# Comparative morphology of the mandibulodental complex in wild and domestic canids

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## ABSTRACT

The relationships between mandibular and dental measurements were investigated in a sample of 60 adult domestic dogs, 17 black-backed jackals *Canis mesomelas*, 18 side-striped jackals *C. adustus* and 16 Cape foxes *Vulpes chama*. Standard mesiodistal and buccolingual tooth measurements, together with 8 mandibular measurements (intercondylar distance, intercarnassial breadth, mandibular length, arch length, condylar height, canine-condylar length, mandibular width, mandibular height) were scaled allometrically to total skull length. Despite wide differences in diet and sexual dimorphism between the 3 wild canid species, larger canids were found to be scaled up versions of smaller canids. While males showed a highly concordant patterning when compared with domestic dogs of equivalent size, females showed a remarkably mosaic pattern. Relative to skull size, the only teeth that appear to be larger than those of equivalently sized domestic dogs were the second molars. It is suggested that those theories of sexual dimorphism and functional integration which apply to skeletodental dimensions in primates may not be applicable to canids.

## INTRODUCTION

Allometric relations of teeth and the jaws that house them have long attracted the attention of comparative anatomists. Much of their attention, however, has been directed at extent and extinct primates. For instance, Wolpoff (1978) studied the scaling of canine size in hominids and found them to be negatively allometric. Corruccini and Henderson (1978) re-examined these data and pronounced the canines to be positively allometric. Wood (1979) and Wood and Stack (1980) followed with more comprehensive analyses and concluded that larger primates tended to have larger canines.

While a positive allometric relationship between molar size and body size was demonstrated in hominoids (Pilbeam & Gould, 1974) a negative relationship was shown in other primates (Kay, 1975). That allometric coefficients in primates differed according to tooth locus has also been well documented (Lauer, 1975; Smith, 1981; Gingerich et al. 1982). Shea (1983), who analysed dentocranial allometry in higher primates, showed that interspecific differences

in tooth size were related to differing dietary habits. Studies on mandibular scaling patterns in primates have cast light on various taxonomic, ecological and biomechanical problems (Hylander, 1979, 1985; Cachel, 1984; Bouvier, 1986; Kieser & Groeneveld, 1987; Kanazawa & Rosenberger, 1989). In contrast, the interspecific morphological variation of the mandibulodental complex in the carnivora has received little attention (Greaves, 1978; Radinsky, 1981; Kieser & Groeneveld, 1991).

The purpose of the present study was to quantify the differences in proportions of the mandibulodental complexes of 3 wild carnivores of southern Africa, *Vulpes chama*, *Canis adustus* and *C. mesomelas*, and to relate these patterns to those in a sample of domestic dogs *C. familiaris* of differing sizes.

## MATERIALS AND METHODS

Measurements were obtained from the mandibles of 60 adult fox-like domestic dogs (30 males), 17 black-backed jackals (10 males), 18 side-striped jackals (9 males) and 16 Cape foxes (8 males). These specimens

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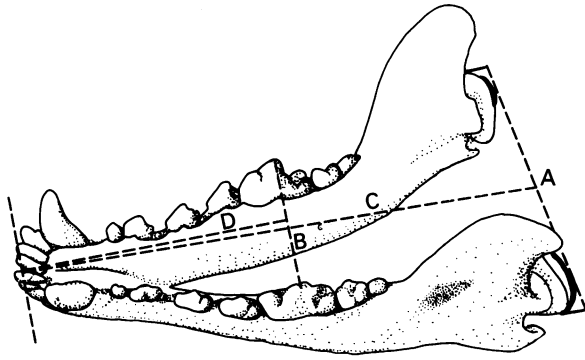
Fig. 1. Stylised mandible showing some of the measurements employed in the study. See text for definitions.
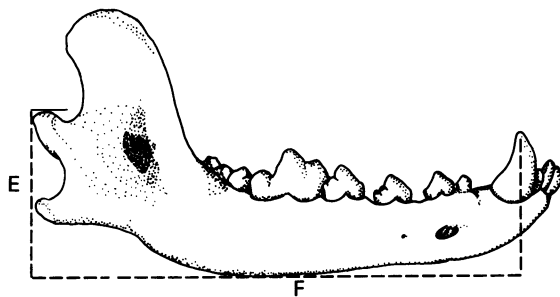


Fig. 2. Lateral view of a stylised mandible showing condylar height (E) and canine condylar length (F). See text for definitions.

had all been collected in the southern African subregion and were housed in the Transvaal Museum, Pretoria, the Kaffrarian Museum in King William's Town and in the State Museum of Namibia, Windhoek. Only adults that had been wild-shot were used.

