

Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals

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Abstract.—Teeth are generally the best-preserved elements among mammal fossil remains and are highly diagnostic characters. Consequently, much mammalian paleontological, systematic, and evolutionary research focuses on teeth, so it is important to understand how they vary and covary with other characters. Dental traits within populations of carnivores appear to be more variable than cranial traits, a pattern that results only partly from their usually smaller size. Furthermore, dental traits, although highly correlated with one another, are not highly correlated with cranial traits, which are also highly correlated with one another. Thus, teeth and cranial bones may be subject to quite different selective pressures and genetic/developmental constraints and may suggest different microevolutionary scenarios. Vestigial teeth show significantly greater variability than expected, reflecting the absence of stabilizing selection.

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Introduction

Mammalian teeth are used in a variety of ecological and evolutionary studies. Teeth figure as indicators of environmental stress (Badyaev 1998; Klevezal and Sokolov 1999), in systematic research (Thackeray 1997), in interspecific and interpopulation comparisons of variation (Harris and Rathbun 1989; Bronner 1996; Suchentrunk and Flux 1996), in studies of community structure (Van Valkenburgh and Wayne 1994; Dayan and Simberloff 1998), and in many other research topics. But first and foremost, teeth are the focus of paleontological research.

Teeth are generally the best-preserved element among vertebrate fossil remains; they are durable and easy to identify to taxon and therefore play a central role in the study of the mammalian fossil record (e.g., West 1979; Chaline and Laurin 1986; MacFadden 1986). Teeth have been used in describing fossil assemblages (Bermudez-De Castro 1993; Mezzabotta et al. 1995), for systematic studies of fossils (Tsoukala 1996), for reconstructing diets (Hunter and Fortelius 1994), for studying evolutionary change through time (Bermudez-De Castro 1993; Jernvall et al. 1996), and for assessing sexual size dimorphism in fossil

populations (Gingerich 1981; Leutenegger and Shell 1987; Fleagle 1989). In many studies tooth size is used as a surrogate for body size, a practice justified by the general relationship between body size and tooth size among mammalian species (e.g., Kurtén 1967; Marshall and Corruccini 1978; Gingerich 1985; Koch 1986; Roth 1992).

Although the extensive use of teeth in paleontological research mostly derives from necessity, researchers often point to its advantages. Chief among them is that tooth crown size is fixed by the cessation of enamel apposition before tooth eruption and is therefore often considered a correlate of body size that is free of ontogenetic change (e.g., Gould and Garwood 1969; Gingerich 1974; Garn et al. 1979; Koch 1986). Moreover, tooth measurements can safely be taken as "adult," whereas termination of cranial growth can be determined only by complete suture closure, a state that is achieved only at a very old age in some mammals and is never quite achieved in others. Even later, bone growth can be modulated by factors such as muscular development and mechanical stress.

Here we explore some tenets of research on mammalian dentitions. We ask whether teeth

vary less than cranial characters do within populations, as many paleontologists perceive. We also attempt to determine to what extent cranial and dental characters covary. Additionally, we ask to what extent natural selection affects patterns of morphological variability, by testing whether the variability of vestigial teeth differs significantly from the general pattern of variation of mammalian teeth. We use original data from single populations of two carnivore species: the wolf (*Canis lupus*) and the wildcat (*Felis silvestris*). We also examine data from many populations of the short-tail weasel (*Mustela erminea*) and the long-tail weasel (*Mustela frenata*) published by Holmes (1987).

Variability of Dental and Cranial Characters.—Simpson et al. (1960; 94) described the rationale that has guided choice of morphological traits for taxonomic purposes:

One of the essentials of good taxonomy is to select characters that are relatively little variable within a taxonomic group, for taxonomic comparisons are more easily and more reliably based on these than on highly variable characters. The coefficient of variation is very useful as a guide in the selection of such characters, too often merely guessed at or accepted with no real criterion. Obviously, a tooth that is extremely variable is not a good taxonomic guide; its variations reflect intraspecific variability and not reliable taxonomic differences.

Some studies have compared the variability of different teeth within populations, assuming the least variable of those has the best diagnostic value (e.g., Gingerich 1974; Gingerich and Schoeninger 1979; Gingerich and Winkler 1979; Roth 1992). Understanding patterns of variation in morphological characters is particularly important because the degree of variation is often considered to indicate the number of species present in a fossil assemblage (Roth 1992; Cope 1993; Cope and Lacy 1995; Carrasco 1998). For red fox (*Vulpes vulpes*), Gingerich and Winkler (1979) found that the largest teeth, the carnassials, were least variable, a fact they attributed to functional integration. Other studies have demonstrated an inverse relationship between size and vari-

ability in mammalian dentitions, which has been variously attributed to developmental complexity (Pengilly 1984) and size-related bias in the coefficient of variation (Polly 1998a).

The ontogenetic considerations discussed above suggest that tooth size may be less variable than cranial or skeletal measurements, but this prediction seems not to have been tested. We studied patterns of variability of dental and cranial characters of carnivores, in light of a growing body of literature on variability in morphological characters (Yablokov 1974; Lande 1977; Soulé 1982; Pankakoski et al. 1987; Kerfoot 1988; Polly 1998a).

Covariation between Dental and Cranial Characters.—We examined the covariation between dental and cranial characters in order to gain insight into patterns of morphological integration among these traits. Morphological integration may be a source of evolutionary constraint (Zelditch 1996); the way characters change may be constrained or facilitated by their intrinsic integration (Cheverud 1982). If dental characters are used to represent evolutionary patterns in fossil mammals, it is important to understand their patterns of covariation with other morphological characters.

