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Variation of cranial and dental measurements and dental correlations in the pampean fox (*Dusicyon gymnocercus*)

F. J. Prevosti[1] & L. Lamas[2]

1 Departamento Científico Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina
2 Facultad de Ciencias Naturales y Museo (UNLP), La Plata, Argentina

Keywords
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Correspondence
Francisco Juan Prevosti,Departamento Científico Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n°, 1900–La Plata, Argentina.
Emails: protocyon@hotmail.com, protocyon@fcnym.unlp.edu.ar

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Abstract

The knowledge of the craniodental variability of South American canids is mainly anecdotal, and the variability and dental correlation of living canids have only been studied in several species of holarctic foxes (*Vulpes vulpes*, *Vulpes lagopus* and *Urocyon cinereoargeteus*) and *Canis lupus*. These studies have shown that the last molars, canines and incisors are the most variable and the central molars and premolars are the least variable, and that correlations are highest among the posterior premolars. This pattern has been accounted for by developmental factors, functional utility and tooth complexity. In this paper the pattern of dental correlation and variability of craniodental measurements in the South American fox *Dusicyon gymnocercus* is studied, with the aim of checking the extension of the pattern observed in other species and contrasting previous hypotheses. The most variable in *D. gymnocercus* measurements are some cranial widths, width of the incisors, lower canine and lower last molar, whereas others such as width of the braincase, length of the upper carnassials, and first and second lower and upper molars have lower variability. The premolar region is the most correlated, in terms of values and number of significant correlation coefficients. The results show that measurement error is negatively correlated with size of the variables, which could explain the bias found in this index as earlier authors have suggested, but the pattern captured by this index cannot be completely considered to be an artefact. The observed results confirm that the patterns of variability and correlation found in holarctic foxes are widespread in the family Canidae, and suggest the presence of an evolutionary constraint.

Introduction

The variability and correlation of the canid dental measurements have been studied by several authors (Kurtén, 1953, 1967; Gingerich & Winkler, 1979, Pengilly, 1984; Ansorge, 1994; Polly, 1998*a*; Szuma, 2000), but with certain exceptions (e.g. Dayan, Wool & Simberloff, 2002; Meiri, Dayan & Simberloff, 2005) these works were mainly restricted to vulpine species (e.g. *Vulpes vulpes*, *Vulpes lagopus* and *Urocyon cinereoargenteus*). The existence of intraspecific dental variation in South American foxes (*Dusicyon* spp.) has been known for a long time (e.g. Mivart, 1890; Kraglievich, 1930), but the information is restricted to anecdotal comments and no clear quantification of this variation is available. The lack of knowledge about the intraspecific variation in recent species restricts the correct recognition of fossil species and specimens. This is evident in several systematic paleontological papers in which fossil species are recognized with a 'quasi-typological' approach (e.g. Kraglievich, 1930; Berman, 1994).

The quantitative aspects of the dentition of recent canids have been studied mainly by means of two indexes, the coefficient of variation (CV) and the Pearson product–moment correlation coefficient *r* (e.g. Kurtén, 1953, 1967; Gingerich & Winkler, 1979; Pengilly, 1984; Polly, 1998*a*; Szuma, 2000; Dayan *et al.*, 2002; Meiri *et al.*, 2005). These two indexes allow the comparison of different aspects of the dentition. The first one has been used to compare the variability of different teeth or measurements (e.g. width vs. length of the same tooth), and to contrast hypotheses of natural selection (functional relevance), structural complexity and developmental factors as causal explanations of dental variability. The second index, *r*, has been used to check the pattern of dental 'integration' of different teeth and, again, to contrast functional and developmental hypotheses (e.g. Polly, 1998*a*; Szuma, 2000; Meiri *et al.*, 2005).

The general pattern for variation coefficient (Gingerich & Winkler, 1979; Pengilly, 1984; Polly, 1998*a*; Szuma, 2000; Dayan *et al.*, 2002) exhibits greatest variability in the last molars (e.g. M_3), canines and incisors, whereas the central molars and premolars are the least variable. This pattern is partly altered if other measurements are used (see below), but the central teeth continue to be less variable and the last molars more variable (e.g. Szuma, 2000). The correlation between upper and lower dental series is highest between homologous teeth or between teeth with complex occlusion, and the highest values have been found in premolars and canines (Gingerich & Winkler, 1979; Pengilly, 1984; Szuma, 2000). When upper or lower series are assessed independently, higher *r* coefficients are found between neighbouring teeth (the neighbour rule), especially at the central cheek teeth (Kurtén, 1953, 1967; Szuma, 2000).

Kurtén (1953, 1967), in studying a sample of European *V. vulpes*, linked the pattern of correlation between teeth in canids to the theory of developmental fields, but he stated that this relationship is complex. In fact, he stated that the high correlation between teeth with complex occlusion (i.e. shear or opposition between P^4/M_1, molars and incisors; see Simpson, 1936) is due to functional value (i.e. adaptation; Kurtén, 1967). Gingerich & Winkler (1979) assigned the lowest CV values to the central teeth and the highest values to the distal ones to functional integration through stabilizing natural selection for more complex interlocking teeth. They found the same pattern of teeth correlations in a population of North American *V. vulpes* as detected by Kurtén in European specimens, and stated that this pattern does not agree with the hypothesis of functional integration, because the highest *r*-values were found at non-occluding premolars (P^2, P^3, P_2, P_3, P_4). However, they suggested that this could be due to an unknown function or to the fact that *r* does not measure functional integration. Gingerich & Winkler (1979) refuted the effect of sexual dimorphism on teeth development and did not find any correlation between CV and sequence of dental eruption. The same patterns of CV and *r* were found in a population of Arctic foxes *V. lagopus* studied by Pengilly (1984) (but in this case highest CV corresponds to M^2, M_2). Pengilly (1984) ascribed this pattern to developmental factors and, following Lande's (1977) statement about the negative relationship between a whole and its parts, explained the lower CV of central molars by the fact that they are more complex ('with more parts') than other teeth. Polly (1998*a*), in the light of an analysis of dental variability in *U. cinereoargenteus* and *Martes americana*, discussed the hypotheses of functional integration, developmental fields and the interplay between sexual dimorphism and sequence of eruption (those teeth that grow later, near or during sexual differentiation are more variable because they are subject to hormonal change), and concluded that the last hypothesis is more congruent with the observed dental CV profile. He also rejected the biases proposed by Lande (1977), including the one followed by Pengilly (1984). Concurrently, Szuma (2000) found positive relationships between CV [and the residuals of standard deviation (SD) on mean] and time of eruption in a population of *V. vulpes* from Poland, but on the basis of correlation patterns she concluded that functional and developmental factors also affect dental variation. The *Canis lupus* sample analysed by Dayan *et al.* (2002) presented the same pattern of variation as the holarctic foxes canids. The authors (Dayan *et al.*, 2002) argued that the high variation of posterior molars results from their being vestigial. On a larger taxonomic scale (order Carnivora), Meiri *et al.* (2005) found that functional integration of the dentition is affected by feeding types and phylogeny. In their study, canines were more variable than carnassials (using CV), a pattern that they suggested could not be completely accounted for by a statistical bias (Meiri *et al.*, 2005). Some of their results also do not agree with the complexity hypothesis adopted by Pengilly (1984).

Polly (1998*a*; see also Lande, 1977 for other possible bias of this coefficient) argued that the CV ratio [SD/mean of the variable (M) × 100] is biased because the error of measurement is constant (added to SD), but the size of the variable (M) can approach zero values, which could explain the pattern observed in several papers (e.g. Gingerich & Winkler, 1979; Pengilly, 1984), showing an inverse but non-linear relationship between these variables (see also Dayan *et al.*, 2002). In Polly's (1998*a*) study, cranial measurements were less variable than dental ones, and his interpretation was that all teeth of his sampled species have a similar variation and that the pattern described by previous researchers is the result of this bias (see below). This author used two other variability measurements – SD of the measures transformed to logarithms and residuals from the regression of SD on M – but he recognized that these are not error-free (Polly, 1998*a*). Other authors (Smith, 1999) have questioned the use of residuals other than for checking the assumptions for regression analysis. Polly (1998*a*) stated that CV could be used in comparisons if the variables have similar size or their measurement error is lower than 0.10. On the other hand, Dayan *et al.* (2002) argued that the new measurements proposed by Polly (1998*a*) are ad hoc and that they obliterate the real relationship between mean and CV, but show that the CV for skull length is similar in a tiny carnivore like *Mustela* and in a large one like *C. lupus*. They concluded that the measurement error cannot produce the entire observed pattern and that the inverse non-linear relationship is real, but that the CV may be used with caution. A recent analysis performed with a large sample of carnivore species and seven craniodental measurements (condylobasal length, zygomatic breadth, skull height, skull width, C^1, P^4 and M_1 lengths) showed that the inverse relationship is present in intraspecific samples, but that it is size-independent in the case of the interspecific sample (Meiri *et al.*, 2005). Meiri *et al.* (2005) also concluded that the CV–mean pattern is real and that the measurement error has only a limited effect on CV.