Buccolingual and mesiodistal dental diameters were determined on all mandibular teeth save the incisors and first 2 premolars using a sliding caliper on which the measuring tips had been sharpened (0.01 mm). The mesiodistal (MD) diameter was accepted as the maximum mesiodistal dimension, parallel to the occlusal plane, while the buccolingual (BL) crown diameter was taken as the greatest distance between the buccal and lingual surfaces of the tooth crown, perpendicular to the MD dimension. Pearson correlation coefficients for intra-observer reliability based on 20 repeated measurements yielded reliability coefficients of 0.997 for MD and 0.934 for BL diameters.

Eight mandibular measurements were also taken: (A) intercondylar distance; (B) arch breadth or intercarnassial distance; (C) mandibular length as the perpendicular distance from the intercondylar line to infradentale; (D) arch length as the perpendicular length from the intersection of the bicarnassial line and the line from infradentale; (E) condylar height; (F) canine-condylar length; (G) mandibular width at the level of the carnassial notch; and (H) mandibular

height at the level of the carnassial notch. These measurements are illustrated in Figures 1 and 2 and are described elsewhere (Wayne, 1986; Kanazawa & Rosenberger, 1989).

All mandibular and dental measurements were scaled to the total skull length of the animal concerned. Allometric relationships were probed by means of Huxley's (1932) power formula: $Y = bX^a$. Here, the exponent is the allometric coefficient, b is a constant and $Y = X^1$ is the isometric base line. All measurements were log-transformed and regressions were fitted by means of a major axis technique (Martin & Barbour, 1989). Because of our relatively small sample sizes, bias was reduced by means of a bootstrap procedure with 300 iterations (Hall & Martin, 1988).

## RESULTS

Univariate statistics for mandibular measurements in the 3 wild carnivore species are listed in Table 1. These data show that while *V. chama* was totally sexually

Table 1. *Univariate statistics for mandibular measurements in the 3 wild canid species examined*

| Variable | Males x̄ | S.D. | t | Females x̄ | S.D. |
|---|---|---|---|---|---|
| *Vulpes chama* | | | | | |
| A | 51.33 | 2.46 | 2.05 | 48.19 | 2.95 |
| B | 23.67 | 1.45 | 1.92 | 22.01 | 1.57 |
| C | 80.30 | 1.91 | 1.25 | 78.13 | 1.81 |
| D | 41.66 | 1.88 | 1.29 | 40.10 | 0.77 |
| E | 20.55 | 0.70 | 0.41 | 20.33 | 1.20 |
| F | 78.71 | 1.65 | 1.87 | 75.69 | 1.69 |
| G | 4.97 | 0.32 | −1.36 | 5.82 | 0.72 |
| H | 10.09 | 1.22 | 1.69 | 9.11 | 0.82 |
| *Canis adustus* | | | | | |
| A | 68.90 | 2.02 | 5.69** | 62.60 | 1.42 |
| B | 31.95 | 1.17 | 2.84* | 27.62 | 1.47 |
| C | 126.87 | 1.02 | 4.38** | 117.74 | 1.34 |
| D | 64.09 | 1.96 | 2.63* | 59.71 | 1.23 |
| E | 31.56 | 1.14 | 1.74 | 29.49 | 1.38 |
| F | 121.30 | 1.71 | 10.09** | 112.31 | 1.00 |
| G | 8.61 | 0.16 | 1.05 | 8.42 | 0.36 |
| H | 16.37 | 0.30 | 5.64** | 14.75 | 0.56 |
| *Canis mesomelas* | | | | | |
| A | 72.50 | 1.53 | 4.63** | 67.89 | 1.12 |
| B | 36.15 | 1.51 | 5.09** | 32.77 | 1.21 |
| C | 116.33 | 0.94 | 4.90** | 107.11 | 0.90 |
| D | 61.77 | 1.97 | 2.93* | 58.66 | 1.02 |
| E | 29.36 | 1.53 | −0.69 | 30.21 | 1.27 |
| F | 107.45 | 2.77 | 2.44 | 101.74 | 1.35 |
| G | 8.36 | 0.62 | 1.47 | 7.94 | 0.49 |
| H | 16.11 | 0.45 | 1.68 | 15.14 | 0.36 |

x̄ = mean; S.D. = standard deviation; t = Student's t test for sexual dimorphism; * = $P < 0.05$; ** = $P < 0.01$.