At a broad taxonomic scale, the significance of studying the allometric relationships between tooth size and body or cranial size has often been emphasized (e.g., Creighton 1980; Legendre and Roth 1988); understanding this relationship allows us to recognize special dental adaptations unrelated to the requirements of size (Gould 1975). A series of "mouse-to-elephant" plots (see Gould 1975) were generated for different taxonomic or ecologically similar groups of mammals, but the particular allometric relationships and their theoretical interpretation are still controversial (e.g., Gould 1975; Kay 1975; Gingerich et al. 1982; Wolpoff 1985; Fortelius 1990).

Size change is so covariant among morphological traits in general that separate body parts are often good estimators of change in other parts (McKinney 1990). However, interspecific allometric relationships cannot safely be extrapolated to predict relationships within species; in fact, it remains unclear whether

intraspecific allometric relationships can be demonstrated at all. Some studies have shown nil correlation within species between dental measurements and skull or body size (e.g., Kurtén 1953; Kieser and Groenveld 1990), and physical anthropologists have long concluded that tooth size cannot be used to predict body size in human populations (e.g., Garn and Lewis 1958; Lavelle 1974; Henderson and Corruccini 1976). Wolpoff (1985) suggested that changes of tooth size may be a passive correlated response to changes in body size, or that they may result from genetic uncoupling of tooth and body size. Likewise, Dayan et al. (1989a,b, 1990, 1992) suggested that morphological patterns in mammalian skull size may be a passive correlated response to natural selection operating on tooth size.

Many studies have dealt with the morphological integration among crania and mandibles (e.g., Cheverud 1989, 1995, 1996; Roth 1996; Smith 1996), but few deal with the morphological integration of dental and cranial characters. Subdividing organisms into natural subunits can be done in different ways (Roth 1996). We ask whether dental and cranial characters can be viewed as parts of an integrated system in which the relationships reflect functional and/or genetic constraints. We address this question by studying patterns of phenotypic covariation between mammalian teeth and cranial characters within carnivore species.

Variability of Vestigial Teeth.—Variation is what natural selection operates on; understanding morphological variation is therefore important for understanding evolutionary processes. A tenet of evolutionary theory is that, under conditions of stabilizing selection, phenotypic variability is inversely related to selection intensity (Tague 1997; see also Hoffmann and Merila 1999 for the possible effects of favorable and unfavorable environments). Many biologists assume that coefficients of variation among traits are, in a very rough way, related to fitness (Soulé 1982); the variability of a trait is seen as inversely related to the effect of the trait on survival and reproduction (Soulé 1982). For example, Gould and Garwood (1969) interpreted the lesser variability in tooth length than in tooth width as

reflecting more stringent limitations on tooth-row length than on tooth-row width.

An extreme case of reduced stabilizing selection is found in vestigial morphological structures. Although biologists have long considered vestigial structures to be highly variable, few studies actually address their morphological variability (Tague 1997). Simpson et al. (1960:94) interpreted the high variability of the third upper premolar of *Ptilodus montanus*, a multi-tuberculate: “p³ in this family is not functional and is being lost. Organs in this condition are usually extremely variable.” In canids, it has been suggested that the great variability in length of the third lower molar is because this tooth is vestigial and is therefore free of strong selective pressures (Kurtén 1953, 1954). Alternatively, it has been interpreted as resulting from the very simple occlusion with the second upper molar (Gingerich and Winkler 1979).

We asked whether this tooth, the small third lower molar of wolves, does indeed exhibit unexpectedly high variability. We also asked whether the second upper premolar and first upper molar of wildcats, minute teeth, can be characterized as vestigial on the basis of their variability, with overall patterns of variation of teeth and skulls as a backdrop. These teeth are exceptionally small and are often absent altogether, and the first peglike upper molar does not occlude with any tooth of the lower jaw.

Materials and Methods

Specimens were measured in the Field Museum of Natural History (Chicago) and the Zoology Museum of the Tel Aviv University Zoological Museum. We studied gross dental morphology, limiting our dental measurements to length and width. We measured a similar number of cranial characters for comparison (Table 1). Measurements were taken with digital calipers to 0.01 mm precision. We considered skulls adult and suitable for measurement at full dental eruption and dorsal suture closure, and we did not use specimens with worn dentitions.

We measured the following:

1. Wolves (*Canis lupus*) (9 females and 13 males) from Israel. We measured 39 cranial

characters and 27 dental characters. Cranial characters were taken according to von den Driesch (1976), Harrison (1968), Radinsky (1981), and Kurtén (personal communication 1983). Tooth crown measurements were the length (L) and width (W) of all teeth (taken according to Kurtén [personal communication 1983]). For upper carnassials we took two length measurements (Le, length of the exterior lobe, and Li, length of the interior lobe) and two width measurements (Wa, anterior width, and Wbl, blade width).

2. Wildcats (*Felis silvestris*) (11 females and 10 males) from the Upper Nile Province, Sudan. We measured 36 cranial characters and 19 dental characters (felids have a reduced number of teeth). Cranial characters were taken according to von den Driesch (1976) and Radinsky (1981). Dental measurements were taken according to Kurtén (personal communication 1983) as for wolves.