This paper has several goals. Firstly, we explore the bias present in CV. Secondly, the study of quantitative variation and correlation of dental measurements in this species could be useful to corroborate the extent of the pattern observed in other canid species and contrast the proposed hypotheses that have been proposed to explain it (e.g. functional integration, developmental factors). Thirdly, the dental and cranial information about a recent species of *Dusicyon* is useful to contrast previous systematic hypotheses (especially paleontological ones).

Table 1 Statistical, morphological and measurement abbreviations used in the text, tables and figures

I, C, P, M: incisors, canines, premolars and molars, respectively (superscript: upper dentition; subscript: lower dentition)
L: anteroposterior length (mesiodistal for all teeth, with the exception of I^1, I^2, I_1, I_2 and I_3, in which it is labiolingual)
W: width (labiolingual for all teeth, with the exception of I^1, I^2, I_1, I_2 and I_3, in which it is mesiodistal)
LCB: condylobasal length of the skull
LOO: distance between the anterior border of the orbits and the occipital condyles
BCW: greatest bizygomatic width
WCP: width of the postorbital constriction
WIM: minimum interorbital width
WPPO: width across the postorbital process
WBC: width of the braincase
PW: palatal width at the position of P^4–M^1 labial contact
WRC^1: greatest width of the rostrum between the external wall of C^1's alveoli
LB: anteroposterior length of the bulla without the styloid process
WB: bulla width, perpendicular to LB
Wcond: greatest transverse length between the lateral borders of the exoccipital condyles
LM: mandibular length between the mandibular condyle and the labial border of I^1's alveolus
HPC: height of the coronoid process
HRH: height of the horizontal ramus between M_1 and M_2
$LLIM^1$: lingual length of M^1
$LLAM^1$: labial length of M^1
$LtrM_1$: length of M_1's trigonid
$WtrM_1$: width of M_1's trigonid
$WtlM_1$: width of M_1's talonid
CV: coefficient of variation
M: arithmetic mean
SD: standard deviation
Res: residuals of the standard deviation regressed onto the mean of each measurement
r: product–moment Pearson correlation coefficient
ME: measurement error
S^2_{ind}: variance of the repeatedly measured specimen
S^2_{pop}: variance of the whole sample
mM: mean of the male sample
fM: mean of the female sample
Ln: natural logarithm
MANOVA: multifactorial analysis of variance

Materials and methods

Specimens studied

We studied a sample of 127 *Dusicyon gymnocercus* specimens hunted by J. J. Bianchini during the years 1967 and 1968 at Laguna Chasicó (38°45′10″S, 62°59′24″W; Buenos Aires, Argentina), currently deposited at Sección Mastozoología – Departamento Zoología Vertebrados of the Museo de La Plata (MLP Ma). We measured only specimens with fully erupted permanent dentition and not showing advanced wear, and with closed basioccipital/basisphenoid suture for skull and mandible measurements. The definitions and acronyms of the measurements are detailed in Table 1, and shown in Figs 1 and 2.

Sequence of tooth eruption

The sequence of dental eruption was constructed on the basis of 11 juvenile specimens from this sample, but the arrangement was ordinal only, as we could not establish absolute eruption time. We considered the time when each tooth reached its adult position with respect to other teeth.

Statistics

Sexual dimorphism was measured using the male mean/female mean (mM/fM) index of each variable and the natural logarithm of these ratios (see Smith, 1999). The significance was evaluated through multifactorial analysis of variance (MANOVA) and the non-parametric Mann–Whitney *U*-test. Notwithstanding the existence of low but significant dimorphism for some variables, the sexes were pooled together in the analyses of variability and correlation, because the patterns of variation were very similar, and the distributions of CV values were not significantly different (see below) and also allowed for comparison with fossil (or unsexed) samples.

The Mann–Whitney *U*-test was also used to check the differences between the CV and residuals (see below) of cranial and dental measurements, between the *r* of neighbouring and non-neighbouring teeth (in each dental series),

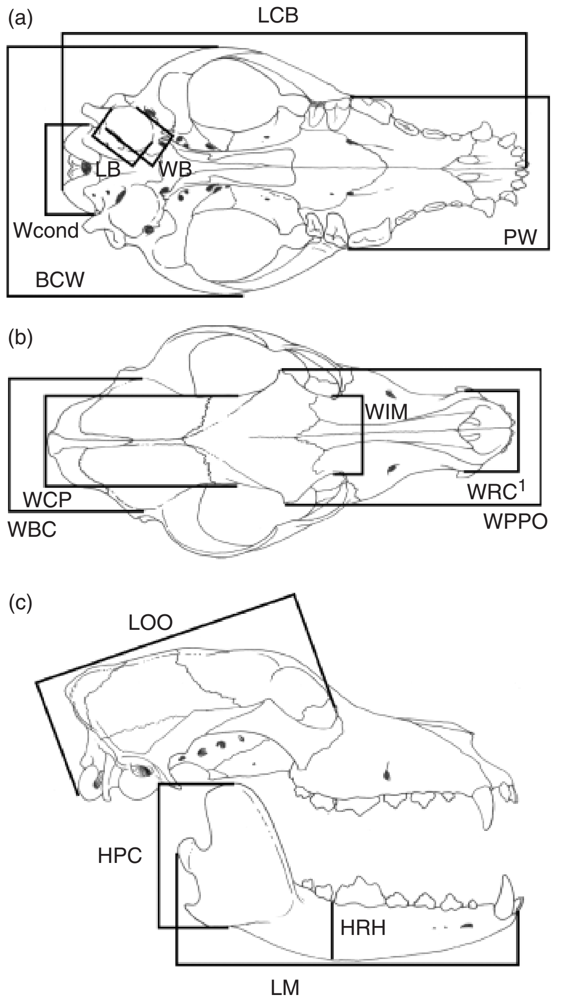

Figure 1 Diagrams showing the cranial variables measured: (a) skull in dorsal view; (b) skull in ventral view; (c) skull and mandible in lateral view.

and between lower and upper homologous and non-homologous teeth. The Kruskal–Wallis test was used for multiple group comparisons. A Mann–Whitney *U*-test was used to check CV differences between sexes, too.

Variability was measured with the variation coefficient $[\mathrm{CV} = (\mathrm{SD}/M) \times 100]$ and the residuals (Res) of the regression of the SD of the variables on their mean (M) (see Polly, 1998*a*; Szuma, 2000). A third measurement (the SD of the log-transformed measures) was estimated, but it was omitted because it showed the same pattern as CV and was highly correlated to the latter ($r > 0.997$, $P < 0.0000$).

Measurement error was estimated by re-measuring one randomly selected specimen 10 times (MLP 13-IV-99-28) and calculating the index: $\mathrm{ME} = [S^2_{\mathrm{ind}}/(S^2_{\mathrm{ind}} + S^2_{\mathrm{pop}})] \times 100$, where S^2_{ind} is the variance of the repeated measurements and S^2_{pop} is the variance of the sample (see Polly, 1998*a*).

Even though this study is 'dentally biased', the inclusion of some cranial measurements allows comparison of the degree of variation between dentition and skull, and an exploration of CV bias within a large size range.

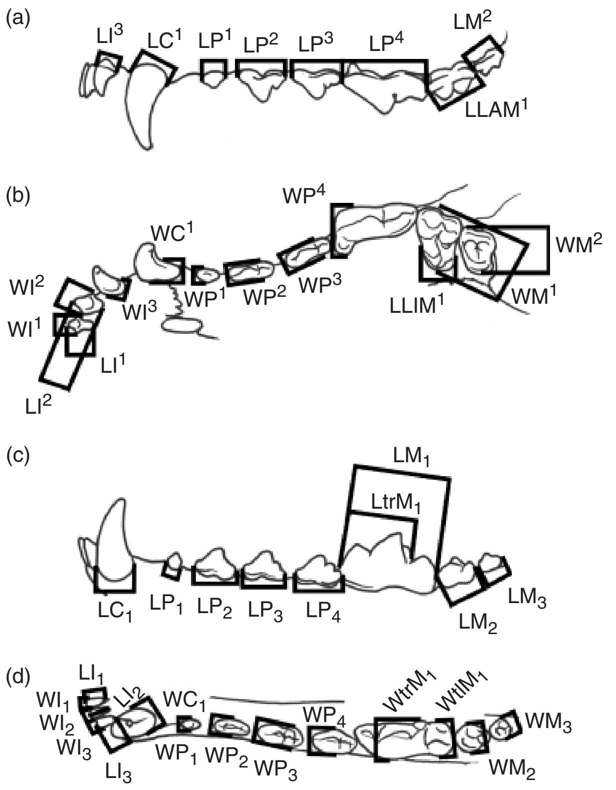

Figure 2 Diagrams showing the dental variables measured: (a) upper dental series in labial view; (b) upper dental series, occlusal view; (c) lower dental series, labial view; (d) lower dental series, occlusal view.

To explore the relationships between CV, SD, M, ME and the sequence of eruption for the dental sub-sample, we used the product–moment Pearson r correlation coefficient, and simple and multiple linear regressions (least squares). The regression analyses were performed with all variables transformed to natural logarithms (Ln) to improve normality and homoscedasticity. The non-parametric Spearman rank coefficient was also calculated, but the results are presented only if they differ from the Pearson r.