Table 2. *Univariate statistic for mandibular dental measurements in the 3 wild canid species examined*

| | | Males | | | Females | |
| --- | --- | --- | --- | --- | --- | --- |
| Variables | | $\bar{x}$ | S.D. | t | $\bar{x}$ | S.D. |
| C | MD | 4.61 | 0.34 | 2.94* | 4.16 | 0.17 |
| | BL | 3.29 | 0.39 | 2.25 | 2.91 | 0.12 |
| $P_3$ | MD | 6.56 | 0.50 | 0.58 | 6.42 | 0.32 |
| | BL | 2.52 | 0.14 | 0.65 | 2.47 | 0.18 |
| $P_4$ | MD | 7.37 | 0.37 | 1.34 | 7.05 | 0.26 |
| | BL | 3.27 | 0.24 | 0.74 | 3.19 | 0.15 |
| $M_1$ | MD | 11.74 | 0.74 | −0.21 | 11.83 | 0.83 |
| | BL | 5.01 | 0.74 | 0.40 | 4.87 | 0.38 |
| $M_3$ | MD | 6.87 | 0.25 | 0.59 | 6.70 | 0.47 |
| | BL | 4.55 | 0.27 | −1.09 | 4.75 | 0.40 |
| *Canis adustus* | | | | | | |
| C | MD | 8.00 | 0.02 | −1.30 | 8.29 | 0.45 |
| | BL | 4.89 | 0.07 | 1.83 | 4.52 | 0.34 |
| $P_3$ | MD | 9.45 | 0.20 | 4.83** | 8.77 | 0.18 |
| | BL | 4.00 | 0.02 | 16.60** | 3.28 | 0.09 |
| $P_4$ | MD | 10.73 | 0.35 | 5.30** | 9.79 | 0.18 |
| | BL | 5.11 | 0.13 | 4.51** | 3.67 | 0.19 |
| $M_1$ | MD | 17.97 | 0.16 | 2.45* | 16.60 | 0.06 |
| | BL | 7.45 | 0.05 | 9.63** | 6.72 | 0.15 |
| $M_2$ | MD | 10.60 | 0.08 | 3.32* | 9.54 | 0.04 |
| | BL | 7.46 | 0.13 | 3.70* | 6.50 | 0.12 |
| *Canis mesomelas* | | | | | | |
| C | MD | 7.89 | 0.07 | 0.78 | 7.53 | 0.09 |
| | BL | 5.18 | 0.27 | 2.50* | 4.89 | 0.16 |
| $P_3$ | MD | 9.42 | 0.03 | 1.75 | 8.77 | 0.14 |
| | BL | 4.04 | 0.12 | 1.62 | 3.82 | 0.03 |
| $P_4$ | MD | 10.68 | 0.19 | 1.77 | 10.26 | 0.14 |
| | BL | 4.86 | 0.24 | 2.11 | 4.57 | 0.27 |
| $M_1$ | MD | 17.84 | 0.04 | −1.10 | 18.49 | 0.03 |
| | BL | 8.03 | 0.15 | 0.62 | 7.88 | 0.26 |
| $M_2$ | MD | 9.22 | 0.40 | 0.57* | 8.55 | 0.55 |
| | BL | 6.91 | 0.10 | 5.40** | 6.16 | 0.33 |

$\bar{x}$ = mean; S.D. = standard deviation; t = Student's t test for sexual dimorphism; * = $P < 0.05$; ** = $P < 0.01$.

monomorphic, *C. adustus* was the most dimorphic. Four of the 8 mandibular measurements in *C. mesomelas* showed significant differences between males and females, namely the intercondylar distance (A), arch breadth (B), mandibular length (C) and arch length (D). The univariate statistics for mandibular dental measurements presented in Table 2 similarly suggest that *C. adustus* is the most dimorphic of the 3 species. Again, *V. chama* emerges as the least dimorphic, with *C. mesomelas* showing only 3 instances of dimorphism out of the 10 measurements taken.