Variability of Dental and Cranial Characters.—We studied variability among dental and cranial characters using the above data plus extensive data on weasels from Holmes (1987). Holmes (1987) divided both *Mustela erminea* and *M. frenata* into a number of local populations (or groups of populations). He separated the sexes and measured eight cranial and five dental measurements. We analyzed all his samples with more than ten individuals (sexes kept separate). These comprised 36 populations of *M. erminea* and 27 populations of *M. frenata*.

We calculated coefficients of variation (CV = sample standard deviation divided by sample mean) for each trait in each sample, then regressed CV linearly on mean. We also attempted to fit the data to a rectangular hyperbola ($CV = a/\text{mean} + b$).

Measurement Error.—Because CV is a relative measure of variation (scaled by the character mean), and because dental characters are smaller, there should be a systematic tendency for measurement errors to be relatively larger in dental characters than in cranial ones and to contribute more to inter-individual variation, measured by CV. In our original data sets, each character was measured once only on each skull. To check the contribution of measurement error to patterns of variability,

we carried out repeated measurements on 15 of the wolf skulls, selected because they were the best preserved and most complete specimens. Fifty-nine characters (37 cranial, 22 dental) were measured on each skull. The entire set of 15 skulls was measured five times. From the original set of measurements, we omitted cranial measurements C–M₃ and vdD^{15a} and dental measurements P²W, P³W, P₂W, P₃W, and P₄W. To be objective, we had the repeated measurements taken by someone unaware of the previous pattern. This person found the seven traits just listed too difficult to measure consistently.

We used single-classification ANOVA, with skulls—a model II factor (Sokal and Rohlf 1981)—as groups and five measurements per skull for each of the 60 variables. The within-group variance component estimates measurement error, as percentage of the total variance. Then the mean of the five measurements of each character was used to recalculate the variance (and CV) among the 15 individuals.

Covariation between Dental and Cranial Characters.—For analyses of the interrelationships of different traits, we used principal components analysis (PCA) on the correlation matrices of the wolf and wildcat data sets. We used the PCA program of the NTSYS-PC package (Rohlf 1986) to extract three components for each data set. We plotted the data in the space of the first two components.

Because there are many more characters than specimens, there is a high null probability that a PCA would show the data to have some structure even if the data had been generated by some random algorithm. To guard against spurious patterns from this source, we attempted cross-validation. We randomly divided the characters in both the wolf and the wildcat data matrices (mixed sexes) into two groups, each containing half the dental and half the cranial characters, then ran the PCA separately on each half.

Variability of Vestigial Teeth.—The third lower molar in wolf dentition may be considered vestigial by developmental criteria. The same criteria suggest that in wildcats the second upper premolar and first upper molar are nonfunctional and perhaps vestigial. We test-

TABLE 1. Cranial measurements taken on wolves and wildcats. vdD indicates von den Driesch 1976. Subscript numbers indicate mandible measurements, and superscript numbers indicate cranial measurements.

Wolves	vdD ₁	Total length: length from condyle process-Infradentale
Wolves	vdD ₂	Length: the angular process-Infradentale
Wolves	vdD ₄	Length: the condyle process-aboral border of the canine alveolus
Wolves	vdD ₇	The aboral border of the alveolus of M ₃ -aboral border of the canine alveolus
Wolves	vdD ₈	Length of the cheek-tooth row, M ₃ -P ₁ , measured along the alveoli
Wolves	vdD ₉	Length of the cheek-tooth row, M ₃ -P ₂ , measured along the alveoli
Wolves	vdD ₁₀	Length of the molar row, measured along the alveoli
Wolves	vdD ₁₁	Length of the premolar row, P ₁ -P ₄ , measured along the alveoli
Wolves	vdD ₁₂	Length of the premolar row, P ₂ -P ₄ , measured along the alveoli
Wolves	vdD ₁₇	Greatest thickness of the body of jaw (below M ₁)
Wolves	vdD ₁₈	Height of the vertical ramus: basal point of the angular process-Coronion
Wolves	vdD ₁₉	Height of the mandible behind M ₁ , measured on the lingual side and at right angles to the basal border
Wolves	vdD ₂₀	Height of the mandible between P ₂ and P ₃ , measured on the lingual side and at right angles to the basal border
Wolves	C-M ₃	Length of the tooth row, canine to M ₃
Wolves	P ₂₋₄	Length of the tooth row, P ₂ -P ₄ , measured at the crown
Wolves	vdD ¹	Total length: Akrokranion-Prosthion
Wolves	vdD ²	Condylbasal length: aboral border of the occipital condyles-Prosthion
Wolves	vdD ⁸	Viscerocranium length: Nasion-Prosthion
Wolves	vdD ¹⁵	Length of cheek-tooth row (measured along the alveoli on the buccal side)
Wolves	vdD ^{15a}	Aboral border of the alveolus of M ³ -oral border of the canine alveolus
Wolves	vdD ¹⁶	Length of the molar row (measured along the alveoli on the buccal side)
Wolves	vdD ¹⁷	Length of the premolar row (measured along the alveoli on the buccal side)
Wolves	vdD ²²	Greatest diameter of the auditory bulla (following Wagner 1930: p. 21): from the most aboral point of the bulla on the suture with the external carotid foramen
Wolves	vdD ^{22a}	Least diameter of the auditory bulla
Wolves	vdD ²³	Greatest mastoid breadth = greatest breadth of the occipital triangle: Otion-Otion
Wolves	vdD ²⁹	Greatest neurocranium breadth = greatest breadth of the braincase: Euryon-Euryon
Wolves	vdD ³⁰	Zygomatic breadth: Zygon-Zygon
Wolves	vdD ³¹	Least breadth of skull = least breadth at the postorbital constriction
Wolves	vdD ³²	Frontal breadth: Ectorbitale-Ectorbitale
Wolves	vdD ³³	Least breadth between the orbits: Entorbitale-Entorbitale
Wolves	vdD ³⁴	Greatest palatal breadth: measured across the outer borders of the alveoli
Wolves	vdD ³⁵	Least palatal breadth: measured behind the canines
Wolves	vdD ³⁶	Breadth at the canine alveoli
Wildcats	vdD ₁	Total length: length from the condyle process-Infradentale
Wildcats	vdD ₂	Length from the indentation between the condyle process and the angular process-Infradentale
Wildcats	vdD ₃	Length: the condyle process-aboral border of the canine alveolus
Wildcats	vdD ₄	Length from the indentation between the condyle process and the angular process-aboral border of the canine alveolus
Wildcats	vdD ₅	Length of the cheek-tooth row, P ₃ -M ₁ , measured along the alveoli
Wildcats	vdD ₈	Height of the vertical ramus: basal point of the angular process-Coronion
Wildcats	vdD ₉	Height of the mandible behind M ₁ , measured on the buccal side
Wildcats	vdD ₁₀	Height of the mandible in front of P ₃ , measured on the buccal side
Wildcats	vdD ¹	Total length: Akrokranion-Prosthion
Wildcats	vdD ²	Condylbasal length: aboral border of the occipital condyles-Prosthion
Wildcats	vdD ³	Basal length: Basion-Prosthion
Wildcats	vdD ⁸	Viscerocranium length: Nasion-Prosthion
Wildcats	vdD ¹⁰	Lateral length of "snout": oral border of the orbit of one side-Prosthion
Wildcats	vdD ¹²	Length of the cheek-tooth row (measured along the alveoli on the buccal side)
Wildcats	vdD ¹³	Length of the premolar row (measured along the alveoli on the buccal side)
Wildcats	vdD ¹⁶	Greatest diameter of the auditory bulla: from the most aborolateral point to the most oromedial point
Wildcats	vdD ¹⁷	Least diameter of the auditory bulla: from the middle of the opening of the external acoustic meatus up to the most medial protrusion of the bulla on the opposite side of the bulla
Wildcats	vdD ¹⁸	Greatest mastoid breadth = greatest breadth of the occipital triangle: Otion-Otion

