overall contribution of late postnatal growth to size change is small. Moreover, static and ontogenetic scaling will coincide even among breeds born at different initial sizes, as long as the static scaling among neonates is similar to the ontogenetic scaling among puppies of different ages. Strict parallelism between ontogenetic and intraspecific allometry follows from the simple requirement that the specific growth rates of cranial dimensions are always changed by the same proportion in the evolution of new breeds.

Such proportional, coordinated changes in overall growth rate of skull measurements explain instances of parallelism between ontogenetic and intraspecific scaling, but not those instances in which adults from small breeds have skulls wider than juveniles of equivalent skull length (breeds located above the ontogenetic regression line; Fig. 6). For these breeds, in addition to an overall decrease in growth rate, the relative rate of growth between characters must be changed. For instance, in Figure 8, the specific growth rates of total skull length (TSL) and zygomatic width (ZW) are plotted against time for a growing Great Dane (hol-

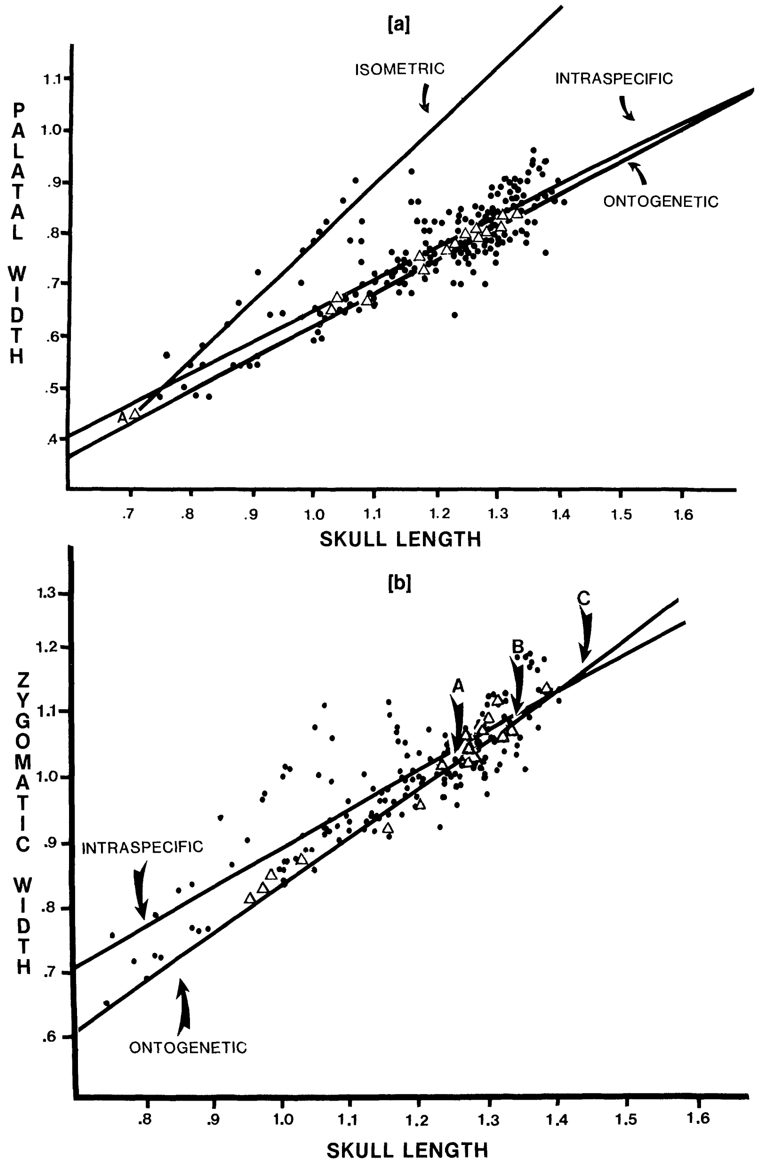


FIG. 6. a) Log/log plots of palatal width (PW) and total skull length for juvenile German Shepherds (triangles; Becker, 1923) and adult domestic dogs (dots). Since the isometric line indicates an extension of neonate proportions (denoted by point A) into large size, many domestic dogs have neonate proportions as adults. b) Log/log plot of zygomatic width (ZW) and total skull length for developing juvenile domestic dogs (symbols) and adult domestic dogs (dots). Ontogenetic data is from measurements on radiographs of developing dog puppies (Wayne, 1984). B is the normal 150-day-old juvenile of the Great Dane. A and C represents the morphology of a 150-day-old juvenile that results if a 60-day-old juvenile grows according to the specific growth rate curves in Figure 7. A is paedomorphic while C is hypermorphic. Ontogenetic and intraspecific regression lines are shown. Measurements in centimeters. Statistics in Table 2 and Figure 4.

low squares) and a Lhasa Apso (solid squares). Apparently, the specific growth rate of zygomatic width is similar in both breeds for much of development (Fig. 8a). In contrast, the growth curve for total skull length of the Lhasa Apso (Fig. 8b) lies below that of the Great Dane. Therefore, relative to the Great Dane, the growth of skull length in