As shown in Table 3, the allometric slopes for mandibular measurements scaled to total skull length do not vary significantly between the wild canids and the domestic dogs. While none of the slopes in males differed significantly from isometry, one measurement in females (mandibular width, G) was significantly

Table 3. *Allometric scaling of mandibular measurements to total skull length in domestic dogs and in the 3 wild canid species examined*

| | | Domestic dogs | | Wild canids[1] | | |
| --- | --- | --- | --- | --- | --- | --- |
| Sex | Variable | a | S.D. | a | S.D. | Difference |
| Male | A | 0.978 | 0.023 | 0.960 | 0.074 | n.s. |
| | B | 0.982 | 0.021 | 0.948 | 0.087 | n.s. |
| | C | 0.990 | 0.003 | 0.991 | 0.005 | n.s. |
| | D | 0.995 | 0.003 | 0.994 | 0.008 | n.s. |
| | E | 0.996 | 0.031 | 0.956 | 0.033 | n.s. |
| | F | 0.993 | 0.002 | 0.988 | 0.013 | n.s. |
| | G | 0.922 | 0.032 | 0.946 | 0.056 | n.s. |
| | H | 0.977 | 0.034 | 0.983 | 0.030 | n.s. |
| Female | A | 0.984 | 0.021 | 0.962 | 0.046 | n.s. |
| | B | 0.938 | 0.038 | 0.920 | 0.063 | n.s. |
| | C | 0.998 | 0.003 | 0.996 | 0.005 | n.s. |
| | D | 0.992 | 0.003 | 0.990 | 0.006 | n.s. |
| | E | 0.963 | 0.059 | 0.958 | 0.055 | n.s. |
| | F | 0.990 | 0.005 | 0.990 | 0.005 | n.s. |
| | G | 0.813* | 0.043 | 0.826* | 0.096 | n.s. |
| | H | 1.027 | 0.010 | 1.024 | 0.023 | n.s. |

[1] = *Vulpes chama*, *Canis adustus* and *C. mesomelas*; * = significantly different from isometry (a = 1.00); a = slope; S.D. = standard deviation.

Table 4. *Allometric scaling of mandibular dental measurements to total skull length in domestic dogs and in the 3 wild canid species examined*

| | | | Domestic dogs | | Wild canids[1] | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Sex | Variable | | a | S.D. | a | S.D. | Difference |
| Male | C | MD | 0.937 | 0.026 | 0.947 | 0.053 | n.s. |
| | | BL | 0.984 | 0.014 | 0.966 | 0.055 | n.s. |
| | $P_3$ | MD | 0.985 | 0.033 | 0.945 | 0.093 | n.s. |
| | | BL | 0.918 | 0.038 | 0.927 | 0.065 | n.s. |
| | $P_4$ | MD | 1.033 | 0.018 | 1.010 | 0.051 | n.s. |
| | | BL | 1.18 | 0.037 | 1.003 | 0.047 | n.s. |
| | $M_1$ | MD | 1.107 | 0.038 | 0.993 | 0.021 | n.s. |
| | | BL | 1.011 | 0.046 | 0.977 | 0.087 | n.s. |
| | $M_2$ | MD | 0.910 | 0.047 | 0.915 | 0.046 | n.s. |
| | | BL | 0.871 | 0.044 | 0.901 | 0.065 | n.s. |
| Female | C | MD | 0.916 | 0.035 | 0.984 | 0.012 | n.s. |
| | | BL | 0.957 | 0.014 | 0.964 | 0.026 | n.s. |
| | $P_3$ | MD | 0.981 | 0.022 | 0.974 | 0.026 | n.s. |
| | | BL | 0.950 | 0.019 | 0.925 | 0.056 | n.s. |
| | P | MD | 1.004 | 0.061 | 0.984 | 0.061 | n.s. |
| | | BL | 0.944 | 0.019 | 0.884 | 0.211 | n.s. |
| | $M_1$ | MD | 1.054 | 0.010 | 1.015 | 0.076 | n.s. |
| | | BL | 0.963 | 0.039 | 0.942 | 0.058 | n.s. |
| | $M_2$ | MD | 0.912 | 0.071 | 0.911 | 0.064 | n.s. |
| | | BL | 0.936 | 0.022 | 0.937 | 0.023 | n.s. |