TABLE 1. Continued.

Wildcats	vdD ¹⁹	Greatest breadth of the occipital condyles
Wildcats	vdD ²⁰	Greatest breadth of the foramen magnum
Wildcats	vdD ²¹	Height of the foramen magnum: Basion–Opisthion
Wildcats	vdD ²²	Greatest neurocranium breadth = greatest breadth of braincase: Euryon–Euryon
Wildcats	vdD ²³	Zygomatic breadth: Zygion–Zygion
Wildcats	vdD ²⁴	Frontal breadth: Ectorbitale–Ectorbitale
Wildcats	vdD ²⁵	Least breadth between the orbits: Entorbitale–Entorbitale
Wildcats	vdD ²⁶	Greatest palatal breadth: measured across the outer borders of the alveoli
Wildcats	vdD ²⁷	Breadth at the canine alveoli
Wildcats	vdD ²⁸	Least breadth aboral of the supraorbital processes = breadth of the postorbital constriction
Wildcats	vdD ²⁹	Facial breadth between the infraorbital foramina (least distance)
Wolves + wildcats	MAM	Moment arm of masseter, measured from the dorsal surface of the condyle to the ventral border of the angular process. An estimator of the moment arm of the superficial masseter
Wolves + wildcats	MAT	Moment arm of temporalis, measured from the condyle to the apex of the coronoid process. An estimator of the moment arm of a portion of the temporalis
Wolves + wildcats	MFL	Maseteric fossa length, measured from the back of the condyle to the most anterior point of the maseteric fossa. An estimator of the size of the deep masseter and of the moment arm of the deep masseter
Wolves + wildcats	OCPH	Occipital height, measured from the midventral border of the foramen magnum to the dorsal rim of the occiput
Wolves + wildcats	TFL	Temporal fossa length, measured from the most posterior point of the lambdoidal crest to the back of the supraorbital process. An estimator of temporalis size
Wolves + wildcats	TRL	Tooth-row length, measured parallel to the palatal midline, from a point level with the back of the last tooth to the front of the medial incisor alveolus

ed whether characters measured on these teeth (M_3L in wolves, P^2L , P^2W , and M^1L in wildcats; Tables 2 and 3) are more variable than other characters with Dixon's and Grubb's tests for outliers (Sokal and Rohlf 1981: p. 413).

Results

Variability of Dental and Cranial Characters.—Male wolves are larger on average than females for both cranial characters (Table 2; paired-comparison t -test: $t = 7.69$, $df = 36$, $p < 0.001$) and dental characters (Table 2; $t = 8.46$, $df = 26$, $p < 0.001$). We therefore separated sexes when studying variation patterns of the different characters. Fossil remains of mammals, however, can rarely be separated to sex. Because we are interested here in the implications of this analysis for paleontological studies, we also analyzed the variation patterns of mixed-sex populations of wolves and wildcats.

For each sex separately and both together, CVs of dental traits tended to exceed those of

cranial ones (Table 2). Mann-Whitney U -tests were all significant at $p < 0.002$.

