



Variability in mammalian dentitions: size-related bias in the coefficient of variation

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The coefficient of variation has been used in many evolutionary studies. However, a strong negative correlation between this index and size may artificially inflate the apparent variability of small traits. This is most pronounced when variables whose size differs by more than an order of magnitude are compared or when the index is applied to variables whose size is within an order of magnitude of their measurement error. When this is likely to affect conclusions, other indexes of variability should be considered. One alternative is to use the standard deviation of log-transformed data; however, this index is sometimes still correlated with variable size so care should be exercised in its use. Another alternative is to regress the standard deviation onto mean variable size; however, this method may also be misleading if variables are not randomly distributed about the regression line. As an example of the effect of bias in the coefficient of variation, previous studies of mammalian dental variability profiles were re-evaluated. It was found that variation among teeth is relatively homogenous, both within and among species. The exception is that the canines of *some* mammalian species have variability that is considerably higher than would be expected from tooth size. Previous explanations of variability patterns that invoked developmental fields are incompatible with the new data.

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ADDITIONAL KEY WORDS:—variability profiles – dental variation – dental fields – carnivore dentitions – primate dentitions – *Martes* – *Urocyon*.

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INTRODUCTION

Because it is a prerequisite for natural selection, variation has been a major focus of biological research for a century and a half (e.g. Darwin, 1859; Bateson, 1894; Yablokov, 1974). A common index of variability is the coefficient of variation ($V = 100 \frac{s}{\bar{x}}$, s —standard deviation, \bar{x} —arithmetic mean)

which is both easily calculated and intended to be size-independent. Both the variability of single traits across populations and multiple traits within a population have been compared using this index (Simpson *et al.*, 1960; Yablokov, 1974; Gingerich, 1974; Pengilly, 1984; Kelley, 1986; Powell & King, 1997). However, because V is calculated as a ratio and because measurement error contributes uniformly to estimated variance, there is significant negative correlation between V and mean variable size—the coefficient of variation may be artificially high if a variable is very small.

Several previous studies noted this negative correlation but attributed it to biological rather than mathematical causes (Bader & Hall, 1960; Yablokov, 1974; Pengilly, 1984). In many cases, including these, the opposite is true. In this paper, I explore the negative correlation between V and \bar{x} , I provide criteria for determining whether size-correlated bias is a problem for any particular study, and I propose an alternative method for indexing variability. As an example, I revisit a series of studies of the mammalian dentition in which the correlation between V and \bar{x} has a significant effect on observed patterns. Reanalysis negates several hypotheses that were proposed to explain differential variability along the tooth row (the selective effect of occlusal complexity and the influence developmental fields) leaving one (the relative timing of tooth formation and the onset of dimorphic growth) that deserves further testing.

ABBREVIATIONS

C	Canine	P	Premolar
H	Crown height	r	Product-moment correlation coefficient
I	Incisor	s	Standard deviation
L	Mesiodistal length	S^2	Variance
M	Molar	V	Coefficient of variation
n	Sample size	W	Buccolingual width
P	Probability that a sample correlation coefficient comes from a population with a parametric coefficient of zero	\bar{x}	Arithmetic mean of variable
		%ME	Percent measurement error

MATERIAL AND METHODS

Original measurements were collected from the dentitions of 61 individuals (30 males, 31 females) of *Martes americana*, the American Marten (Mustelidae, Carnivora), all from a single population in British Columbia, and from 42 individuals (21 males,

TABLE 1. Percent measurement error for the variables used in this study based on the variance of 20 successive measurements of a single individual of *Urocyon cinereoargenteus* (s_{ind}^2) compared to the measured variance in a population of 42 individuals (s_{pop}^2)

Position	Upper dentition			Position	Lower dentition		
	s_{ind}^2	s_{pop}^2	%ME		s_{ind}^2	s_{pop}^2	%ME
I ¹ L	0.02	0.10	14	I ₁ L	0.01	0.11	10
W	0.00	0.04	08	W	0.04	0.06	42
I ² L	0.04	0.06	41	I ₂ L	0.03	0.22	10
W	0.01	0.03	27	W	0.00	0.10	04
I ³ L	0.01	0.10	06	I ₃ L	0.05	0.10	32
W	0.00	0.06	07	W	0.02	0.06	25
C ¹ L	0.04	0.18	17	C ₁ L	0.04	0.32	12
W	0.02	0.08	18	W	0.04	0.11	30
H	0.06	1.58	04	H	0.04	0.83	05
P ¹ L	0.01	0.06	14	P ₁ L	0.01	0.07	13
W	0.00	0.02	16	W	0.02	0.03	34
P ² L	0.01	0.07	16	P ₂ L	0.00	0.08	04
W	0.01	0.06	17	W	0.00	0.04	10
P ³ L	0.01	0.13	04	P ₃ L	0.01	0.14	05
W	0.02	0.06	23	W	0.01	0.05	20
P ⁴ L	0.01	0.40	03	P ₄ L	0.00	0.21	01
W	0.02	0.21	07	W	0.01	0.11	05
M ¹ L	0.00	0.26	02	M ₁ L	0.02	0.41	04
W	0.02	0.46	04	W	0.04	0.16	19
M ² L	0.01	0.17	07	M ₂ L	0.02	0.24	08
W	0.00	0.32	01	W	0.07	0.13	34
				M ₃ L	0.01	0.14	05
				W	0.00	0.09	04

14 females, 7 unknown sex) of *Urocyon cinereoargenteus*, the Grey Fox (Canidae, Carnivora) from populations across North America. All specimens are housed in the University of Michigan Museum of Zoology. Measurements—recorded to the nearest 0.01 millimeter, and rounded to the nearest 0.1 millimeter—were taken with Mitotuyo digital calipers following Gingerich & Winkler (1979). Broken teeth were not measured. As shown in Table 1, percent measurement error (see below) ranged from 1% to 42% and averaged 13%.