The correlation coefficient of the dental measures was assessed using the Pearson r of the raw measurements. Normal distribution was checked with the Shapiro–Wilk's test. In the serial tests, the P-levels were adjusted with the sharpened P-plots Bonferroni method (García, 2004); $P = 0.05$ was used elsewhere.

All statistical analyses were performed with Excel 2002 (Microsoft Corporation, 2001) and Statistica 6.0 (StatSoft Inc., 2001).

Results

Sexual dimorphism

Sexual dimorphism is low with a mean of 1.025 in comparison to other carnivores and to the mean value of the family (see Gittleman & Van Valkenburgh, 1997; Van Valkenburgh & Sacco, 2002), and a range of 0.999 (LB)–1.091 (WI$_1$) (Table 2).

Table 2 Mean (*M*; mm), standard deviation (SD; mm), coefficient of variation (CV), measurement error (ME; %), sexual dimorphism (DI) and sample size (*n*) of the studied quantitative variables

	M	SD	CV	ME	DI (*U*, *P*)	*n*
LCB	141.64	6.09	4.30	0.13	1.007 (722.50, 0.0001)	113
LOO	86.43	3.59	4.16	1.13	1.009 (674.50, 0.0001)	114
BCW	74.58	3.45	4.63	0.38	1.009 (773.00, 0.0001)	113
WCP	25.61	1.65	6.45	3.84	1.001 (1452.00, 0.6078)	114
WIM	26.45	1.71	6.45	1.65	1.001 (974.00, 0.0009)	114
WPPO	36.07	2.55	7.08	0.04	1.009 (1099.00, 0.0094)	114
WBC	47.02	1.64	3.48	4.28	1.005 (1020.00, 0.0014)	115
PW	41.32	1.70	4.12	5.68	1.006 (1152.00, 0.0156)	115
WRC^1	23.09	1.40	6.04	2.02	1.017 (799.00, 0.0001)	114
LB	20.36	0.99	4.88	23.50	0.999 (1495.00, 0.6730)	115
WB	13.26	0.93	6.98	10.84	1.007 (1360.50, 0.2897)	114
Wcond	26.10	1.16	4.43	2.63	1.010 (829.00, 0.0001)	113
LM	108.02	4.92	4.56	0.50	1.009 (735.50, 0.0001)	115
HPC	36.50	2.09	5.72	1.89	1.018 (551.00, 0.0001)	115
HRH	14.21	1.08	7.57	14.13	1.018 (957.00, 0.0004)	115
LI^1	2.82	0.21	7.43	2.13	1.035 (750.00, 0.0236)	94
WI^1	2.58	0.29	11.13	3.00	1.055 (816.50, 0.0827)	94
LI^2	3.38	0.25	7.34	5.42	1.040 (678.00, 0.0003)	100
WI^2	3.28	0.29	8.92	10.16	1.041 (860.50, 0.0228)	100
LI^3	4.32	0.30	6.95	10.28	1.029 (893.00, 0.0028)	107
WI^3	3.42	0.35	10.34	6.41	1.083 (582.00, 0.0001)	107
LC^1	6.66	0.47	7.07	28.77	1.027 (797.50, 0.0003)	107
WC^1	4.31	0.34	7.92	3.34	1.047 (750.50, 0.0001)	111
LP^1	4.01	0.30	7.39	2.15	1.013 (931.00, 0.2490)	95
WP^1	2.72	0.22	7.91	11.80	1.046 (754.50, 0.0044)	97
LP^2	7.58	0.49	6.51	1.11	1.019 (1075.50, 0.0029)	116
WP^2	3.07	0.26	8.59	10.96	1.031 (1254.50, 0.0516)	116
LP^3	8.31	0.53	6.32	4.08	1.019 (1152.00, 0.0016)	121
WP^3	3.23	0.27	8.39	3.12	1.036 (1255.00, 0.0062)	122
LP^4	13.32	0.74	5.55	1.44	1.015 (1171.00, 0.0002)	127
AP^4	7.11	0.57	8.00	0.75	1.015 (1458.00, 0.0538)	124
LLIM^1	7.79	0.52	6.68	1.01	1.025 (1053.50, 0.0001)	127
LLAM^1	9.88	0.55	5.55	2.11	1.010 (1428.00, 0.0136)	127
WM^1	11.78	0.64	5.47	2.41	1.011 (1398.00, 0.0089)	127
LM^2	6.46	0.46	7.10	15.40	1.027 (1141.50, 0.0002)	125
WM^2	9.67	0.59	6.14	1.43	1.012 (1440.50, 0.0315)	125
LI$_1$	2.20	0.18	8.40	2.98	1.041 (649.50, 0.1060)	88
WI$_1$	1.78	0.19	10.48	45.94	1.091 (737.00, 0.1060)	88
LI$_2$	2.72	0.22	7.96	5.43	1.027 (752.00, 0.0246)	93
WI$_2$	2.37	0.32	13.65	3.90	1.007 (998.00, 0.7689)	93
LI$_3$	3.10	0.26	8.36	6.63	1.042 (672.00, 0.0061)	92
WI$_3$	3.49	0.40	11.39	33.88	1.031 (872.50, 0.1970)	93
LC$_1$	7.10	0.68	9.61	15.56	1.039 (889.50, 0.0001)	116
WC$_1$	4.65	0.44	9.43	4.48	1.061 (704.00, 0.0001)	116
LP$_1$	3.57	0.28	7.77	8.83	1.024 (1077.00, 0.1016)	105
WP$_1$	2.42	0.21	8.58	2.43	1.023 (1096.00, 0.1306)	105
LP$_2$	7.14	0.48	6.77	0.62	1.024 (972.00, 0.0002)	117
WP$_2$	3.13	0.25	8.06	8.26	1.050 (1011.50, 0.0005)	117
LP$_3$	8.11	0.51	6.27	0.27	1.019 (1163.50, 0.0006)	124
WP$_3$	3.21	0.25	7.85	3.64	1.043 (1143.00, 0.0004)	124
LP$_4$	8.53	0.50	5.88	0.79	1.018 (1124.00, 0.0006)	122
WP$_4$	3.66	0.30	8.28	19.10	1.034 (1214.50, 0.0021)	123
LM$_1$	15.12	0.72	4.74	9.25	1.010 (1214.15, 0.0021)	123
LtrM$_1$	10.10	0.54	5.35	2.60	1.019 (1000.00, 0.0001)	122
WtrM$_1$	6.09	0.39	6.36	3.39	1.016 (1371.50, 0.0246)	123
WtlM$_1$	5.83	0.40	6.85	4.16	1.017 (1341.00, 0.0185)	122
LM$_2$	7.92	0.42	5.27	7.27	1.011 (1303.00, 0.0185)	121
WM$_2$	5.72	0.34	5.88	2.41	1.014 (1248.00, 0.0080)	121
LM$_3$	3.80	0.42	11.04	0.92	1.022 (981.00, 0.2114)	96
WM$_3$	3.26	0.29	8.99	0.34	1.018 (1014.00, 0.2451)	97

U, *U*-value of the Mann–Whitney test; *P*, probability value.

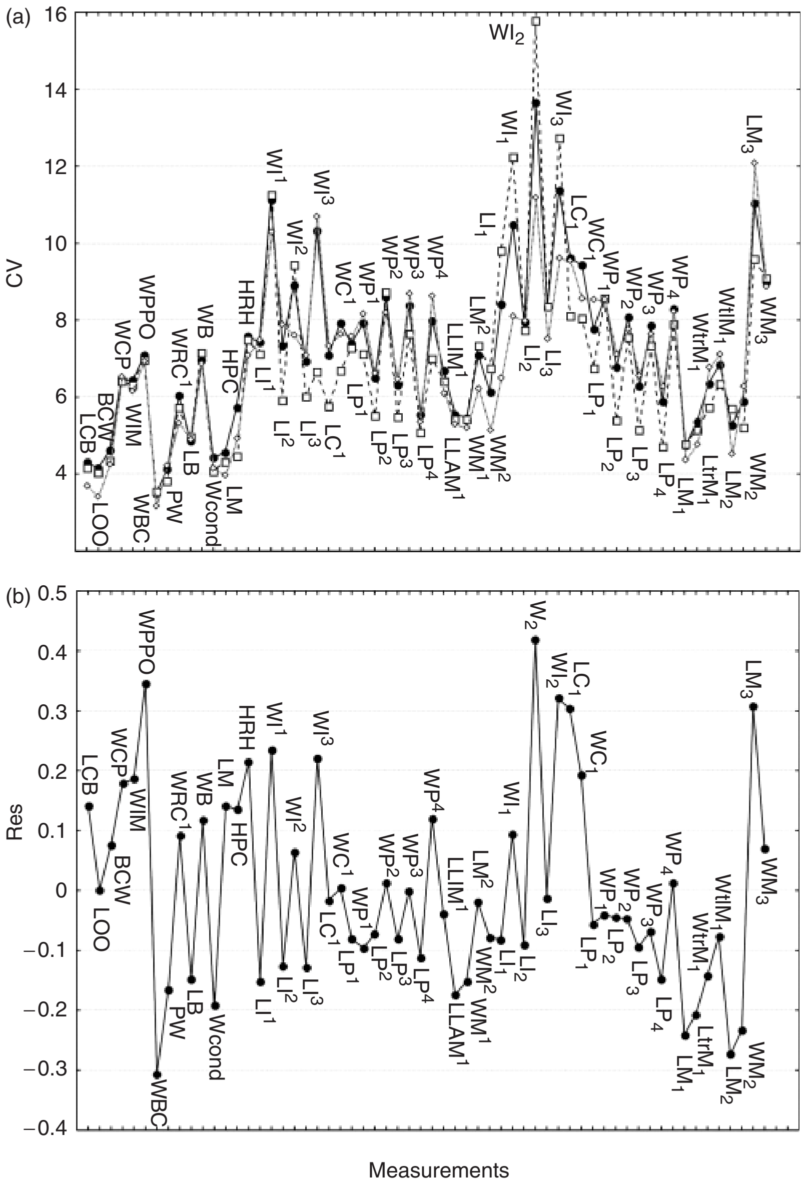

Figure 3 Profile of variation in cranial and dental measurements of *Dusicyon gymnocercus*. (a) Coefficient of variation (CV). Black dot and solid line: pooled sexes; empty square and broken line: females; empty diamond and dotted line: males. (b) Residuals of the standard deviation (SD) of measurements with respect to the mean (*M*; mm).