Within sexes and in the mixed-sex sample (Fig. 1 top), a linear regression of CV on mean for all traits together yielded a highly significant negative relationship ($p < 0.002$ for all regressions), although the fraction of the variation explained was not large (0.171 for males, 0.316 for females, and 0.286 for mixed sexes). In each case, a rectangular hyperbolic regression produced a better fit ($p < 0.001$ for each regression), and the improvement was always significant (at $p < 0.005$) by ANOVA (Keeping 1962). The regressions still explain a minority of the variation (0.295 for males, 0.491 for females, and 0.403 for mixed sexes). Heteroscedasticity was substantial, with variance tending to be greater for small means, so the probabilities must be interpreted cautiously. No transformation eliminated this problem.

Finally, in the hyperbolic regressions the dental and cranial traits appeared to fall on the same line. Most cranial traits are larger than most dental ones, so the magnitude of

TABLE 2. Means, CVs, SDs, and principal component scores for the wolf data set. vdD indicates von den Driesch 1976. Subscript numbers indicate mandible measurements, and superscript numbers indicate cranial measurements.

	Males		Females		Males and females			Principal component (males and females)		
	Mean	CV	Mean	CV	Mean	SD	CV	1	2	3
vdD ₁	165.08	3.33	159.16	3.82	162.28	6.24	3.85	0.83414	-0.45362	0.04978
vdD ₂	165.21	3.42	158.42	4.19	162.09	6.75	4.17	0.88821	-0.41575	0.11968
vdD ₄	145.54	3.71	140.58	4.38	143.15	6.11	4.27	0.84365	-0.43854	0.13925
vdD ₇	93.92	2.43	90.68	3.04	92.52	2.86	3.09	0.95213	-0.13146	-0.05186
vdD ₈	88.43	3.04	84.21	2.19	86.77	3.05	3.52	0.90778	-0.05310	-0.33831
vdD ₉	81.68	2.68	77.85	2.59	80.22	2.77	3.45	0.90890	-0.04209	-0.31798
vdD ₁₀	40.74	4.43	39.12	2.57	40.18	1.70	4.23	0.73521	0.50006	-0.00829
vdD ₁₁	48.10	4.93	45.59	3.57	47.03	2.35	4.99	0.69328	-0.41733	-0.47822
vdD ₁₂	41.30	4.87	39.29	4.49	40.44	2.07	5.13	0.67773	-0.45172	-0.44986
vdD ₁₇	11.77	4.90	11.02	7.52	11.41	0.77	6.77	0.82752	-0.18604	-0.44986
vdD ₁₈	66.99	5.22	61.54	6.56	64.88	4.36	6.72	0.81379	-0.25479	0.11947
vdD ₁₉	25.89	5.40	25.19	6.43	25.44	1.56	6.13	0.53210	-0.52537	0.26312
vdD ₂₀	20.67	8.17	20.36	7.88	20.47	1.68	8.22	0.72386	-0.28068	0.25678
C-M ₃	107.19	3.13	103.55	2.87	105.70	3.58	3.39	0.98820	-0.08569	-0.08142
P ₂₋₄	42.10	3.84	40.47	3.80	41.44	1.72	4.14	0.71278	-0.37203	-0.46422
vdD ¹	225.57	4.26	219.03	2.58	222.58	8.86	3.98	0.85758	-0.40223	0.14775
vdD ²	210.66	3.76	204.79	2.69	208.07	3.56	3.56	0.84800	-0.37292	0.15405
vdD ⁸	110.74	4.95	104.89	3.40	108.23	5.37	4.97	0.87326	-0.12805	0.08023
vdD ¹⁵	77.58	3.54	74.30	2.51	76.23	2.79	3.66	0.90656	-0.14761	-0.06935
vdD ^{15a}	94.27	3.53	90.43	3.35	90.51	11.55	3.81	0.92083	-0.15307	-0.09883
vdD ¹⁶	19.35	5.90	19.18	4.14	19.30	0.98	5.10	0.62284	0.54658	0.30028
vdD ¹⁷	60.83	3.32	57.33	3.98	59.43	2.61	4.39	0.85168	-0.31002	-0.14604
vdD ²²	28.85	4.92	28.79	2.35	28.79	1.45	5.04	0.53351	-0.31832	0.27343
vdD ^{22a}	17.46	7.42	16.77	3.99	17.16	1.30	7.58	0.57434	-0.29234	-0.27388
vdD ²³	70.89	4.57	70.00	3.59	70.40	3.01	4.28	0.77254	-0.53275	-0.01333
vdD ²⁹	66.86	3.97	65.24	1.82	66.21	6.70	3.64	0.75122	-0.45340	-0.18953
vdD ³⁰	118.33	5.79	121.71	5.03	118.84	2.04	5.64	0.42965	-0.48784	0.55538
vdD ³¹	39.39	5.57	38.12	4.12	38.81	4.39	5.27	0.27091	-0.33934	-0.33048
vdD ³²	57.59	9.05	56.14	3.43	56.82	2.22	7.72	0.51962	-0.09510	0.01487
vdD ³³	40.53	6.25	39.49	3.67	40.05	2.99	5.55	0.60789	-0.30067	0.00776
vdD ³⁴	69.60	3.81	67.53	4.75	68.67	2.21	4.36	0.80806	-0.14407	0.11444
vdD ³⁵	38.55	4.06	36.45	6.32	37.53	2.25	5.88	0.73927	0.02883	-0.06742
vdD ³⁶	40.42	4.75	39.10	6.41	39.70	2.41	5.67	0.86279	0.12731	0.06364
MAM	31.51	6.25	30.32	7.87	31.00	2.14	6.91	0.72478	-0.40706	0.26196
MAT	49.48	5.44	46.32	5.61	48.27	2.94	6.10	0.72578	-0.39072	0.40587
MFL	54.97	6.34	52.83	6.34	53.57	3.71	6.92	0.59289	-0.31085	0.40587
OCPH	54.94	5.39	52.51	3.63	54.04	2.76	5.10	0.81723	-0.30684	-0.13953
TFL	108.38	11.69	102.07	3.62	105.55	10.55	10.00	0.65480	-0.17713	0.48771
TRL	113.58	3.16	109.23	2.73	111.86	3.81	3.40	0.91695	-0.10317	-0.11655
C ^{sup} L	12.42	5.74	11.69	6.67	12.11	0.80	6.57	0.76118	0.23239	-0.08963
C ^{sup} W	7.48	6.84	7.23	8.90	7.35	0.59	8.05	0.70283	0.19831	0.33794
P ¹ L	7.53	5.75	7.08	4.45	7.32	0.44	5.99	0.60068	0.49190	-0.19443
P ² L	12.67	5.94	11.78	6.26	12.30	0.82	6.69	0.72605	0.41388	-0.40025
P ² W	5.18	8.24	4.88	7.88	5.05	0.42	8.37	0.68275	0.37359	0.05633
P ³ L	14.09	5.12	13.25	3.88	13.79	0.75	5.47	0.73565	0.36864	-0.43580
P ³ W	5.96	8.83	5.53	8.21	5.79	0.53	9.21	0.77600	0.28152	0.08157
P ⁴ Le	22.85	4.29	21.61	5.23	22.40	1.17	5.24	0.74407	0.45848	0.00013
P ⁴ Li	23.56	3.68	22.20	6.06	23.07	1.25	5.22	0.83454	0.31141	0.02481
P ⁴ Wa	11.49	7.34	10.86	6.74	11.23	0.81	7.25	0.65778	0.10838	-0.28524
P ⁴ Wb1	8.77	5.30	8.25	7.79	8.57	0.57	6.61	0.77629	0.43098	0.09559
M ¹ L	14.92	4.60	14.64	4.42	14.84	0.66	4.42	0.62015	0.41168	0.40398
M ¹ Win	17.47	5.16	16.52	4.56	17.06	0.92	5.41	0.72868	0.39802	0.10286
M ² L	8.11	4.76	8.11	4.90	8.09	0.38	4.75	0.48386	0.35944	0.35969
M ² W	11.40	6.96	10.89	4.65	11.22	0.73	6.53	0.57428	0.36834	-0.00201
Cin ^f L	13.23	5.24	12.42	4.13	12.85	0.72	5.59	0.78949	0.05927	-0.00321
Cin ^f W	7.66	6.26	7.37	6.53	7.53	0.50	6.68	0.64687	0.12700	0.24729
P ₂ L	11.05	5.71	10.28	5.69	10.76	0.70	6.47	0.58118	0.56503	-0.22143
P ₂ W	5.17	7.15	5.07	7.19	5.12	0.36	7.01	0.55762	0.54440	0.32455
P ₃ L	12.63	3.91	11.81	5.92	12.31	0.68	5.56	0.73622	0.37343	-0.35390