Previously published data—selected from studies on the mammalian dentition which reported V , \bar{x} , and measurement precision—were also used in this study. Four species of indriids, the African indri and sifakas (Gingerich & Ryan, 1979); 13 subspecies of cercopithecids, the African guenons (Cope & Lacy, 1995); and one species of canid, the red fox (Gingerich & Winkler, 1979) were included. The average number of individuals in these samples was 27, the minimum was 7, and the maximum 112. The data in each of these studies was taken using hand calipers to the nearest 0.1 millimeter. The coefficients of variation of each tooth were averaged across these species and reported as a single dental variability profile (Fig. 5C). The same procedure was used with regression residuals to produce Figure 6C.

The arithmetic mean (\bar{x}), standard deviation (s), and coefficient of variation (V) was calculated for each variable. Correlation coefficients (r) between \bar{x} and both s and V were calculated for each data set. The *Martes americana* data were log transformed (\ln) and the summary statistics and correlations were recalculated. Finally, a regression analysis was run on each untransformed data set and the residuals used as an alternative to V for measuring variability.

To assess measurement error, 20 repeated sets of measurements were taken from a single specimen of *U. cinereoargenteus* following the procedure outlined above. Summary statistics and correlation coefficients between \bar{x} and both V and s were calculated. Percent measurement error, reported in Table 1, was also calculated using a formula modified from Bailey and Byrnes (1990):

$$\%ME = 100 \cdot \frac{s_{ind}^2}{s_{ind}^2 + s_{pop}^2}$$

s_{ind}^2 = variance of measurements of a single individual

s_{pop}^2 = variance of measurements among individuals in a population.

RESULTS

All of the data used in this study have a significant negative correlation between the mean variable size and the coefficient of variation (Fig. 1). This includes both the newly collected data (Fig. 1A,B) and data from previously published studies (Fig. 1C). As \bar{x} approaches zero in all three of these data sets, V increases exponentially ($P < 0.01$). In most cases, the data tightly fit a curvilinear regression, although some variables—particularly canine measurements—fall well above the line. This observation is considered in more detail below. These data seem to suggest that small variables have proportionately more variation than larger ones; however this is not the case. The standard deviations of these variables have a positive linear correlation with their means ($P < 0.01$) (Fig. 2A–C). This relationship is expected because s is an absolute measure of dispersion about the mean. Because some of the observations of a given variable must be less than \bar{x} , s must be close to zero when \bar{x} is close to zero. As \bar{x} increases, s may also increase. With the exception of some canine variables, it appears, contrary to the data in Figure 1, that s is constant relative to variable size and that variability is not proportionally greater in small teeth than in larger ones.

It is this correlation between s and \bar{x} , in fact, that V is designed remove. But why doesn't it? Lande (1977) said that a negative correlation between V and \bar{x} may be found: (1) when measurement error is disproportionately large for smaller measurements, (2) when V of a whole is compared to its parts, or (3) when a variable has a significant probability of a zero measurement. In the present study, however, the last two cases are not applicable. All variables are linear measurements of teeth with no probability of a zero measurement and no wholes are compared to constituent parts (*contra* Pengilly, 1984). But is there a negative correlation between measurement error and variable size? A single individual of *Urocyon cinereoargenteus* was remeasured 20 times to assess the relationship between measurement error and \bar{x} (Table 1, Figs 1D, 2D). When the coefficient of variation is used as an index, it appears that there is a negative correlation with \bar{x} (Fig. 1D). But there is no significant correlation between the standard deviation of a remeasured variable and its mean (Fig. 2D). This indicates that there is no bias in measurement error relative to variable size in the data collected for this study. None of Lande's explanations for a negative relationship between \bar{x} and V fit these data.

The inverse correlation between the coefficient of variation and variable mean can be explained, however, by a combination of measurement error and the