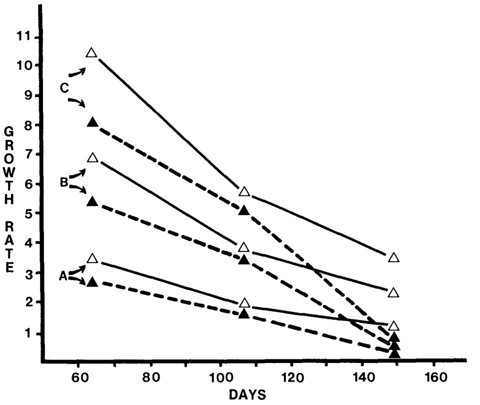


FIG. 7. Hypothetical and observed specific growth rates of zygomatic width (broken lines) and total skull length (solid lines) for 90 days of develoment in the Great Dane. The measured growth rates (B) are multiplied by 1.5 (C) in the upper two lines or by 0.5 (A) in the lower two lines. Specific growth rate in units of 1/day times 1,000.

the Lhasa Apso does not keep pace with that of zygomatic width. Accordingly, the bivariate slope of ZW against TSL will be larger for the Lhasa Apso than for the Great Dane. If the y-intercept values are the same in the Lhasa Apso and Great Dane, then, for a given skull length, the Lhasa Apso will always have a larger zygomatic width. Why only small breeds show this pattern is as yet uncertain.

Theoretically, the specific growth rate of TSL may be increased relative to that of other skull dimensions. This would result in adults with long, narrow faces and skulls, as seen in Russian Wolfhounds and Salukis. But if the overall somatic growth rate were reduced in tandem with an increase in the relative growth rate of TSL, then a small breed with a narrow face and cranium similar to foxes could be produced. None of the sampled small breeds has such a conformation. Neonate dogs are approximately half the size of an adult fox, but they are profoundly different in morphology (ontogenetic intercepts are much larger than interspecific intercepts in Fig. 4). A dramatic departure in the relative growth of TSL and in the overall growth rate of all cranial dimensions would be necessary to produce a small, narrow-skulled adult dog similar to a fox. This suggests that small domestic dogs differ from foxes because puppies of small dogs cannot grow out of their distinctive neonate morphology.

This conclusion implies that differences between dogs and fox-like species stem from discrepancies between the conformation of their neonates. Among wild canids there is a broad similarity in fetal growth rate (Frazer and Hugget, 1974; Calder, 1982). Thus, the neonate size of wild canids increases with gestation time. In contrast, there are significant differences in the neonate size of domestic dogs, yet all dogs have the same 60–63 day gestation period as their progenitor, the grey wolf (Wayne, 1986). Most fox-size wild canids have gestation times of approximately 52 days, and hence, relative to a domestic dog of any size, all fox-like canids are born immature or altricial. If fetal