TABLE 2. Continued.

	Males		Females		Males and females			Principal component (males and females)		
	Mean	CV	Mean	CV	Mean	SD	CV	1	2	3
P ₃ W	5.78	7.06	5.58	7.59	5.68	0.41	7.16	0.67103	0.44174	0.27629
P ₄ L	14.50	5.46	13.64	5.16	14.16	0.86	6.07	0.78587	0.27129	-0.17745
P ₄ W	6.85	8.07	6.60	8.42	6.75	0.54	8.03	0.62570	0.45064	0.16296
M ₁ L	24.93	4.22	23.81	3.92	24.47	1.11	4.52	0.91057	0.21341	0.08664
M ₁ W	9.49	5.61	8.79	6.39	9.22	0.61	6.67	0.78905	0.46532	-0.06925
M ₂ L	10.40	5.83	10.03	4.71	10.30	0.63	6.09	0.31017	0.49030	-0.03109
M ₃ L	5.24	9.11	5.10	8.41	5.17	0.47	9.04	0.02804	0.48258	-0.35416

the residuals of dental traits tended to exceed those of the cranial ones because of the heteroscedasticity noted above; however, there was no systematic tendency for the residuals of one category to differ in sign from those of the other category. Of 27 dental measurements, 10 exceeded the smallest cranial one, whereas of 39 cranial traits 3 were smaller than the largest dental one. Within this joint domain of mean size, there appeared to be no tendency for CV of either class of trait to exceed CV of the other class for approximately equal means.

Male wildcats are larger than females in both cranial and dental traits (Table 3; cranial traits: $t = 6.83$, $df = 34$, $p < 0.001$; dental traits: $t = 6.89$, $df = 18$, $p < 0.001$). Thus we again analyzed the two sexes separately as well as together. As with wolves, dental CVs tended to exceed cranial CVs (Table 3). All three Mann-Whitney U -tests were significant at $p < 0.001$.