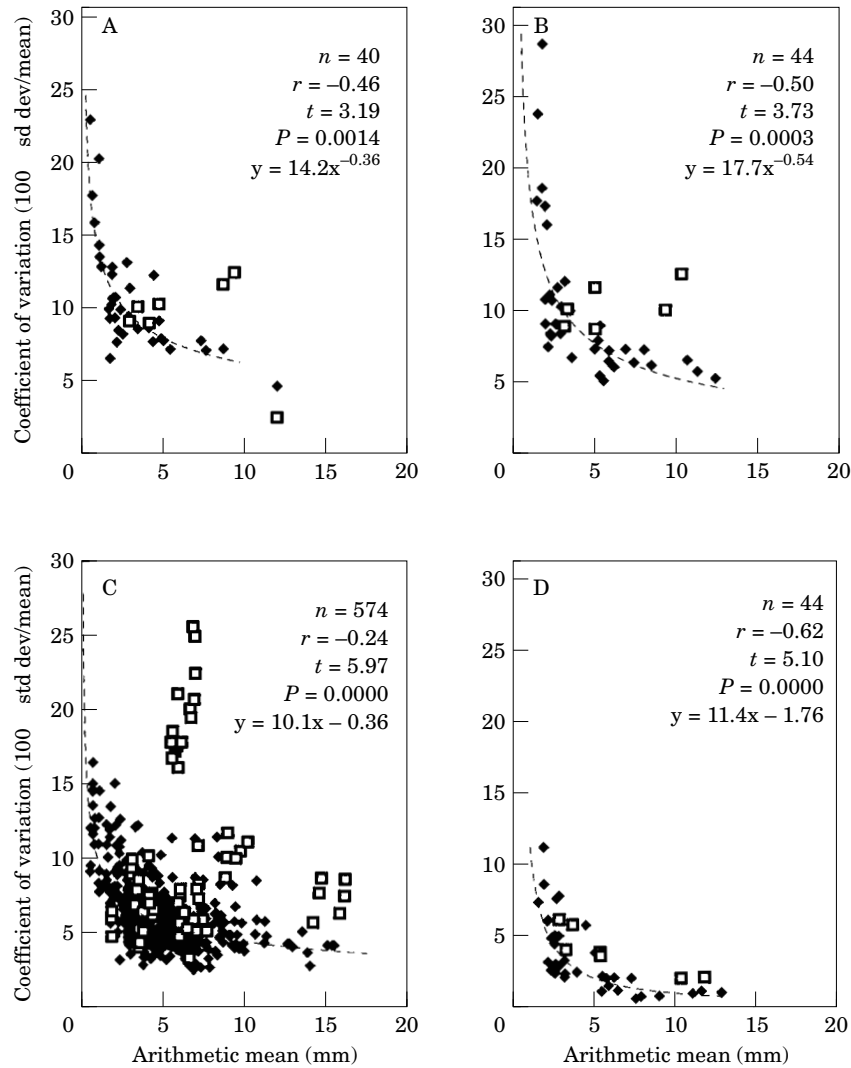


Figure 1. The relationship between the coefficient of variation and mean variable size. All variables are buccolingual widths and mesiodistal heights of mammal teeth. A, data from 61 individuals of *Martes americana* (40 variables). B, data from 42 individuals of *Urocyon cinereoargenteus* (44 variables). C, data from published literature on variability in the mammalian dentition (574 variables). D, data from a single multiply-remeasured individual of *Urocyon cinereoargenteus* (44 variables). In all four graphs, including the data in D which is from a single individual, there is a strong negative correlation between V and \bar{x} . Canine variables (\square); other teeth (\blacklozenge). The regression lines are fit to non-canine variables only, but r and other statistics are calculated using all of the data.

properties of ratios. Figure 3A shows why a ratio with size in the denominator, such as V , may not always remove the effect of size from an equation (Pearson, 1897; Atchley *et al.*, 1976; Albrecht, 1977; Bookstein *et al.*, 1985). The inset shows three possible linear relationships between s and \bar{x} —one passes through the origin while the others have positive y-intercepts—and the main chart shows the relationship

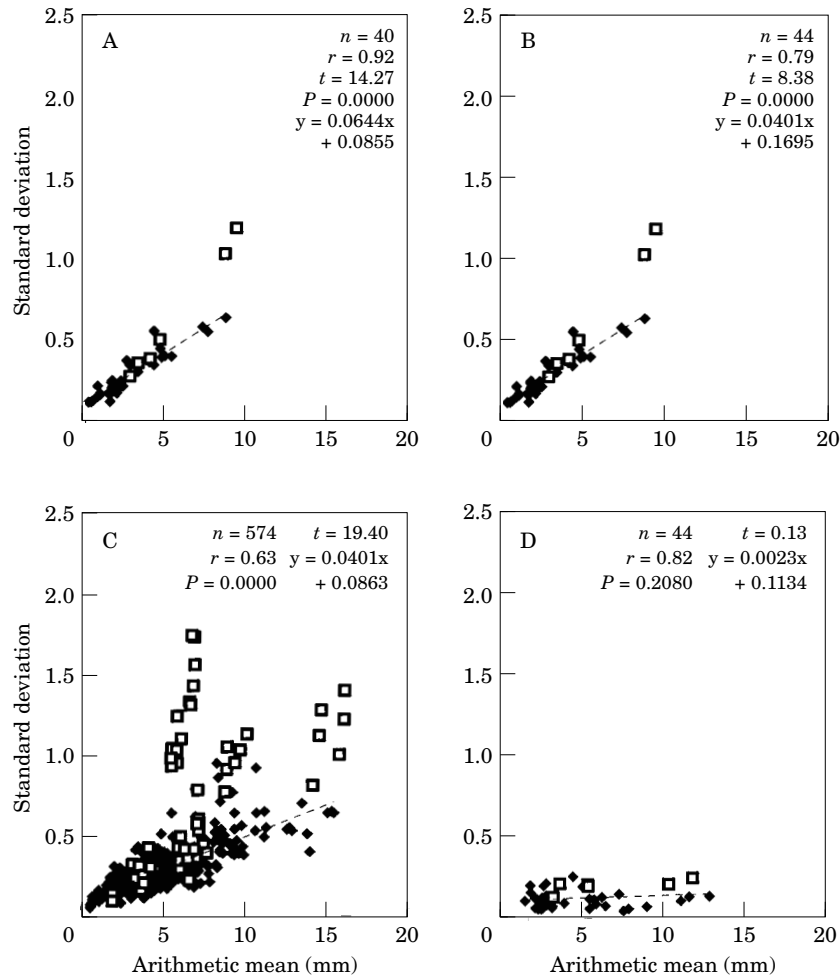


Figure 2. The relationship between standard deviation and mean variable size. A, data from *Martes americana*. B, data from *Urocyon cinereoargenteus*. C, data from published literature. D, data from a single individual of *Urocyon cinereoargenteus*. In the first three cases—all populations of multiple individuals—there is a strong positive relationship between s and \bar{x} , but in D—a single remeasured individual—there is no significant correlation. Canine variables (\square); other teeth (\blacklozenge). The regression lines are fit to non-canine variables only, but r and other statistics are calculated using all of the data.

between V and \bar{x} for those three cases. Only in the first example is size effectively removed using a simple ratio like V (line A, Fig. 3A). In the other cases, V becomes exponentially large as \bar{x} decreases even though there is a linear relationship between s and \bar{x} (lines B and C, Fig. 3A). This is the case with the data in this study. Even though there is a linear relationship between s and \bar{x} , the coefficient of variation has a negative correlation with \bar{x} because s does not approach zero in very small variables (Fig. 2A–C). The inverse correlation between V and \bar{x} in the remeasured data (Fig. 1D) is simply the result of a constant s (Fig. 2D) being divided by an ever decreasing mean.