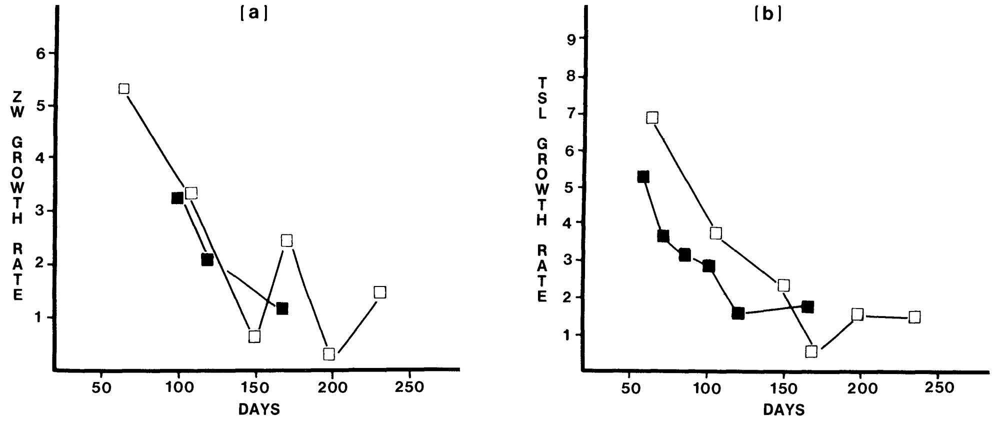


FIG. 8. Specific growth rates of a) zygomatic width and b) total skull length against time for the Great Dane (hollow squares) and the Lhasa Apso (solid squares). Specific growth rate in units of 1/day times 1,000.

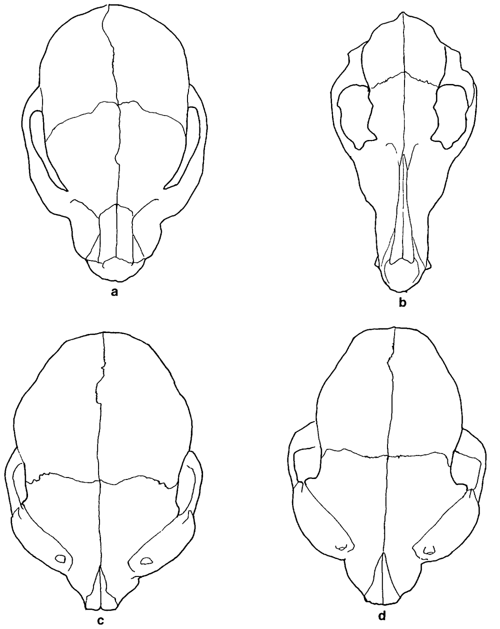


FIG. 9. Dorsal view of a skull of a) a domestic dog neonate and b) an adult, contrasted with that of c) a domestic cat neonate and d) an adult cat. All skulls are drawn to the same length. Adult dog skull is from Evans and Christensen (1979).

growth rates of cranial dimensions are similar in small dogs and fox-like canids and if skull growth is not isometric for most measurements, domestic dogs will be born with a different conformation due to their longer gestation time. As suggested above, this initial difference between dogs and fox-size wild canids may be difficult to overcome. Hence, in domestic dogs the apparent lack of variability in gestation time may act as a fundamental developmental constraint on the morphological diversity of dog breeds.

Evolutionary Implications

Despite the uncertain role of developmental mechanisms in breed evolution, the similarity between static and ontogenetic allometry in the domestic dog suggests a causal relationship between the process of ontogeny and the generation of diverse adult morphologies (i.e., breeds). Dramatic shape changes in ontogeny apparently translate into strong allometry among adults. Puppies have wide, rounded crania, large orbits and broad palates. The average large adult dog has a long, narrow rostrum with a tapered cranium (Fig. 9a and b). To some extent, many dog breeds represent morphological snapshots between these developmental endpoints. This may prove to be a general rule for domestic mammals: diversity under domestication is dependent on the morphological discrepancy between neonate and adult. Furthermore, since many dog breeds appear behaviorally paedomorphic (Zimen, 1971; Fox, 1978) the behavioral diversity among adults may stem from that expressed in ontogeny.