The MANOVA (all effects) did not find significant differences between sexes (Shapiro–Wilk's test = 0.010, $F = 2.31$, $P = 0.4850$); however, the Mann–Whitney U-test (with Bonferroni adjustment: 0.0029) found significant difference in several traits, especially the canines, P_2–M_1, and some incisor, molar and cranial measurements (Table 2).

The CV pattern between sexes is similar (Fig. 3), and the distributions of CV values between the sexes were not significantly different (Mann–Whitney $U = 1661$, $P = 0.4686$). Both show similar relationships with other variables (measurement error, sequence of eruption, variable size); thus we present only the combined sample.

Pattern of dental variability

CV shows a non-linear negative relationship (raw values; $r = -0.55$, $P < 0.0001$) with the size of the variables (M), with cranial measures having significantly lower CV values than dental ones (Mann–Whitney $U = 96$, $P < 0.0001$; Fig. 4). It must be noted that when correlation is calculated using cranial and dental measurements separately, the relationship is similar. Among the skull measurements, LCB, LOO, PW, WBC, LB, Wcond and LM have lower CV, and WCP, WIM, WPPO, WRC^1, WB, HPC and HRH have high CV values. In the upper tooth series the incisors, canines and P^1–P_1 are more variable than the cheek teeth, but the values gradually diminish towards M^1 (the least variable) and increase somewhat in M^2. Variation in the inferior series is similar to the upper series value; C_1, I_1, I_2, I_3 and P_1 are highly variable, CVs diminish from P_2 to M_1–M_2, but M_3 is as variable as the incisors (Fig. 3a).

The Res of the dental and cranial variables are not significantly different (Mann–Whitney $U = 246$,

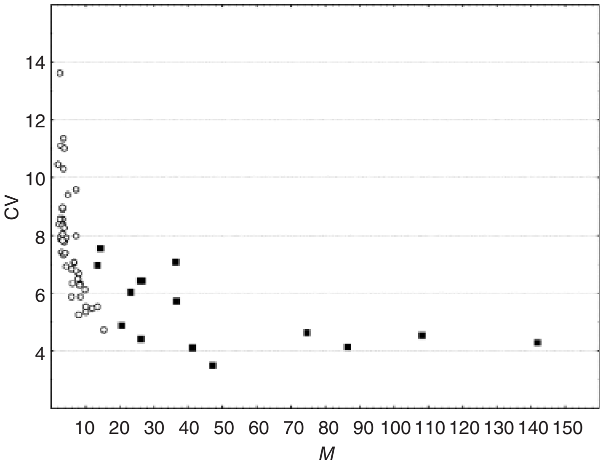

Figure 4 Biplot of coefficient of variation (CV) versus measurement size (*M*) in mm. Open circles: dental measurements; black squares: cranial measurements.

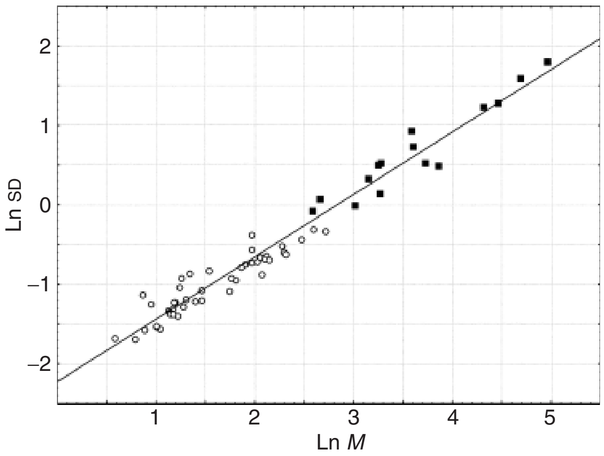

Figure 5 Biplot of natural logarithms of the standard deviation (SD) versus natural logarithm of variable size (*M*) in mm. Solid line: least-squares regression line ($\text{SD} = -2.226 + 0.786M$, $r = 0.96$). Open circles: dental measurements; black squares: cranial measurements.

Table 3 Sequence of dental eruption

Tooth	Sequence of eruption
P_1	1
P^1, I^1	2
I_1	3
I^2, I_2, M^1, M_1, M_2	4
I^3, I_3	5
P^4	6
M^2, P^2	7
M_3, P_2	8
P^3	9
P_3	10
P_4	11
C^1, C_1	12

$P = 0.1180$) and the pattern contrasts with CV (Fig. 3b), but WCP, WIM, WPPO, WRC^1, WB, HPC, HRH, width of I^1,I^2, I^3, I_1, I_2, I_3, LC_1, WC_1 and M_3 have higher variability, whereas WCC, LB, Wcond, LP^4, M^1, M^2, M_1 and M_2 have lower variability in both indexes. The pattern of intratooth variability is similar, width is more variable than length, but the difference is higher in the incisors and less clear in lower premolars. On the other hand, in this case incisor lengths have low variability and LCB and LM show high variation. The regression of SD on M is highly significant ($a = -2.226$, $P < 0.0001$; $b = 0.786$, $P < 0.0001$; standard error of the estimate = 0.1666; $r = 0.98$) and explains a large fraction of the variance (96.26%) (Fig. 5). As Polly (1998*a*) has noted, some variables are outliers (WPPO, WI_2), and the natural logarithm of SD and M are not normally distributed (Shapiro–Wilk's test = 0.8990, $P = 0.0001$ and 0.9113, $P = 0.0004$, respectively). The effect of the outliers on the slope of the fitted line is not clear, because both are placed on the same side of the line and on opposite ends. But the exclusion of these variables does not change the results; in addition, the plot of the residuals onto the independent variable (M) does not show any pattern, and they have a normal distribution (Shapiro–Wilk's test = 0.9655, $P = 0.0879$).

Measurement error, sexual dimorphism, sequence of eruption and variability

The mean measurement error obtained is 6.55%, and the range is 0.04% (WPPO) to 45.94% (WI^1) (Table 2). ME is negatively correlated with SD and M ($r = -0.46$, $P = 0.0002$ and $r = -0.44$, $P = 0.0004$, respectively), but not with Res ($r = -0.11$, $P = 0.4181$). The correlation with CV is positive and significant ($r = 0.30$, $P = 0.0209$) but not after Bonferroni adjustment ($P = 0.0170$).

The sequence of eruption (Table 3) has significant, and positive, correlation with SD ($r = 0.43$, $P = 0.0030$) and M ($r = 0.32$, $P = 0.0310$), but not with CV, ME or sexual dimorphism. The relationship with the size of the variable is not significant after Bonferroni adjustment. With the Spearman r the sequence of eruption is correlated to Res ($r = 0.31$, $P = 0.0410$), but the correlation is not significant when Bonferroni adjustment is applied.

Sexual dimorphism is negatively correlated with M ($r = -0.659$, $P < 0.0001$) and SD ($r = -0.60$, $P < 0.0004$) and positively correlated with CV ($r = 0.55$, $P < 0.0001$) and Res ($r = 0.45$, $P = 0.0020$). It is not significantly correlated with sequence of eruption ($r = 0.02$, $P = 0.8849$). The CV of cranial measurements alone is not significantly correlated with sexual dimorphism ($r = 0.23$, $P = 0.3998$).