The reason that s remains positive as \bar{x} approaches zero—hence the reason why

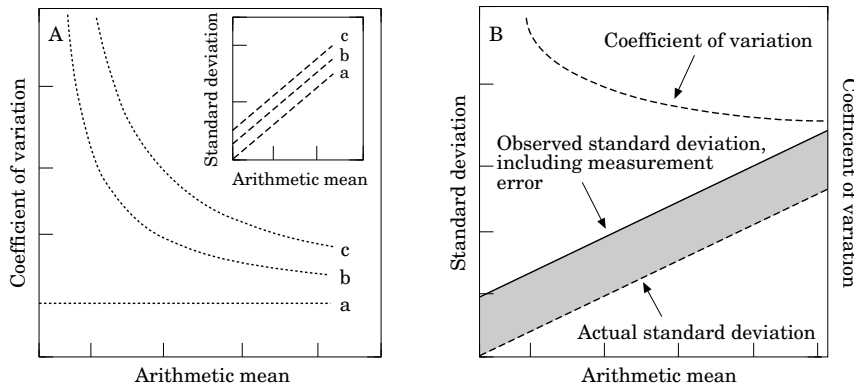


Figure 3. The relationship between the coefficient of variation, standard deviation, and variable mean size. A, there is no correlation between V and \bar{x} when the relationship between s and \bar{x} is linear and passes through the origin; however, there is a negative relationship between V and \bar{x} when the line does not pass through the origin. B, size-independent measurement error contributes to the standard deviation of each variable so that the relationship between s and \bar{x} does not pass through the origin, causing V to be exponentially large for very small variables. (Part A modified from Albrecht, 1978).

there is a negative correlation between V and \bar{x} —is that measurement error acts as a constant added to the standard deviation of each variable (Fig. 3B). The standard deviation of very small variables is expected to be close to zero because, by definition, s cannot be larger than \bar{x} . The data in Figure 2A–C predict, however, that a variable with a mean of zero will have a standard deviation of about 0.1. It is no coincidence that this value is approximately the average standard deviation of the repeated measurements of a single individual (Fig. 2D). Measurement error is not negatively correlated with \bar{x} , but is a constant that increases the standard deviation of each variable by the same amount (Fig. 3B). This creates a situation like that of examples B and C (Fig. 3A)—the coefficient of variation becomes exponentially larger as the variable mean gets smaller because s does not approach zero (Fig. 3B). Even though it is not correlated with variable size as suggested by Lande (1977), measurement error is still responsible for the negative correlation between V and \bar{x} .

TOWARDS A SIZE-INDEPENDENT INDEX OF VARIABILITY

The negative correlation between V and \bar{x} makes the coefficient of variation inappropriate for some studies of variability. If the variables being compared have a large range of means—like those considered in this study—or if variable size is within an order of magnitude of its measurement error then V is likely to be misleading. The coefficient of variation may be used with impunity, however, when percent measurement error (Bailey & Byrnes, 1990) is less than 10 or when all of the variables being compared are of similar size (this is confirmed by inspection of Figs 1 & 2).

In cases where the negative correlation is likely to cause problems, alternative measures may be used. One widely used method for removing the effect of size is to use the standard deviation of log-transformed data rather than the coefficient of

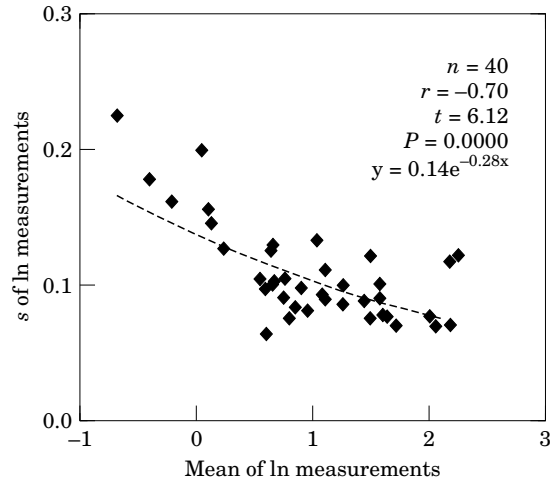


Figure 4. The relationship between the standard deviation and mean variable size of log-transformed data. Note that, although the effect has been dampened, there is a negative correlation between s and \bar{x} similar to that between V and \bar{x} in Fig. 1.

variation (Hills, 1978; Falconer, 1989; Sokal & Rohlf, 1995). But this simply transforms the data, turning the positive correlation between s and \bar{x} (Fig. 2A–C) into a negative correlation (Fig. 4). An alternative method is to remove the effect of measurement error from s before calculating V . This makes the relationship between s and \bar{x} pass through the origin so that size can be factored out successfully using the coefficient of variation (Fig. 3A). While the data in this study suggest that this can be accomplished by calculating s for multiple measurements of the same variable on the same individual and subtracting it from s of the population

$$\left(V = 100 * \frac{s_{pop} - s_{ind}}{\bar{x}} \right)$$

this is hard to justify statistically.

When many similar variables are being considered (as in the data used in this study), a third index may be calculated by regressing s on \bar{x} . Regression is the most common method for removing the effect of one variable on another (Sokal & Rohlf, 1995), although it may not be appropriate if variables are not randomly distributed on either side of the regression line. Unfortunately, this method cannot be applied if only a few similar sized variables are being considered because the significance of the regression will be diminished. Below, the regression index is used to reassess previous studies of the pattern variability in the mammalian dentition.