The morphological similarity between dog breeds and wolf-like species (Figs. 1, 2, 3) suggests that there may be similarities between the mechanics of morphological change under domestication and in nature. For example, Jolicoeur (1959), in a multivariate analysis, found that wolf populations differ primarily in relative skull width. Similar differences have been found among wolves and wolf-size dog breeds in this study (Figs. 2 and 3). Presumably, such differences stem from the strong allometric scaling of skull width measurements in ontogeny. To answer the question posed in the introduction, in the absence of appreciable genetic change, ontogenetic scaling may be the common determinant of adult patterns of allometry. This may be especially valid for species (such as species in *Canis*) in which selection may favor differences in size alone (rather than shape) as a means of mitigating interspecific competition (Rosenzweig, 1968; McNab, 1971; Kleiman and Eisenberg, 1973). In general, under conditions of rapid evolutionary change but minimal genetic change, and where selection favors differences in size apart from morphology, ontogenetic scaling may limit the extent of morphological diversity among adults.

Examples from other Domestic Mammals.—The influence of ontogenetic shape diversity on morphological diversity of adults is apparent in other mammal taxa. The domestic cat (*Felis catus*) has been domesticated for as long as 9,500 year (Clutton-Brock, 1981 p. 111). Yet, among cat breeds there is minimal variability in size or shape. Cat breeds differ primarily in coat color and texture and only slightly in skull morphology (Robinson, 1977). Since the crania of kittens and adult cats differ considerably in size but not in shape (Fig. 9c and d), the ontogenetic scaling of most cranial dimensions more closely approaches isometry than in the domestic dog. Hence, in contrast to the domestic dog, simple changes in the overall growth rate of the cranium (or in the duration of growth) will not result in shape differences among adult cats. There is a striking resemblance between the neonates and adults of small wild cat species as well (Fagan and Wiley, 1978), which in part may explain the observation that there are only minor differences in skull proportions among many, especially the smaller, felids (Davis, 1962; Ewer, 1973).

Horses are an example of a domestic species that varies in size almost as much as the domestic dog but is considerably less variable in cranial shape (Zeuner, 1963; Epstein, 1971). As with domestic dogs, the skull shape diversity among adults is related to that within an age series of juvenile horses (Hilzheimer, 1935; Hammond, 1935; Robb, 1935; Epstein, 1971; Radinsky, 1984; Devillers et al., 1984). The importance of ontogenetic allometry for the extent of morphologic evolution in horses is also suggested by the work of Woodburne and MacFadden (1982). These authors demonstrate a relationship between size increase, relative maturity, and morphologic change in horse evolution.

In contrast to cats and horses, pigs (*Sus scofa*) show considerable change in skull proportions with growth. Piglets are born with extremely wide palates, broad crania, and short faces. Adults have narrow crania and long faces. For instance, the ratio of palate length to width in piglets changes from 3:1 at one month to 5:1 at six months of age (Epstein, 1971 p. 365). This ontogenetic shape change is paralleled by considerable cranial diversity among adults of different breeds. Pig breeds number in the hundreds, and among domestic mammals, pigs appear to be second only to domestic dogs in morphologic diversity (Epstein, 1971). Many pig breeds clearly show juvenile skull proportions. Hilzheimer (1926) asserted that the skull morphology of adults in some races of pigs resemble juveniles of more "primitive" races, and he suggested that "advanced" races terminate development prematurely. As shown previously, paedomorphic adults could also result from a change in relative or overall somatic growth rates. In either case, the general observation is unchanged; cranial shape diversity among adult pigs might be predicted from growth curves. Since extant wild species are morphologically very similar, morphological diversity in wild suids does not seem to reflect ontogenetic allometry. However, pigs were morphologically more diverse in the Pleistocene (Cooke and Wilkanson, 1978), and thus an allometric study of these extinct forms might alter this conclusion.

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Appendix 1

The following 21 measurements were taken on each skull except when skulls were incomplete or lacking measured features (e.g., Speothos has no M^2). Figure A-1 shows most of these 21 traits digrammatically.