Using multiple regression, with SD as the dependent variable and M, ME, sequence of eruption and sexual dimorphism as the independent variables, only two models were found that include other measurements beside M: M + sexual dimorphism, multiple $r = 0.98$, $P < 0.0001$, standard error of estimate = 0.1620; and only for dental measurements, M + sequence of eruption, multiple $r = 0.938$, $P < 0.0001$, standard error of estimate = 0.1357. These

Table 4 Correlation coefficients of upper dental series

	WI^1	LI^2	WI^2	LI^3	WI^3	LC^1	WC^1	LP^1	WP^1	LP^2	WP^2	LP^3	WP^3	LP^4	WP^4	LLIM^1	LLAM^1	WM^1	LM^2	WM^2
LI^1	0.32*	0.60**	0.30*	0.61**	0.40**	0.49**	0.60**	0.29*	0.45**	0.36*	0.60**	0.40**	0.51**	0.50**	0.43**	0.35*	0.41**	0.48**	0.30*	0.35*
WI^1		0.38*	0.57**	0.40*	0.24*	0.15	0.31*	0.24*	0.27*	0.36*	0.25*	0.32*	0.22	0.27*	0.19	0.28*	0.27*	0.21	0.34*	0.15
LI^2			0.29*	0.64**	0.37*	0.52**	0.48**	0.39*	0.43**	0.40*	0.48**	0.53**	0.43**	0.53**	0.36*	0.45**	0.43*	0.50**	0.33*	0.39*
WI^2				0.33*	0.21	0.27*	0.44**	0.14*	0.25*	0.37**	0.39*	0.32*	0.27*	0.28*	0.21	0.31*	0.24*	0.16	0.14	0.16
LI^3					0.46**	0.55**	0.65**	0.45**	0.55**	0.54**	0.60**	0.64**	0.63**	0.56**	0.50**	0.44**	0.36*	0.57**	0.35*	0.32*
WI^3						0.41*	0.50**	0.32*	0.37*	0.37*	0.49**	0.35*	0.53**	0.47**	0.22	0.35*	0.26*	0.34*	0.35*	0.37*
LC^1							0.59**	0.34*	0.32*	0.38*	0.48**	0.44**	0.52**	0.47**	0.40*	0.42*	0.35*	0.40*	0.14	0.26*
WC^1								0.42**	0.48**	0.51**	0.71**	0.51**	0.62**	0.59**	0.48**	0.46**	0.33*	0.48**	0.28*	0.33*
LP^1									0.52**	0.49**	0.46**	0.57**	0.56**	0.65**	0.63**	0.53**	0.48**	0.58**	0.41**	0.33*
WP^1										0.36*	0.65**	0.46**	0.67**	0.50**	0.49**	0.53**	0.42**	0.53**	0.40*	0.30*
LP^2											0.51**	0.73**	0.55**	0.57**	0.48**	0.50**	0.43**	0.50**	0.38*	0.40**
WP^2												0.53**	0.80**	0.55**	0.47**	0.43**	0.49**	0.55**	0.42**	0.38*
LP^3													0.53**	0.60**	0.52**	0.51**	0.45**	0.58**	0.41**	0.36*
WP^3														0.59**	0.56**	0.52**	0.51**	0.64**	0.35*	0.39*
LP^4															0.61**	0.65**	0.59**	0.74**	0.44**	0.48**
WP^4																0.61**	0.61**	0.56**	0.39*	0.40*
LLIM^1																	0.73**	0.67**	0.49**	0.43**
LLAM^1																		0.68**	0.60**	0.50**
WM^1																			0.58**	0.68**
LM^2																				0.68**

*Significant at $P<0.05$.

**Significant with Bonferroni adjustment, $P<0.0003$.

models explain only little more variance than M alone (96.53 vs. 96.26% and 86.17 vs. 86.15, respectively). In the two models, sequence of eruption and sexual dimorphism contributed little compared with M, and their partial correlation coefficients were lower (0.266 vs. 0.973 and 0.368 vs. 0.924, respectively). Multiple regressions with the interactions of these variables results did not significantly improve the model.

Pattern of dental correlation

In the upper series the I^3, C^1, premolars and M^1 measurements are more correlated with other tooth measurements (i.e. show more significant r with sharpened Bonferroni adjustment, $P = 0.0003$, and higher r-values; Table 4). The mean r is 0.44, with a range of 0.14–0.80. The M^2 and widths of incisors are less correlated than other measurements. The premolar region has higher r values (0.70–0.80), but its mean and median are similar to the molar region, while the incisors have lower mean, median and raw values. A Kruskal–Wallis test found marginally significant differences between tooth classes, but not with the Bonferroni adjustment ($P<0.0177$, $H = 6.1336$, $P = 0.0466$). However, the differences between incisors and premolars + molars are significant with a Mann–Whitney test ($U = 105$, $P = 0.0133$). The correlations are higher for neighbouring elements than for non-neighbouring ones, and the differences are highly significant (Mann–Whitney $U = 1717$, $P<0.0001$). The inferior series shows a similar pattern, but the incisors are practically not significantly correlated with the premolars (Table 5). The mean r is 0.32 and the range is -0.20 to 0.89. The M_2 have a low number of significant r but the lowest numbers correspond to P_1 and M_3. Again, the higher r, mean and median values are found in the premolar region (P_2, P_3, P_4), but now the lower values are in the molar region. These differences are only marginally significant (Kruskal–Wallis test $H = 8.6208$, $P = 0.0134$) when M_3 is included, but not when it is excluded ($H = 2.3554$, $P = 0.3080$). Neighbouring teeth have significantly higher r than non-contiguous ones (Mann–Whitney $U = 2643$, $P<0.0001$).

Between lower and upper series, nearly all homologous teeth are significantly correlated (Table 6). The lengths of incisors are more highly correlated than their widths in terms of significant correlation coefficients. The M_3, M^2 and incisors have less significant r with other teeth, especially the first two. Some of the higher r values occur between homologous (LI^1–LI_1, WC^1–WC_1, WM^1–LM_1, LP^4–LP_4) or occluding teeth (LM_1–LP^4), but others do not (WP^3–WP_4, LP^4–LP_3, WP^2–WP_3, LP^3–LP_4, WP_3–WP_4). The difference in r between homologous upper and lower teeth and between non-homologous ones is highly significant (Mann–Whitney $U = 2576$, $P<0.0001$). The first group shows higher values. The lower values correspond to the incisor region but are similar in other regions. A Mann–Whitney test between incisors and the other teeth shows significant differences ($U = 92.00$, $P = 0.0030$). The correlations between occluding teeth (I/I, P^4/M_1, M^1/M_1, M^2/M_2) are significantly higher than between non-occluding ones (Mann–Whitney $U = 4734$, $P<0.0001$).

Discussion

The general pattern of dental variation and correlation in *D. gymnocercus* is similar to that observed in other canids (e.g. Kurtén, 1953, 1967; Gingerich & Winkler, 1979; Pengilly, 1984; Polly, 1998*a*; Szuma, 2000; Dayan *et al*., 2002).

Table 5 Correlation coefficients of lower dental series

	WI$_1$	LI$_2$	WI$_2$	LI$_3$	WI$_3$	LC$_1$	WC$_1$	LP$_1$	WP$_1$	LP$_2$	WP$_2$	LP$_3$	WP$_3$	LP$_4$	WP$_4$	LM$_1$	LtrM$_1$	WtrM$_1$	WtlM$_1$	LM$_2$	WM$_2$	LM$_3$	WM$_3$
LI$_1$	0.54**	0.55**	0.40**	0.48**	0.48**	0.36*	0.45**	0.34*	0.23	0.32*	0.30*	0.25*	0.31*	0.34*	0.32*	0.57**	0.44**	0.36*	0.41*	0.23*	0.26*	0.01*	0.16*
WI$_1$		0.43*	0.59*	0.21*	0.50**	0.35*	0.44*	0.22	0.16	0.19	0.19	0.18	0.11	0.218	0.137	0.37*	0.38*	0.23	0.12	0.34*	0.22	0.18	0.23
LI$_2$			0.26*	0.46**	0.42*	0.36*	0.38*	0.30*	0.24	0.2	0.35*	0.23	0.36*	0.26*	0.32*	0.33*	0.29*	0.13	0.45**	0.01	0.29*	−0.2	0.07
WI$_2$				0.1732	0.70**	0.20	0.40*	0.06	−0.04	0.19	0.18	0.21	0.03	0.15	−0.03	0.31	0.23	0.24	0.17	0.23	0.32*	0.17	0.19
LI$_3$					0.34*	0.38*	0.38*	0.43**	0.22	0.47**	0.36*	0.39*	0.47**	0.40*	0.53**	0.50**	0.42*	0.37*	0.47**	0.15	0.28*	−0.03	0.03
WI$_3$						0.42*	0.55**	0.15	−0.02	0.29*	0.27*	0.35*	0.1857	0.38*	0.193	0.54**	0.40*	0.38*	0.31*	0.32*	0.34*	0.12	0.13
LC$_1$							0.52**	0.35*	0.30*	0.54**	0.39*	0.47**	0.42*	0.52**	0.59**	0.56**	0.42*	0.39*	0.31*	0.31*	0.26*	0.17	0.25*
WC$_1$								0.29*	0.19	0.47**	0.47**	0.53**	0.51**	0.52**	0.49**	0.63**	0.68**	0.57**	0.37*	0.29*	0.22	0.18	0.26*
LP$_1$									0.49**	0.34*	0.31*	0.17	0.26*	0.26*	0.43*	0.43*	0.37*	0.28*	0.35*	0.09	0.09	−0.05	0.00
WP$_1$										0.2	0.49**	0.12	0.42*	0.16	0.47**	0.20	0.10	0.09	0.07	0.03	0.05	−0.08	0.01
LP$_2$											0.34*	0.80**	0.38*	0.79**	0.49**	0.65**	0.59**	0.60**	0.41*	0.29*	0.37*	0.13	0.25*
WP$_2$												0.50**	0.47**	0.51**	0.52**	0.40*	0.43*	0.30*	0.28*	0.13	0.30*	0.09	0.15
LP$_3$													0.36*	0.89**	0.48**	0.56**	0.59**	0.62**	0.42*	0.40*	0.45**	0.14	0.29*
WP$_3$														0.41*	0.80**	0.48**	0.50**	0.35*	0.42*	0.01	0.38*	−0.02	0.10
LP$_4$															0.60**	0.64**	0.61**	0.56**	0.42**	0.36*	0.46*	0.11*	0.28*
WP$_4$																0.61**	0.56**	0.47**	0.46**	0.10	0.36*	0.01	0.21
LM$_1$																	0.78**	0.54**	0.60**	0.38*	0.34*	0.21	0.26*
LtrM$_1$																		0.65**	0.53**	0.33*	0.36*	0.16	0.21
WtrM$_1$																			0.52**	0.37*	0.48**	0.18	0.25*
WtlM$_1$																				0.20	0.50**	0.01	0.34*
LM$_2$																					0.33*	0.57**	0.48**
WM$_2$																						0.07	0.32*
LM$_3$																							0.66**

*Significant at $P<0.05$.