VARIABILITY IN THE MAMMALIAN DENTITION: AN EXAMPLE

The coefficient of variation has been used in several studies of the differential variability along the mammalian tooth row (Van Valen, 1962; Gould & Garwood,

1969; Yablokov, 1974; Gingerich, 1974; Gingerich & Ryan, 1979; Gingerich & Schoeninger, 1979; Gingerich & Winkler, 1979; Pengilly, 1984; Cope, 1993; Plavcan, 1993). The subtle bias in V detrimentally contributed to the observed patterns of variability in these studies so that small teeth—incisors, anterior premolars, and third molars—appeared to be more variable than larger ones. Scenarios that were constructed to explain the pattern of high variability in small teeth (especially Pengilly, 1984) may be unnecessary when the data are reanalysed because much of that pattern disappears when an alternative index of variability is used. As an example of the influence of the negative correlation between V and \bar{x} , these studies are reviewed here and supplemented with new data.

These studies have documented fairly consistent patterns among primate and carnivoran species—canines, on average, are the most variable teeth, incisors the second most variable, and anterior molars are the least variable (Fig. 5C). It has been particularly noted that the lower first molar is, with few exceptions, the least variable tooth in the dentition and probably the best for distinguishing closely related species in the fossil record (Gingerich, 1974; Pengilly, 1984; Cope, 1993). These results are confirmed by new data from *Martes americana* and *Urocyon cinereoargenteus* (although canines are not as variable as incisors in these new data) (Fig. 5). Three evolutionary scenarios have been proposed to explain these patterns: functional integration, developmental fields, and the effect of tooth eruption patterns on sexual dimorphism. These are explained and critiqued below.

The data on which these patterns are based show a strong correlation between mean variable size and both the coefficient of variation and the standard deviation, as we have seen (Figs 1, 2). With the exception of some canines (differentiated by open squares in these figures), those teeth with high coefficients of variation are small and those with low coefficients are large. When size is accounted for, the variability of incisors, anterior premolars, and posterior molars is no greater than that of anterior molars (i.e. variability in all of these teeth is linear with respect to size). This is most apparent when the standard deviation is compared directly with mean variable size (Fig. 2) or when the residuals of the regression of s on \bar{x} are examined (Fig. 6, insets). For the most part, size variation in the dentition is remarkably homogenous, except that the canines of some species (primarily sexually dimorphic primates, but *not* sexually dimorphic carnivorans like *Martes americana*) are more variable than other teeth.

When the residuals of s on \bar{x} are plotted as variability profiles, the pattern seen in the coefficient of variation profiles changes (Fig. 6). Most notable is that the incisors have lower variability than before in *Martes americana* (Fig. 6A) and in the species average data (Fig. 6C). In these profiles, anterior molars still appear to have below-average variability and posterior molars higher than average. Comparison with the raw residuals, however, shows that this method of indexing variation has its own problems. The extreme outliers in the inset graphs—almost all canine variables—lie exclusively above the regression line. Because the data are not randomly distributed about the regression line, the line is ‘pulled up’ from the main cloud of points as variable size increases. Compare the path the regression lines in Figure 6, which are fit to both canine and non-canine variables, to those in Figure 2, which are fit to non-canines only. The outliers cause the residuals of large teeth (such as the anterior molars) to appear artificially low. The apparent difference between the variability of anterior and posterior molars is again due to their size