[1] = *Vulpes chama*, *Canis adustus* and *C. mesomelas*; * = significantly different from isometry (a = 1.00); a = slope; S.D. = standard deviation.

Table 5. *Distances from species centroids for mandibular measurements to the relevant regressions in domestic dogs*

| Variable | Vulpes chama | Canis adustus | C. mesomelas |
|---|---|---|---|
| **Males** | | | |
| A | −0.020 | −0.085 | −0.013 |
| B | −0.106* | −0.167* | −0.044 |
| C | −0.042 | −0.008 | −0.015 |
| D | −0.063 | −0.028 | −0.017 |
| E | −0.117* | −0.096* | −0.111* |
| F | −0.012 | 0.023 | −0.025 |
| G | −0.213* | −0.118* | −0.101* |
| H | −0.241* | −0.168* | −0.144* |
| **Females** | | | |
| A | −0.017 | −0.104* | 0.018 |
| B | −0.086 | −0.211* | −0.023 |
| C | −0.020 | −0.001 | −0.005 |
| D | −0.056 | −0.045 | 0.008 |
| E | −0.118* | −0.133* | −0.051 |
| F | 0.112* | 0.098* | 0.100* |
| G | −0.073 | −0.097* | −0.064 |
| H | −0.155 | −0.085 | −0.001 |

\* = significant at the 5% level.

Table 6. *Distances from species centroids for dental measurements to the relevant regressions in domestic dogs*

| | Variable | Vulpes chama | Canis adustus | C. mesomelas |
|---|---|---|---|---|
| **Males** | | | | |
| C | MD | −0.254* | −0.155* | −0.129 |
| | BL | −0.232* | −0.220* | −0.143* |
| $P_3$ | MD | −0.038 | −0.052 | −0.020 |
| | BL | −0.234* | −0.201* | −0.156* |
| $P_4$ | MD | 0.009 | −0.031 | 0.002 |
| | BL | −0.172* | −0.121* | −0.120* |
| $M_1$ | MD | −0.137* | −0.074 | −0.069 |
| | BL | −0.089* | −0.067 | 0.020 |
| $M_2$ | MD | 0.207* | 0.216* | 0.161* |
| | BL | 0.089* | 0.138* | 0.128* |
| **Females** | | | | |
| C | MD | −0.270* | −0.085 | −0.084 |
| | BL | −0.242* | −0.216* | −0.092* |
| $P_3$ | MD | −0.006 | −0.052 | 0.012 |
| | BL | −0.201* | −0.280* | −0.110* |
| $P_4$ | MD | −0.009 | −0.044 | 0.053 |
| | BL | −0.123* | −0.304* | −0.073 |
| $M_1$ | MD | −0.082 | −0.098* | 0.081 |
| | BL | −0.035 | −0.084 | 0.093 |
| $M_2$ | MD | 0.182* | 0.144* | 0.139* |
| | BL | 0.132* | 0.068 | 0.100* |

\* = significant at the 5% level.

negatively allometric. The data presented in Table 4 show a similar pattern: all the allometric slopes for dental dimensions scaled isometrically to skull length. This pattern was, moreover, not significantly different between sexes or between wild and domestic canids.

Table 5 lists the distances from the centroids of individual species and the relevant regression lines in domestic dogs. It appears that, as far as mandibular dimensions are concerned, males and females do not share the same patterns of variation. In males of all 3 species, differences from the dog regressions centred on condylar height (E), mandibular height, (H) and mandibular width (G), each of these being significantly smaller than those of equivalently sized dogs. In females, however, condylar height was significantly smaller than dogs, but the canine-condylar length (F) was found to be significantly larger than the dog regression.