For each sex separately as well as for combined sexes, a regression of CV on mean (Fig. 1 bottom) yielded a highly significant negative relationship ($p < 0.005$ for all regressions). As with wolves, these regressions explained only a small fraction of the variation: 0.167 for males, 0.321 for females, 0.204 for the mixed sample. All three wildcat data sets were better fit by a rectangular hyperbola, and the improvement in fit was always significant at $p < 0.005$. The fraction of the variation explained was considerably greater: 0.531 for males, 0.430 for females, and 0.463 for the mixed sample. Heteroscedasticity was similar to that for wolves. Again dental and cranial traits appeared to fall on the same hyperbolic line. Although cranial traits tended to exceed dental

ones, one of 19 dental traits was larger than the smallest cranial trait, whereas one of 35 cranial traits in males (two in females) was smaller than the largest dental one. Over this joint domain there did not appear to be a trend for cranial CVs to exceed dental ones or vice versa.

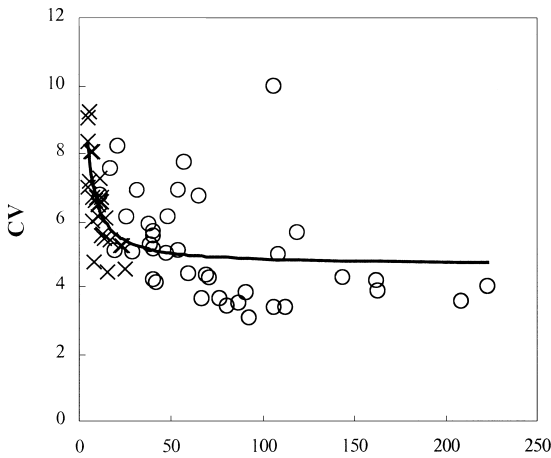
Both weasel species resemble wolves and wildcats in that dental CVs tended to exceed cranial ones. Most samples yielded significant negative linear regressions of CV on mean. Usually a rectangular hyperbola fit the data better. For *M. erminea*, 30 of 36 samples were better fit by the hyperbola (9 of these were significant improvements at $p < 0.05$). No sample was significantly better fit by a straight line. The hyperbolic regression explained an average of 0.595 of the variation, a figure that rose to 0.646 when three anomalous samples were omitted. For *M. frenata*, 24 of 27 samples were better fit by a hyperbola, 13 significantly so ($p < 0.05$). No sample was significantly better fit by a straight line. On average, a hyperbolic regression explained 0.640 of the variation. For both weasels, all five dental traits were smaller than all eight cranial ones, rendering more difficult judgments about whether all points fall on the same line. A visual inspection suggested no tendency for the signs of the residuals to differ between categories.

Measurement Error.—Measurement error in dental characters exceeded that in cranial ones (Table 4). Magnitude of measurement error exceeded 5% in only 8 of 37 cranial characters versus 19 of 22 dental ones (18 cranial but no dental characters had less than 1% error). The distributions are skewed, so the medians are better estimates of central tendency than the means are. The median measurement error of

TABLE 3. Means, CVs, SDs, and principal component scores for the wildcat data set. vdD indicates von den Driesch 1976. Subscript numbers indicate mandible measurements, and superscript numbers indicate cranial measurements.