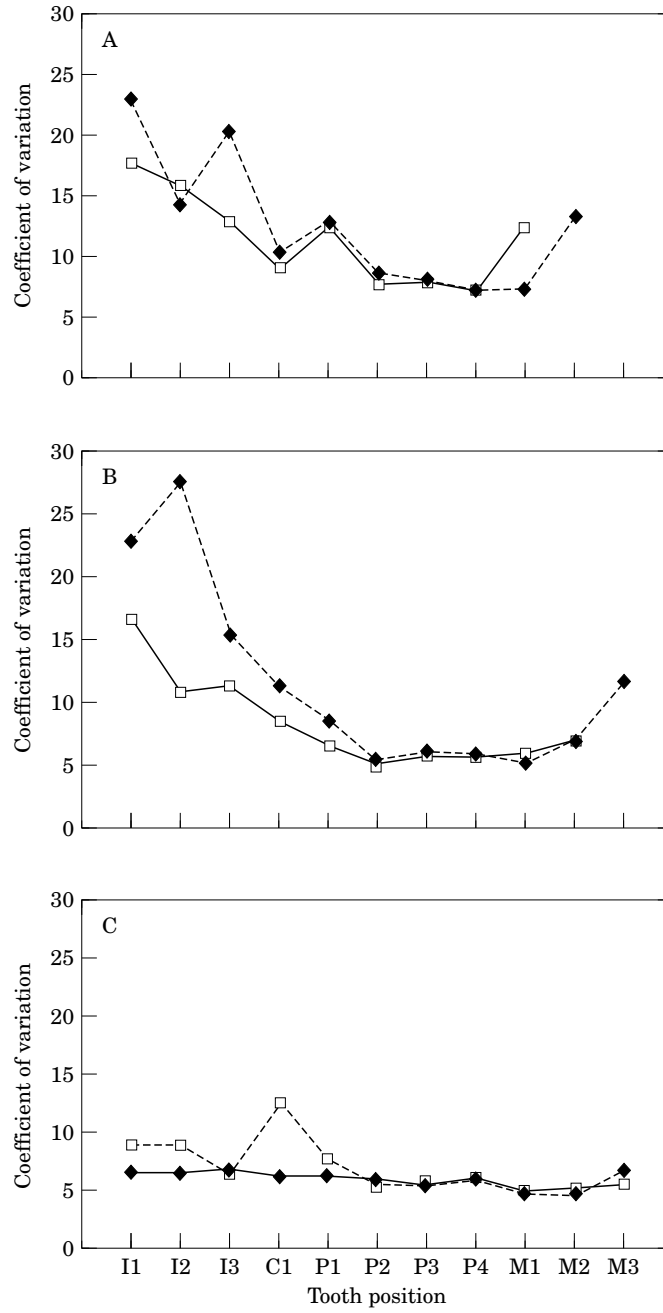


Figure 5. Dental variability profiles showing the coefficient of variation of mesio-distal tooth lengths by their position in the jaw. A, newly collected data on *Martes americana*. B, newly collected data on *Urocyon cinereoargenteus*. C, averages of previously published data on 18 primate and carnivoran species and subspecies. Upper teeth (□); lower teeth (◆).

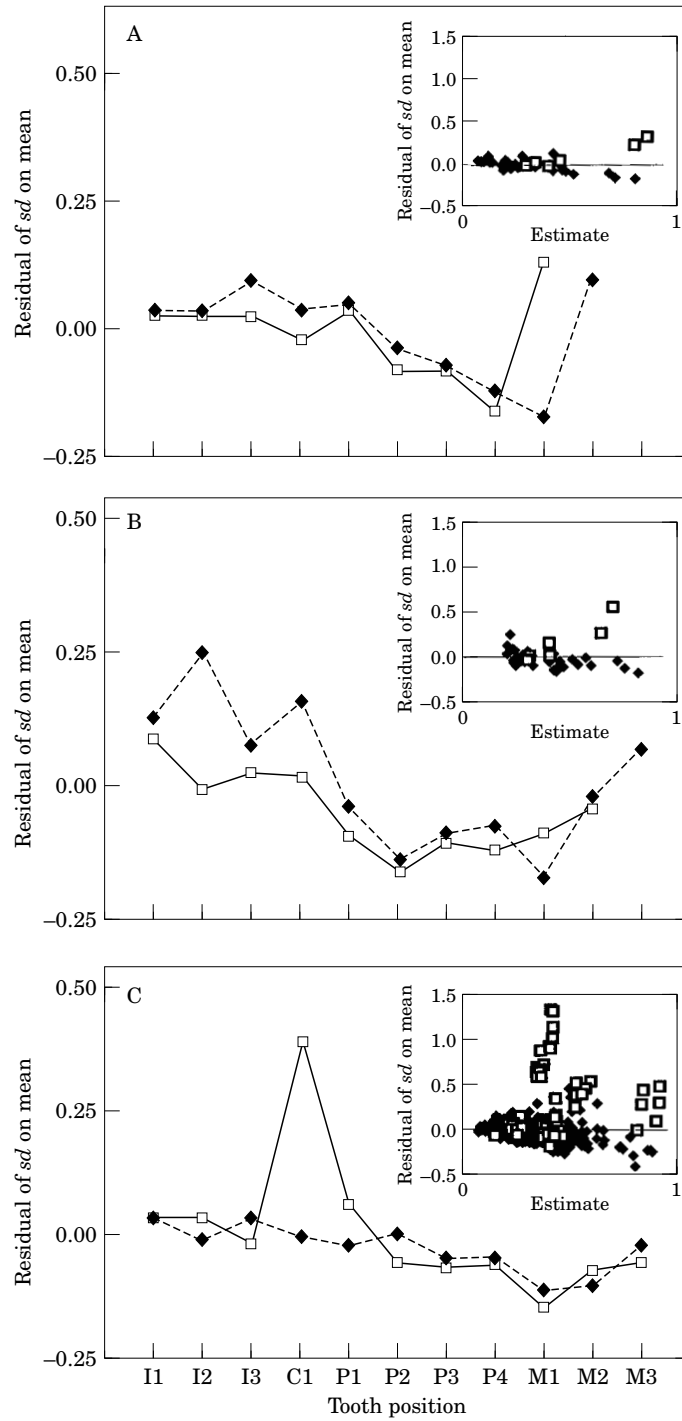


Figure 6. Adjusted variability profiles showing variation in tooth length for each position in the dentition. These plots use the residual of standard deviation on mean variable size instead of the coefficient of variation. The insets shows the complete results of regression analysis for each particular data set. A, *Martes americana*. B, *Urocyon cinereoargenteus*. C, the average for eighteen species and subspecies of primates and carnivorans. Upper teeth (\square); lower teeth (\blacklozenge). In the inset canine data are symbolized by an open box and other teeth by solid diamonds.

difference rather than true difference in variability. For this reason as much caution should be used with regression residuals as with the coefficient of variation.

It should be clear, however, that most teeth except the canines of some sexually dimorphic primates (the extreme outliers in Figs 1, 2, 6) have roughly the same level of variability. Relative to their size, anterior molars are no less variable and incisors are no more variable than other teeth. This finding has implications for the scenarios proposed to explain the original variability patterns.

Functional integration

The first of these scenarios is that natural selection differentially reduces variability in those teeth that are the most functionally integrated into the dentition (Yablokov, 1974; Gingerich, 1974; Gingerich & Ryan, 1979; Gingerich & Schoeninger, 1979; Gingerich & Winkler, 1979). According to this explanation, anterior molars have low variability because they have a more complexly interlocking occlusion than other teeth—even subtle variants might interfere with proper mastication and reduce fitness. Stabilizing selection should, therefore, lower their variability. Canines, anterior premolars, and incisors, on the other hand, have very simple occlusion and even extreme variation in the size of these teeth is unlikely to affect function (but see Gittleman & Van Valkenburgh, 1997; Biknevicius & Van Valkenburgh, 1997). This scenario fits the originally observed patterns in which canine, incisor and anterior premolars had higher variability than posterior premolars and anterior molars. However, it does not fit the reanalysed data in which incisors, premolars and molars have roughly the same variability. Furthermore, it does not explain why some species have extremely variable canines and others do not. While the logic of this scenario is extremely compelling—indeed it may prove to be true when shape rather than size variation is studied—it does not adequately explain differential variability in the tooth row.