Estimates of distances for mandibular dental measurements from the regressions in dogs are listed in Table 6. Females and males showed more concordant values; while canines tended to be relatively smaller than those of equivalently sized dogs, second molars tended to be larger.

## DISCUSSION

### Mandibular morphology

The Cape fox *V. chama*, side-striped jackal *C. adustus* and black-backed jackal *C. mesomelas* are 3 members of the family Canidae found in the southern African subregion. *C. adustus* is the heaviest of the 3 and also the most robust (Smithers, 1983). It is also the most dimorphic of the 3 and is the only species which regularly consumes vegetable matter (Smithers, 1983). In contrast, *V. chama* is the smallest, the least dimorphic and consumes insects and small mammals such as mice. Theoretically, it would be expected that species of different sizes, of different levels of sexual dimorphism and of different diets would have different mandibular morphologies. Yet it has been shown frequently that functionally and developmentally related morphological characters will tend to be correlated in their expression and, as a result, will tend to evolve together as a unit (Lande, 1980; Cheverud, 1982, 1990; Atchley et al. 1985; Cheverud et al. 1991).

The similarity of the allometric slopes for male and female wild canids and domestic dogs (Table 3) indicates a high degree of concordance in mandibular morphology. Larger canids, be they domestic or wild, are simply scaled up versions of smaller canids, the only exception to this rule being mandibular width in females which scales negatively allometric in both groups. Hence larger female canids will tend to have disproportionately narrower mandibular dimensions at the carnassial notch.

Against this general pattern of isometric uniformity the differences in centroidal distances (Table 5) are

especially noteworthy. The largest of the 3 species, *C. adustus*, and the smallest, *V. chama* are also the most significantly removed from the regressions for dogs. Interestingly, *C. mesomelas* appears to have a diet intermediate between the other 2: it feeds on insects, small mammals, carrion and sometimes on vegetable matter (Smithers, 1983).

In the present analysis, males of all 3 species showed a highly concordant pattern. Relative to skull length, these animals shared 4 measurements that were smaller than those of equivalently sized dogs: arch breadth (B), condylar height (E) and mandibular height and width (G and H). Females, in contrast showed little uniformity. Only 3 measurements, mandibular length (C), arch length (D) and mandibular height (H) were similar to equivalently sized dogs in all 3 species.

Although females showed a mosaic pattern of centroidal dispersal about the dog regressions, one measure, the canine condylar length (F), proved to be significantly enlarged in all 3 species (Table 5). Lucas (1981), who studied jaw shape in primates, drew attention to the relationship between jaw length, position and size of the canine and the height of the mandibular condyle. Citing Herring and Herring (1974), he pointed out that the position of the temporomandibular joint is crucial to the mechanical advantage of the masticatory musculature, and hence the ratio of condylar height to jaw length is intimately related to masticatory demands. Here it is of interest to note that in females the larger length is associated with a relatively smaller condylar height.

## Dental size

Comparison of allometric results for tooth size scaled to skull length in male and female wild and domestic canids (Table 4) suggests total conformity to isometry. Larger animals have scaled up sizes of their mandibular teeth. Relative to skull size, the only teeth that appear to be larger than those of equivalently sized dogs are the second molars, a pattern which is consistent among the 3 species considered (Table 6).

These results have several implications. First, unlike the situation in primates, there is no different pattern of scaling corresponding to canine, premolar and molar teeth in the canids examined. Gingerich and Smith (1985) have found, for instance, that posterior and anterior cheek teeth in primates become larger with increasing body size. Smaller primates have disproportionately smaller canine and first molars. The second implication is that, in spite of differences

in size, diet and sexual dimorphism, *V. chama*, *C. mesomelas* and *C. adustus* have similar patterns of relative tooth size. Thirdly, unlike primates, which show strong positive allometry for canine size dimorphism with respect to canine size (Leutenegger & Cheverud, 1985), dimorphism in canine size in carnivores is unrelated to allometric phenomena.

## Conclusions

From the foregoing we conclude that the recognition of an overall pattern of isometry in canid dental size relative to skull length will require a reassessment of those theories of sexual dimorphism and functional integration that have been applied to the primate dentition. As was the case in mandibular dimensions, the teeth of canids appear to have evolved in concert with one another and relatively independently of differences in dimorphism, size or functional demands.

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