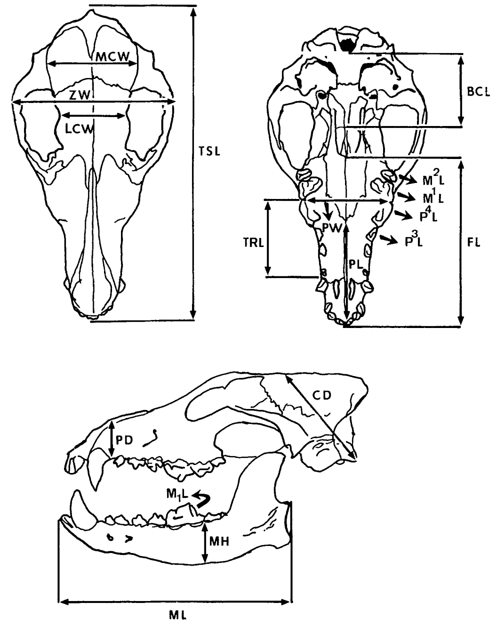

FIG. A-1. Diagrams showing measurements taken on each skull.

SKULL LENGTH

Total skull length (TSL)
Face length (FL)
Palatal length (PL)
Basicranial length (BCL)
Upper premolar tooth row length (TRL)
Mandible length (ML)

SKULL WIDTH AND DEPTH

Palatal width (PW)
Maximum cranial width (MCW)
Zygomatic width (ZW)
Least cranial width (LCW)
Cranial depth (CD)
Premaxilla depth (PD)
Mandible width (MW): Medial/lateral width at posterior end of P^4
Mandible height (MH)

DENTAL LENGTH AND WIDTH (maximum)

P^3 Length (P^3L)
P^4 Length (P^4L)
M^1 Length (M^1L)
M^2 Length (M^2L)
M^1 Width (M^1W): Maximum medial/lateral width
M^2 Width (M^2W): Maximum medial/lateral width
M_1 Length (M_1L)

These measurements were made with vernier calipers on skulls from 75 dog breeds (202 skulls) and 26 wild canid species (95 skulls). Two to sixteen skulls were measured for each species. One to eight skulls were measured for each breed. Cranial measurements only were taken on 25 juvenile domestic dog skulls in museum collections. In addition, data from museum skulls measured by Becker (1923) and from radiographs of developing dogs measured by the author were used to augment the sparse museum collections. A list of skulls measured with museum location and number is available from the author.

Appendix 2. List of names, average body weight (if known), and code number of species used in the Figures. Weight references in Wayne (1984) and Nowak and Paradiso (1983).

	Weight (kg)	Code number
Wolf-like species:		
Canis familiaris (domestic dog)	0.5–90	1
Canis lupus (grey wolf)	45	1
Canis latrans (coyote)	15	1
Canis aureus (golden jackel)	7	1
Canis adustus (side-striped jackel)	6	1
Canis mesomelas (black-backed jackel)	7	1
Cuon alpinus (dhole)	17	1
Lycaon pictus (Cape hunting dog)	25	1
Vulpine foxes:		
Vulpes vulpes (red fox)	8.5	2
Vulpes velox (swift fox)	2	2
Vulpes bengalensis (Bengal fox)	3	2
Vulpes rueppelli (sand fox)	2.7	2
Vulpes chama (cape fox)	4	2
Vulpes pallida (pale fox)	2.6	2
Alopex lagopus (arctic fox)	5.2	2
South American foxes:		
Dusicyon culpaeus	3.5	3
Dusicyon griseus (chico grey fox)	6.5	3
Dusicyon gymnocercus (pampas fox)	4.4	3
Cerdocyon thos (crab-eating fox)	6.5	3
The Fennec:		
Fennecus zerda (fennec)	1.2	4
Grey fox:		
Urocyon cinereoargenteus (grey fox)	4.5	5
Urocyon littoralis	4	5
Aberrant canids:		
Nyctereutes procyonoides (raccoon dog)	7	6
Speothos venaticus (bushdog)	6	6
Chrysocyon brachyurus (maned-wolf)	22	6
Otocyon megalotis (bat-earred fox)	4.2	6
Atelocynus microtis (zorro)	9.5	6