Developmental fields

The second scenario is that morphogenic or developmental fields independently coordinate the variability of blocks of multiple teeth (Gould & Garwood, 1969; Gingerich & Ryan, 1979; Pengilly, 1984). Developmental fields were originally hypothesized to explain differences in morphology among the four classes of teeth: incisors, canines, premolars and molars (Butler, 1939; Dahlberg, 1945; Van Valen, 1962). Pengilly (1984), the most adamant promoter of the field scenario, said that the inverse correlation between V and \bar{x} itself was due to developmental fields. Drawing on Lande's (1977) observation that an inverse correlation is produced when wholes are compared to their constituent parts, Pengilly argued that the correlation in dental variables is a consequence of individual teeth being parts of larger developmental fields. But Lande's effect would only appear if field variables were directly compared with individual tooth variables. Sadly, this was not the case—rather the negative correlation observed by Pengilly was a consequence of the mathematical properties of the coefficient of variation itself. Gould & Garwood (1969) used fields to explain the high variability in posterior molars. They argued that large anterior molars exert a developmental influence on the smaller posterior ones that increases variability in the latter. As we have seen, however, the

difference in the level of variability of anterior and posterior molars is an artifact. The observations of both Pengilly and Gould & Garwood are best explained simply by the effect of size on V , not by developmental fields.

Sexual dimorphism and tooth eruption sequences

The last scenario advanced to explain variability patterns involves the relative timing of tooth formation and sexually dimorphic hormonal activity (Gingerich, 1974). Teeth that form before the beginning of sex-linked differentiation in hormonal balance should be less dimorphic—and less variable—than those that form later. Those that form during sexually differentiated growth should have higher variability indexes when males and females are pooled. While the relationship between eruption time, variability, and hormonal activity has not been thoroughly explored, changes in dimorphism during ontogeny are known in other mineralized structures, such as the pelvis of the squirrel monkey (Gingerich, 1972). The adjusted dental variability profiles are potentially consistent with this hypothesis. The most variable teeth in any of the data included in this study are the canines of *Cercopithecus* (the 15 outlying points with means of approximately 6.0 in Fig. 1C), which are noted for their sexual dimorphism (Cope, 1993; Cope & Lacy, 1995). The cheek teeth and incisors of *Cercopithecus*, however, are not remarkably variable (i.e. they fall close to the regression line in Fig. 6C). The canines are formed (or at least erupt) later than all other teeth in the cercopithecoid dentition except the M_3 (which is variable in its time of eruption relative to the canine). The canine erupts long after sexual maturity and dimorphic hormonal activity could have affected most of its growth (Smith, 1992; Schultz, 1960). In comparison the adjusted dental variability profiles of non-dimorphic species—like indriids (Gingerich & Ryan, 1979) and foxes (Polly, 1997)—are relatively flat. Since there is little sexual differentiation in growth, there is no opportunity for some teeth to be more affected by it than others. Interestingly, the adjusted variability profile of *Mustela americana* is quite flat, even though it is extremely dimorphic (Fig. 6A: this is best seen in the raw residual data since the final tooth in the dentition is the smallest, making the apparent difference between it and the penultimate teeth an artifact). The teeth of *Mustela* form in extremely quick succession (Aulerich & Swindler, 1968) and dental development is less likely to straddle the onset of dimorphic differentiation than in *Cercopithecus*. All teeth may be equally affected by dimorphic hormonal activity giving them uniformly high variability indexes. It has been demonstrated elsewhere that variability in each sex of *Mustela americana* is similar to that of an entire non-dimorphic species, but that the pooled-sex data of *M. americana* have elevated variability indexes (Polly, 1997). Many data that would be required to test the hypothesis that variability profiles are related to dimorphism and eruption sequence—such as the timings of hormonal activity or tooth initiation—are not readily available. However, this hypothesis remains viable in light of the data reanalyzed here and deserves further study.

CONCLUSION

Even though the coefficient of variation—like many ratio-based indexes (Atchley *et al.*, 1976; Albrecht, 1977; Bookstein *et al.*, 1985)—was designed to be size-independent, in many cases it is not. Dividing the standard deviation by the mean

will only produce an unbiased measure of variability when the standard deviations of included variables fit a linear function that approaches zero as the mean decreases. In cases where the standard deviation is constant or does not approach zero, a strong inverse correlation between the coefficient of variation and the variable mean results. This phenomenon is not necessarily caused by size-correlated measurement error, but results from the uniform addition of error to measured variation. The effects could be significant and should be explored before drawing conclusions about levels of relative variability in biological studies.

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APPENDIX 1

Summaries of dental measurements of *Urocyon cinereoargenteus* from North America. This sample includes a mixture of males and females from a variety of localities across North America. All measurements are in millimeters.