**Significant with Bonferroni adjustment, $P<0.0003$.

Table 6 Correlation coefficients between lower and upper dental series

	LI^1	WI^1	LI^2	WI^2	LI^3	WI^3	LC^1	WC^1	LP^1	WP^1	LP^2	WP^2	LP^3	WP^3	LP^4	WP^4	$LLIM^1$	$LLAM^1$	WM^1	LM^2	WM^2
LI_1	0.71**	0.37*	0.53**	0.13	0.52**	0.29*	0.32	0.49*	0.36	0.53**	0.34*	0.46*	0.33*	0.41*	0.37*	0.33*	0.35*	0.35*	0.49**	0.31*	0.38*
WI_1	0.35*	0.40*	0.32*	0.43*	0.31*	0.19	0.14*	0.42*	0.19	0.39*	0.23	0.34*	0.24	0.24	0.25	0.23	0.34*	0.39*	0.35*	0.29*	0.37
LI_2	0.69**	0.49**	0.55**	0.27	0.52**	0.30*	0.39*	0.45*	0.24	0.44*	0.30*	0.27	0.26	0.24	0.32*	0.24	0.26	0.12	0.23	0.14	0.11
WI_2	0.23	0.47*	0.29*	0.35*	0.27	0.13	0.01	0.34*	0.15	0.15*	0.24	0.17	0.24	0.12	0.18	0.16	0.19	0.33*	0.33*	0.26	0.30*
LI_3	0.65*	0.25*	0.43*	0.20	0.67**	0.37*	0.51**	0.53**	0.51**	0.45*	0.48**	0.56**	0.39*	0.45*	0.53**	0.41*	0.32*	0.1977	0.44*	0.29*	0.36*
WI_3	0.47*	0.46*	0.47*	0.22	0.51**	0.39*	0.37*	0.46*	0.48*	0.39*	0.26	0.43*	0.33*	0.39*	0.53**	0.45*	0.38*	0.44*	0.56**	0.39*	0.34*
LC_1	0.41*	0.36*	0.40*	0.14*	0.55**	0.32*	0.68**	0.49**	0.4275	0.49**	0.41*	0.51**	0.45*	0.51*	0.53**	0.39*	0.50**	0.48**	0.42*	0.37*	0.18
WC_1	0.60**	0.31*	0.46*	0.30*	0.64**	0.51**	0.46*	0.76**	0.41*	0.43*	0.46*	0.65**	0.43*	0.63**	0.64**	0.34*	0.36*	0.38*	0.54**	0.31*	0.37*
LP_1	0.41*	0.05	0.24	0.10	0.31*	0.24	0.49**	0.43*	0.52**	0.51**	0.37*	0.50**	0.21	0.49**	0.40*	0.43*	0.62**	0.39*	0.37*	0.13	0.11
WP_1	0.28*	0.03	0.27	−0.03	0.26	0.24	0.19	0.27*	0.46*	0.53**	0.09	0.54**	0.17	0.52**	0.16	0.18	0.19	0.22	0.19	0.04	0
LP_2	0.38*	0.37*	0.47*	0.30*	0.56**	0.42*	0.54**	0.50**	0.61**	0.41*	0.74**	0.50**	0.74**	0.59**	0.69**	0.36*	0.55**	0.44*	0.63**	0.37*	0.37*
WP_2	0.38*	0.17*	0.33*	0.17	0.38*	0.33*	0.34*	0.46*	0.41*	0.35*	0.33*	0.54**	0.41**	0.46*	0.51**	0.24	0.14	0.25*	0.40*	0.16	0.16
LP_3	0.42*	0.20	0.49**	0.37*	0.56**	0.37*	0.57**	0.54**	0.52**	0.34*	0.70**	0.54**	0.76**	0.61**	0.74**	0.34*	0.42*	0.32*	0.63**	0.24	0.40*
WP_3	0.63**	0.21	0.45*	0.36*	0.72**	0.43*	0.46*	0.64**	0.36*	0.59**	0.43*	0.78**	0.50**	0.69**	0.50**	0.46*	0.45*	0.46*	0.47*	0.34*	0.34*
LP_4	0.49**	0.22	0.46*	0.26	0.61**	0.41*	0.53**	0.54**	0.65**	0.52**	0.76**	0.64**	0.78**	0.67**	0.75**	0.50**	0.45*	0.43*	0.63**	0.31*	0.37*
WP_4	0.60**	0.14	0.34*	0.27	0.66**	0.40*	0.55**	0.60**	0.54**	0.69**	0.55**	0.79**	0.53**	0.79**	0.62**	0.58**	0.54**	0.46*	0.50**	0.27*	0.33*
LM_1	0.62**	0.44*	0.46*	0.39*	0.59**	0.39*	0.53**	0.59**	0.58**	0.58**	0.54*	0.58**	0.56**	0.61**	0.79**	0.58**	0.73**	0.64**	0.77**	0.41*	0.49**
$LtrM_1$	0.50**	0.28*	0.26	0.36*	0.52**	0.40*	0.42*	0.62**	0.49**	0.50**	0.57**	0.57**	0.56**	0.65**	0.72**	0.49**	0.64**	0.53**	0.65**	0.32*	0.34*
$WtrM_1$	0.42*	0.27	0.28*	0.12	0.56**	0.44*	0.42*	0.52**	0.37*	0.39*	0.62**	0.56**	0.48*	0.65**	0.66**	0.28*	0.47*	0.45*	0.60**	0.41*	0.42*
$WtlM_1$	0.54**	0.37*	0.45*	0.32*	0.60**	0.25	0.45*	0.45*	0.36*	0.52**	0.43*	0.41*	0.45*	0.47*	0.61**	0.38*	0.53*	0.46*	0.58**	0.32*	0.24
LM_2	0.09	0.31*	0.21	0.29*	0.31*	0.21	0.20	0.26*	0.24	0.21	0.30*	0.36*	0.35*	0.31*	0.30*	0.23	0.43*	0.42*	0.58**	0.63	0.58**
WM_2	0.33*	0.42*	0.22*	0.32*	0.47*	0.20	0.18	0.48*	0.37*	0.47*	0.60**	0.46*	0.55**	0.50**	0.49**	0.48**	0.51**	0.52**	0.58**	0.56**	0.44*
LM_3	−0.13	0.14	0.00	0.07	0.09	0.10	−0.1	−0.05	0.11	−0.04	0.05	0.05	0.04	0.09	0.07	0.01	0.16	0.26	0.38*	0.65**	0.55**
WM_3	0.09	0.40*	0.19	0.37*	0.30*	0.1673	0.09	0.17*	0.19	0.20	0.22	0.19	0.33*	0.23	0.25	0.14	0.28*	0.26	0.38*	0.59**	0.45*

*Significant at $P<0.05$.

**Significant with Bonferroni adjustment, $P<0.0003$. The *r*s of measurements of homologous teeth are enclosed in black lines; the *r*'s between complex occluding teeth are in grey blocks.

In spite of the problems presented by the two variability indexes used (*vide supra*), both agree in indicating that some measurements (e.g. some cranial widths, widths of incisors, lower canine, lower last molar; see Table 2 and Fig. 3) are more variable, whereas others (e.g. carnassials, upper molars) show lesser variation. The higher variability of incisor and P^2–P^3 width with respect to their length is also recovered for the two variability indexes. In his analysis of *U. cinereoargenteus* and *M. americana*, Polly (1998*a*) found that the pattern observed in CV is a result of the constant error added to SD when measurement size (the mean of the variable) decreases (e.g. Fig. 4). In his study the measurement error was not correlated with the size of the measurements. The results obtained in the *D. gymnocercus* population studied are consistent with the existence of a bias in CV, but contrary to Polly's (1998*a*) results, in our study the measurement error is negatively correlated to size of the variable, which implies that the error of smaller measurements is higher than the error of the larger ones. This appears to partly explain the inverse and non-linear relationship between CV and the size of the measurements, as Lande (1977) suggested, but does not necessarily invalidate CV as a variability gauge (Meiri *et al.*, 2005). Some results show that not the entire pattern is a product of this bias. First, CV and the residuals of SD on the mean of the variables agree in identifying several measurements as possessing high or low variability (Fig. 4). Another point to be noted is that variables with sharp differences in size may have similar CV or vice versa (see Table 2; Figs 3 and 4). Additionally, sexual dimorphism is positively correlated with CV (*vide supra*), a fact logically expected for a variability measure. The relationship between these variables has been discovered by other authors too (e.g. Van Valkenburgh & Sacco, 2002). These facts support the idea that the pattern of dental variability observed by means of CV is not completely due to the use of an inappropriate statistic to measure variability, as Dayan *et al.* (2002) and Meiri *et al.* (2005) have suggested (see also Szuma, 2000).