Position	Upper dentition				Lower dentition				Position	n	Range	Mean	s	V
	n	Range	Mean	s	n	Range	Mean	s						
I ¹ L	82	1.52-2.45	1.95	0.2037	10.43	I ₁ L	74	0.92-1.82	1.42	0.2418	17.04			
W	82	1.34-2.63	1.92	0.3214	16.70	W	75	0.92-1.98	1.47	0.3363	22.88			
I ² L	80	1.76-2.63	2.29	0.1863	8.12	I ₂ L	76	1.14-2.24	1.75	0.3132	17.90			
W	80	1.62-2.89	2.27	0.2437	10.75	W	75	0.94-2.52	1.72	0.4736	27.55			
I ³ L	82	2.49-3.82	2.91	0.2363	8.13	I ₃ L	76	1.90-2.97	2.33	0.2438	10.47			
W	82	2.49-3.82	2.91	0.2363	8.13	W	76	1.38-2.70	2.07	0.3194	15.42			
C ¹ L	84	4.35-6.23	5.04	0.4253	8.44	C ₁ L	81	3.90-6.39	5.00	0.5618	11.23			
W	84	2.53-3.82	3.19	0.2738	8.60	W	82	2.58-4.17	3.34	0.3264	9.79			
H	76	6.68-12.62	10.33	1.2566	12.17	H	74	6.24-11.18	9.33	0.9095	9.75			
P ¹ L	79	3.10-4.20	3.61	0.2353	6.52	P ₁ L	70	2.45-3.68	3.17	0.2681	8.47			
W	80	1.78-2.54	2.17	0.1567	7.23	W	70	1.68-2.66	2.01	0.1763	8.78			
P ² L	81	5.08-6.31	5.56	0.2767	4.98	P ₂ L	74	4.65-5.92	5.34	0.2834	5.30			
W	80	1.91-3.15	2.39	0.2479	10.38	W	75	1.92-2.78	2.35	0.1872	7.96			
P ³ L	79	5.26-6.82	6.18	0.3646	5.90	P ₃ L	81	5.07-7.07	5.87	0.3677	6.27			
W	78	2.16-3.47	2.71	0.2368	8.74	W	81	2.08-3.25	2.59	0.2270	8.77			
P ⁴ L	82	9.25-12.37	11.30	0.6327	5.60	P ₄ L	79	6.54-8.39	7.39	0.4595	6.21			
W	82	4.28-6.24	5.33	0.4630	8.69	W	79	2.56-4.42	3.50	0.3387	9.67			
M ¹ L	83	7.20-9.57	8.48	0.5107	6.02	M ₁ L	81	11.13-14.47	12.41	0.6418	5.17			
W	83	9.22-11.92	10.68	0.6792	6.36	W	81	4.27-6.50	5.21	0.4005	7.68			
M ² L	82	4.78-7.05	5.88	0.4101	6.98	M ₂ L	81	4.83-7.80	6.89	0.4892	7.09			
W	82	6.08-9.09	8.02	0.5653	7.05	M ₃ L	81	3.82-5.75	5.02	0.3566	7.11			
						W	69	2.43-4.15	3.17	0.3690	11.64			
						W	69	2.41-3.92	2.94	0.2925	9.95			

APPENDIX 2

Summary of dental measurements of the American marten (*Martes americana*) from British Columbia. This sample includes both male and female individuals. All measurements in millimeters.

Position	<i>n</i>	Upper dentition			<i>V</i>	Position	<i>n</i>	Lower dentition			<i>V</i>
		Range	Mean	<i>s</i>				Range	Mean	<i>s</i>	
I ¹ L	90	1.55-2.58	1.96	0.2080	10.64	I ₁ L	80	0.54-1.54	1.14	0.1540	13.47
W	90	0.39-0.99	0.68	0.1197	17.71	W	80	0.29-0.84	0.51	0.1177	22.95
I ² L	90	1.54-2.74	2.14	0.2295	10.72	I ₂ L	90	1.54-2.38	1.91	0.1947	10.21
W	90	0.50-1.12	0.81	0.1286	15.85	W	90	0.52-1.49	1.12	0.1596	14.29
I ³ L	94	2.36-3.85	3.02	0.3426	11.33	I ₃ L	91	0.97-2.10	1.73	0.1713	9.91
W	94	0.97-1.76	1.27	0.1624	12.81	W	91	0.62-1.57	1.06	0.2146	20.28
C ¹ L	122	3.58-5.00	4.26	0.3803	8.93	C ₁ L	120	3.77-6.11	4.86	0.4961	10.22
W	122	2.53-3.57	3.03	0.2751	9.08	W	121	2.73-4.25	3.54	0.3563	10.06
H	113	7.30-12.93	9.50	1.1779	12.40	H	118	6.27-10.66	8.81	1.0222	11.60
P ¹ L	116	1.34-2.41	1.91	0.2351	12.29	P ₁ L	115	1.37-2.63	1.94	0.2475	12.78
W	115	1.56-2.12	1.83	0.1189	6.50	W	115	0.99-2.29	1.81	0.1677	9.26
P ² L	120	3.72-5.46	4.47	0.3426	7.66	P ₂ L	119	2.87-4.92	4.21	0.3622	8.60
W	120	1.76-2.74	2.12	0.1971	9.31	W	120	1.72-2.56	2.24	0.1705	7.62
P ³ L	121	4.36-6.00	5.14	0.3982	7.74	P ₃ L	121	4.20-6.13	4.97	0.3914	7.87
W	122	1.98-3.04	2.47	0.2439	9.86	W	121	1.92-2.88	2.34	0.1974	8.43
P ⁴ L	121	6.38-9.16	7.76	0.5483	7.06	P ₄ L	120	4.58-6.44	5.55	0.3961	7.13
W	121	4.06-5.82	4.86	0.4425	9.11	W	120	2.20-3.13	2.61	0.2137	8.19
M ¹ L	121	3.36-5.56	4.50	0.5510	12.24	M ₁ L	121	7.71-10.10	8.84	0.6327	7.16
W	120	6.33-8.74	7.44	0.5752	7.73	W	121	2.65-4.16	3.53	0.3021	8.55
						M ₂ L	120	2.06-3.66	2.84	0.3720	13.11
						W	120	1.12-3.63	2.96	0.2789	9.42