As previously noted (e.g. Polly, 1998*a*; Szuma, 2000), the variability pattern appears to be related to developmental factors. This may be seen in the correlation between the sequence of eruption and SD, which is consistent with the pattern observed in *V. vulpes*. The use of the residuals and the bias occurring in CV could obscure the relationship between dental variability and sequence of eruption as observed in the relationship between SD and sequence of eruption. On the other hand, other criteria to establish eruption sequence, such as the termination of crown mineralization, could be a better gauge of the conclusion of tooth development, but this information is not available at the present time.

The absence of correlation between sexual dimorphism and sequence of dental eruption does not agree with the hypothesis suggested by Polly (1998*a*) of a combination of these factors as a causal explanation of the pattern of dental variability. This lack could be explained by the low dimorphism present in *D. gymnocercus*.

The pattern of correlation is similar to the one recorded for other species by other authors (e.g. Kurtén, 1953, 1967; Gingerich & Winkler, 1979; Pengilly, 1984; Szuma, 2000). The occurrence of the neighbour rule and the correlation between homologous upper and lower teeth agree with developmental integration as a cause of this pattern. The higher correlation coefficients between canines and incisors could be interpreted in the same way. The absence of sharp differences between the correlations of complex and simple occluding teeth (i.e. upper/lower carnassials and molars, shearing and opposition vs. upper/lower canines and premolars, alternating) argues against the hypothesis of functional integration. The only exceptions are the lower values of incisors of the upper series and between occluding incisors in comparison with other tooth types, but the lower incisors have similar *r*-values as the premolars and molars (excluding the last lower molar) in the lower series. On the other hand, the significant higher *r*-values between complex occluding teeth with respect to simple occluding ones are consistent with the functional explanation. It must be remarked that, with the exception of the carnassial pair, occluding teeth are a sub-sample of the upper and lower homologous teeth, and it is difficult to separate developmental and functional aspects at this level. As other authors have noted (e.g. Szuma, 2000), simple occluding teeth such as the canines could possess functional relevance; the incisors, canines and premolars other than the upper carnassial could be important as a guide for occlusion, during chase and prey capture, and in food consumption (e.g. Biknevicius & Van Valkenburgh, 1996; Van Valkenburgh, 1996). In *V. vulpes* the canines could also be important tools in social interactions (Szuma, 2000), and this factor could affect the dental pattern of *D. gymnocercus* if the latter species has a similar behaviour. At any rate, the comparatively high *r*-values observed in premolars cannot be explained by a functional hypothesis alone.

Interestingly, the presence of a similar pattern of variation and correlation in several canid species of different clades (see Tedford, Taylor & Wang, 1995; Zrzavý & Řičánková, 2004; Bardeleben, Moore & Wayne, 2005; Lindblad-Toh *et al.*, 2005) could be interpreted as a constraint (e.g. Gould, 2002; Schwenk & Wagner, 2003), caused by the underlying developmental programme. On the other hand, the observed pattern might be generated by selective pressures, associated with a similar diet. *D. gymnocercus*, *V. vulpes*, *V. lagopus* and *U. cinereoargenteus* share an opportunistic and omnivorous diet, comprising rodents, birds, insects and fruits (see Sillero Zubiri, Hoffmann & Macdonald, 2004), but is this enough to assert that they live under the same selective pressures? These species inhabit different habitats (e.g. Pampas grasslands, Arctic tundra) and some species are more omnivorous (e.g. *U. cinereoargenteus*; see Sillero Zubiri *et al.*, 2004). *Canis lupus* is clearly more carnivorous than these foxes and has very different hunting behaviour, but possesses a similar pattern of dental variation (Dayan *et al.*, 2002). These facts are not in line with a 'selective pressure' hypothesis. Moreover, this issue should be explored with an increased taxonomic sample and the use of statistical tests for the comparison between these taxa (e.g. Steppan, 1997; Arnold & Phillips, 1999; Phillips & Arnold, 1999; Polly, 2005).

The dental variability profile and correlation pattern indicate that some of the more variable measurements (e.g. last lower molar, width of incisors) are less correlated with other teeth (i.e. with low raw *r* and lowest significant *r*; Tables 4–6). The combination of these two aspects points to the influence of developmental pathways (e.g. Kurtén, 1953, 1967; Pengilly, 1984; Wolsan, 1984, 1988, 1989; Jernvall, 1995; Polly, 1998*a,b*, 2000; Sharpe, 2000; Szuma, 2000; Zhao, Weiss & Stock, 2000; McCollum & Sharpe, 2001) in the pattern of dental variation and correlation. The last lower molar is occasionally absent in several canid species (see Huxley, 1880; Kraglievich, 1930; Buchalczyk, Dynowski & Szteyn, 1981; Steenkamp & Borrel, 1999; Andersone & Ozoliņŝ, 2000; Szuma, 2002, 2003), another expression of the relatively high variation presented by this tooth (Dayan *et al.*, 2002). This pattern was observed in other vestigial structures (e.g. Tague, 1997). Absence of the last lower molar may happen when the tooth does not reach the threshold size during development (e.g. Wolsan, 1988, 1989; Jernvall, 1995; Szuma, 2002, 2003), which may be related to the size variation observed in M_3 when it is developed. Along these lines, Szuma (2002) stated that this could be due to a weaker genetic control on this molar, which allows it to be more easily influenced by non-genetic factors. To some extent, the high variability and low integration of the last lower molar could also be explained by its low functional relevance (see Kurtén, 1953, 1967; Dayan *et al.*, 2002), which could be linked to a weakening of the genetic control. These possible causes are not mutually exclusive. The pattern shown by other teeth is not clear, and certainly does not agree with their vestigial status. For example, the incisors and the lower canine show high variability (Fig. 3), but they are correlated with other teeth and have an important functional role in food capture and consumption (see Van Valkenburgh, 1996). On the other hand, the incisors present high variation only in their widths but not in the lengths.

Much of the dental integration discussion assumes that the correlation pattern reflects the dental integration generated by developmental or functional causes, but other causes (e.g. epigenetic, environmental) are implicated and could create a fuzzy blueprint (Kurtén, 1953).

As early authors have mentioned (e.g. Polly, 1998*a*), CV could be used for comparisons when the measurements (or species) possess similar size; unfortunately the residuals of SD (regressed on the measurement's mean) do not allow this type of comparison. CV values and the variability profile obtained here could be used to compare the variability of fossil species with respect to *D. gymnocercus* (e.g. Kraglievich, 1930; Berman, 1994), and contrast their validity. For example, some specimens assigned to *Dusicyon cultridens* by Berman (1994) [the type of '*Canis*' *bonaerensis*, MLP 10-65 (Departamento Científico Paleontología Vertebrados, Museo de La Plata)] fall within the range of variation of the present sample (F. J. Prevosti, pers. obs.), which argues for a review of these species (see Prevosti *et al.*, 2005 for a similar assertion). It must be noted that the variability observed in this population does not represent the full variation of the species because geographical and temporal variation is not considered, and therefore these results underestimate the variability of the recent representatives of the species.

Conclusions

CV is biased by the increase of the measurement error when the size of the measurements decreases. However, the pattern shown by CV is not entirely generated by this bias, and this index could be used in combination with others as an indicator of relative variation of measurements.

The pattern of variability and correlation observed in *D. gymnocercus* is similar to the published values for other canid species (e.g. Kurtén, 1953, 1967; Gingerich & Winkler, 1979; Pengilly, 1984; Polly, 1998*a*; Szuma, 2000; Dayan *et al.*, 2002). The most variable measurements are some cranial measurements, width of incisors, lower canine and the last lower molar (Fig. 3), where measurements of other teeth (e.g. carnassials; Fig. 3) have lower variability values. The similarities between the patterns of variability in different canid clades could reflect a constraint of the underlying developmental programme. We did not find significant differences between cranial and dental measurements. Both sexual dimorphism and dental eruption sequence contribute to the variability of measurements.

Neighbouring teeth are more correlated than distant ones, in agreement with the neighbour rule. The premolar region is more 'integrated' with respect to *r*-values and number of significant correlations. Homologous and occluding upper and lower teeth are significantly more correlated than non-homologous or non-occluding ones. There are small differences between tooth types, with the exception of the lower values in the lower incisors.

The observed patterns of variation and correlation appear to represent the effect of developmental factors, but functional explanations (natural selection) could explain the low correlation and high variability of the last lower molar.

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References

Andersone, Ž. & Ozoliņš, J. (2000). Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia. *Acta Theriol.* **45**, 549–558.

Ansorge, H. (1994). Intrapopular skull variability in the red fox, *Vulpes vulpes* (Mammalia: Carnivora: Canidae). *Zool. Abh. Sta. Mus. Tierk. Dresden* **48**(6), 103–123.

Arnold, S.J. & Phillips, P.C. (1999). Hierarchical comparison of genetic variance–covariance matrices. II. Coastal–inland divergence in the garter snake, *Thamnophis elegans*. *Evolution* **53**, 1516–1527.

Bardeleben, C., Moore, R.L. & Wayne, R.K. (2005). A molecular phylogeny of Canidae, based on six nuclear loci. *Mol. Phylogenet. Evol.* **37**, 815–831.

Berman, W.D. (1994). *Los carnívoros continentales (Mammalia, Carnivora) del Cenozoico en la provincia de Buenos Aires*. PhD dissertation, La Plata.

Biknevicius, A.R. & Van Valkenburgh, B. (1996). Design for killing: craniodental adaptations of predators. In *Carnivore behavior, ecology, and evolution*, Vol. 2: 393–428. Gittleman, J.L. (Ed.). Ithaca, NY: Cornell University Press.

Buchalczyk, T., Dynowski, J. & Szteyn, S. (1981). Variations in number and asymmetry of the skull in the wolf. *Acta Theriol.* **26**, 23–30.

Dayan, T., Wool, D. & Simberloff, D. (2002). Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology* **28**, 508–526.

García, L.V. (2004). Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**, 657–663.

Gingerich, P.D. & Winkler, D.A. (1979). Pattern of variation and correlation in the dentition of the red fox, *Vulpes vulpes*. *J. Mammal.* **60**, 691–704.

Gittleman, J.L. & Van Valkenburgh, B. (1997). Sexual dimorphism in the canines and skulls of carnivores: effect of size, phylogeny, and behavioural ecology. *J. Zool. (Lond.)* **242**, 97–117.

Gould, S.J. (2002). *The structure of evolutionary theory*. Cambridge: Harvard University Press.

Huxley, T.H. (1880). On the cranial and dental characters of the Canidae. *Proc. Zool. Soc. Lond.* **12**, 238–288.

Jernvall, J. (1995). Mammalian molar cusp patterns: developmental mechanism of diversity. *Acta Zool. Fenn.* **198**, 1–61.

Kraglievich, L. (1930). Craneometría y clasificación de los cánidos sudamericanos, especialmente los argentinos actuales y fósiles. *Physis* **10**, 35–73.

Kurtén, B. (1953). On the variation and population dynamics of fossil and recent mammals populations. *Acta Zool. Fenn.* **76**, 1–122.

Kurtén, B. (1967). Some dental quantitative approaches to dental microevolution. *J. Dent. Res.* **46**, 817–828.

Lande, R. (1977). On comparing coefficients of variation. *Syst. Zool.* **26**, 214–217.

Lindblad-Toh, K., Wade, C.M., Mikkelsen, T.S., Karlsson, E.K., Jaffe, D.B., Kamal, M., Clamp, M., Chang, J.L., Kulbokas, E.J. III, Zody, M.C., Mauceli, E., Xie, X., Breen, M., Wayne, R.K., Ostrander, E.A., Ponting, C.P., Galibert, F., Smith, D.R., de Jong, P.J., Kirkness, E., Alvarez, P., Biagi, T., Brockman, W., Butler, J., Chin, C.-W., Cook, A., Cuff, J., Daly, M.J., DeCaprio, D., Gnerre1, S., Grabherr1, M., Kellis, M.M., Kleber, M., Bardeleben, C., Goodstadt, L., Heger, A., Hitte, C., Kim, L., Koepfli, K.-P., Parker, H.G., Pollinger, J.P., Searle, S.M.J., Sutter, N.B., Thomas, R., Webber, C., Broad Institute Genome Sequencing Platform & Lander, E.S. (2005). Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* **438**, 803–819.

McCollum, M. & Sharpe, P.T. (2001). Evolution and development of teeth. *J. Anat.* **199**, 153–159.

Meiri, S., Dayan, T. & Simberloff, D. (2005). Variability and correlations in large carnivore crania and dentition. *Funct. Ecol.* **19**, 337–343.

Microsoft Corporation (2001). *Microsoft Excel 2002*. www.microsoft.com.

Mivart, St. G. (1890). *Dogs, jackals, wolves and foxes. A monograph of the Canidae*. London: R. H. Porter.

Pengilly, D. (1984). Developmental versus functional explanations for patterns of variability and correlation in the dentitions of foxes. *J. Mammal.* **65**, 34–43.

Phillips, P.C. & Arnold, S.J. (1999). Hierarchical comparison of genetic variance–covariance matrices. I. Using the Flury hierarchy. *Evolution* **53**, 1506–1515.

Polly, P.D. (1998*a*). Variability in mammalian dentitions: size-related bias in the coefficient of variation. *Biol. J. Linn. Soc.* **64**, 83–99.

Polly, P.D. (1998*b*). Variability, selection, and constraints: development and evolution in viverravid (Carnivora, Mammalia) molar morphology. *Paleobiology* **24**, 409–429.

Polly, P.D. (2000). Development and evolution occlude: evolution of development in mammalian teeth. *Proc. Natl. Acad. Sci. USA* **97**, 14019–14021.

Polly, P.D. (2005). Development and phenotypic correlations: the evolution of tooth shape in *Sorex araneus*. *Evol. Dev.* **7**, 29–41.

Prevosti, F.J., Noriega, J.I., García Esponda, C.M. & Ferrero, B.S. (2005). Primer registro de *Dusicyon gymnocercus* (Fischer, 1814) (Carnivora: Canidae) en el Pleistoceno de Entre Ríos (Argentina). *Rev. Esp. Pal.* **20**, 159–167.

Schwenk, K. & Wagner, G.P. (2003). Constraint. In *Key concepts and approaches in evolutionary developmental biology*: 1–5. Hall, B.K. & Olson, W.M. (Eds). Cambridge: Harvard University Press.

Sharpe, P.T. (2000). Homeobox genes in initiation and shape of teeth during development in mammalian embryos. In *Development, function and evolution of teeth*: 3–12. Teaford, M., Meredith, S. & Ferguson, W.J. (Eds). Cambridge: Cambridge University Press.

Sillero Zubiri, C., Hoffmann, M. & Macdonald, D.W. (2004). *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan*. Gland: IUCN Species Programme.

Simpson, G.G. (1936). Studies of the earliest mammalian dentitions. *Dent. Cosmos* **78**, 791–800, 940–953.

Smith, R.J. (1999). Statistics of sexual size dimorphism. *J. Hum. Evol.* **36**, 423–459.

StatSoft Inc. (2001). *STATISTICA 6.0 (data analysis software system*). www.statsoft.com.

Steenkamp, G. & Borrel, C.G. (1999). Oral and dental conditions in adult African wild dog skull: a preliminary report. *J. Vet. Dent.* **16**, 65–68.

Steppan, S.J. (1997). Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. *Evolution* **51**, 571–586.

Szuma, E. (2000). Variation and correlation patterns in the dentition of the red fox from Poland. *Ann. Zool. Fenn.* **37**, 113–127.

Szuma, E. (2002). Dental polymorphism in a population of the red fox (*Vulpes vulpes*) from Poland. *J. Zool. (Lond.)* **256**, 243–253.

Szuma, E. (2003). Microevolutionary trends in the dentition of red fox (*Vulpes vulpes*). *J. Zool. Syst. Evol. Res.* **41**, 47–56.

Tague, R.G. (1997). Variability of a vestigial structure: first metacarpal in the *Colobus guereza* and *Ateles geoffroyi*. *Evolution* **51**, 595–605.

Tedford, R., Taylor, B.E. & Wang, X. (1995). Phylogeny of the Caninae (Carnivore: Canidae): the living taxa. *Am. Mus. Novitates* **3146**, 1–37.

Van Valkenburgh, B. (1996). Feeding behaviour in free-ranging, large African carnivores. *J. Mammal.* **77**, 240–254.

Van Valkenburgh, B. & Sacco, T. (2002). Sexual dimorphism, social behaviour, and intrasexual competition in large Pleistocene carnivorans. *J. Vert. Pal.* **22**, 164–169.

Wolsan, M. (1984). Concerning the variation in the number, shape and size of incisors in fissiped carnivores. *Acta Zool. Cracov.* **27**, 107–120.

Wolsan, M. (1988). Morphological variations of the first upper molar in the genus *Martes* (Carnivora, Mustelidae). *Mém. Mus. Natl. Hist. Nat. Ser. C Sci. Terre* **53**, 241–254.

Wolsan, M. (1989). Dental polymorphism in the genus *Martes* (Carnivora: Mustelidae) and its evolutionary significance. *Acta Theriol.* **34**, 545–593.

Zhao, Z., Weiss, K.M. & Stock, D.W. (2000). Development and evolution of dentition patterns and their genetic basis. In *Development, function and evolution of teeth*: 152–172. Teaford, M., Meredith, S. & Ferguson, W.J. (Eds). Cambridge: Cambridge University Press.

Zrzavý, J. & Řičánková, V. (2004). Phylogeny of recent Canidae (Mammalia, Carnivora): relative reliability and the utility of morphological and molecular datasets. *Zool. Scrip.* **33**, 311–333.