	Males		Females		Males and females			Principal component (males and females)		
	Mean	CV	Mean	CV	Mean	SD	CV	1	2	3
vdD ₁	63.36	4.52	58.55	4.30	60.85	3.52	5.78	0.920	-0.340	-0.116
vdD ₂	59.85	4.47	55.23	4.24	57.42	3.34	5.82	0.929	-0.333	-0.088
vdD ₃	56.47	4.50	52.28	4.50	54.28	3.13	5.77	0.886	-0.390	-0.121
vdD ₄	53.13	4.33	49.04	4.39	50.98	2.95	5.78	0.894	-0.388	-0.070
vdD ₅	20.90	4.87	20.06	5.58	20.50	1.09	5.30	0.796	0.377	-0.025
vdD ₈	27.09	7.32	24.48	7.50	25.64	2.22	8.66	0.768	-0.515	-0.130
vdD ₉	10.79	6.35	9.73	7.93	10.22	0.87	5.55	0.904	-0.128	0.105
vdD ₁₀	8.97	5.95	8.01	5.94	8.48	0.69	8.17	0.777	0.034	0.446
vdD ¹	96.80	3.64	89.16	3.81	92.38	5.03	5.44	0.944	-0.305	0.005
vdD ²	88.93	4.31	82.04	3.75	85.01	4.68	5.51	0.947	-0.264	-0.123
vdD ³	81.95	4.27	75.01	4.01	78.07	4.55	5.83	0.952	-0.282	-0.083
vdD ⁸	36.61	5.88	33.18	5.73	34.81	2.53	7.25	0.842	-0.103	-0.183
vdD ¹⁰	25.88	5.24	23.33	4.34	24.55	1.72	6.99	0.915	-0.204	0.129
vdD ¹²	22.67	5.06	21.75	5.09	22.08	1.17	5.28	0.817	-0.180	-0.251
vdD ¹³	21.74	4.97	20.67	5.07	21.06	1.13	5.38	0.848	-0.053	-0.078
vdD ¹⁶	21.59	5.56	20.19	3.38	20.70	1.15	5.56	0.695	-0.067	-0.120
vdD ¹⁷	13.83	4.65	12.80	6.88	13.67	0.90	6.75	0.695	0.022	0.135
vdD ¹⁸	40.40	4.42	39.39	3.45	39.81	1.53	3.85	0.789	0.134	-0.087
vdD ¹⁹	22.45	4.39	22.13	3.93	22.21	0.88	3.98	0.585	0.325	-0.190
vdD ²⁰	14.29	7.51	14.24	4.47	14.20	0.84	5.90	0.426	0.536	-0.472
vdD ²¹	12.00	9.56	12.39	7.38	12.11	1.04	8.57	0.177	0.622	-0.564
vdD ²²	43.41	3.57	43.35	2.32	43.43	2.70	2.70	0.567	0.554	-0.153
vdD ²³	65.74	4.83	61.50	2.43	63.68	3.32	5.22	0.934	-0.182	-0.033
vdD ²⁴	48.58	6.02	45.38	4.48	46.95	2.91	6.19	0.723	-0.457	0.060
vdD ²⁵	17.19	7.17	15.64	7.49	16.41	1.38	8.40	0.696	-0.544	-0.035
vdD ²⁶	38.90	4.40	36.49	3.34	37.76	1.92	5.08	0.917	-0.043	0.049
vdD ²⁷	23.78	4.98	21.96	5.03	22.85	1.47	6.45	0.899	-0.096	0.079
vdD ²⁸	32.03	2.37	32.12	4.39	32.12	1.11	3.47	0.074	0.520	0.394
vdD ²⁹	25.48	4.46	23.88	5.34	24.72	1.49	6.05	0.900	-0.094	0.119
MAM	12.09	8.28	10.74	7.57	11.37	1.07	9.43	0.560	-0.608	0.028
MAT	19.21	6.08	17.60	7.27	18.30	1.42	7.73	0.818	-0.351	-0.182
MFL	26.51	5.19	24.57	8.55	25.39	2.05	8.08	0.692	-0.462	-0.300
OCPH	26.24	3.88	25.50	3.49	25.94	1.01	3.91	0.740	0.206	-0.079
TFL	55.12	3.49	50.51	4.73	52.33	7.67	5.95	0.833	-0.503	0.148
TRL	37.73	3.87	35.01	3.91	36.28	5.57	5.21	0.916	-0.241	0.111
C ^{sup} L	4.66	6.96	4.15	9.37	4.38	0.42	9.63	0.778	0.262	0.195
C ^{sup} W	3.52	5.84	3.16	8.11	3.33	0.29	8.72	0.798	0.181	0.316
P ² L	2.03	25.19	2.18	17.80	2.17	0.45	20.90	0.238	0.401	-0.630
P ² W	1.46	24.17	1.51	10.91	1.50	0.23	15.57	0.240	0.313	-0.606
P ³ L	6.77	4.93	6.39	6.34	6.57	0.40	6.11	0.637	0.466	-0.166
P ³ W	3.37	7.55	3.16	5.93	3.27	0.24	7.20	0.749	0.352	0.124
P ⁴ Le	11.00	6.15	10.51	6.18	10.72	0.70	6.50	0.618	0.545	-0.071
P ⁴ Li	11.54	5.78	10.99	6.43	11.21	0.72	6.40	0.654	0.427	0.066
P ⁴ Wa	5.45	8.65	5.05	12.07	5.23	0.55	10.51	0.629	0.548	0.176
P ⁴ Wb1	3.50	6.03	3.17	6.71	3.32	0.26	7.75	0.665	0.286	0.351
M ¹ L	3.69	19.20	3.14	19.92	3.38	0.70	20.76	0.590	0.130	-0.414
Cin ^f L	4.37	7.60	3.83	10.96	4.09	0.47	11.40	0.781	0.161	0.240
Cin ^f W	3.26	6.41	2.84	9.13	3.06	0.31	10.29	0.819	0.186	0.218
P ₃ L	5.56	7.38	5.32	7.57	5.45	0.41	7.43	0.713	0.526	-0.159
P ₃ W	2.73	6.33	2.59	6.23	2.67	0.18	6.73	0.586	0.366	0.284
P ₄ L	7.39	6.65	6.99	7.91	7.19	0.53	7.32	0.771	0.443	-0.137
P ₄ W	3.16	5.27	2.98	5.94	3.08	0.19	6.14	0.686	0.473	0.362
M ₁ L	8.30	6.20	8.08	8.74	8.18	0.60	7.35	0.433	0.633	0.201
M ₁ W	3.44	5.13	3.24	6.43	3.35	0.21	6.31	0.698	0.414	0.243

WOLVES



WILDCATS

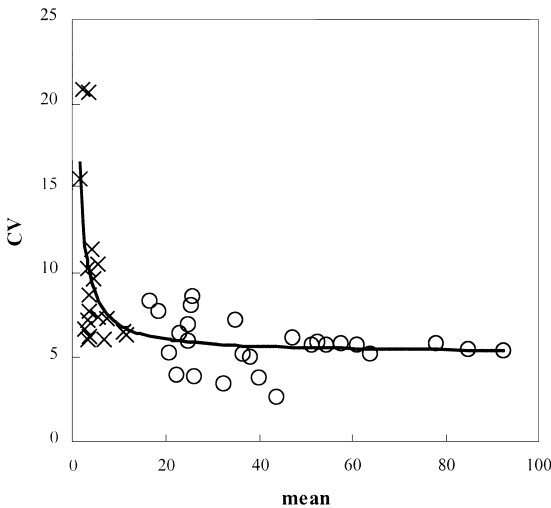


FIGURE 1. Top, hyperbolic regression of coefficient of variation on mean for dental traits (X) and cranial ones (O) for wolves (both sexes mixed). Bottom, hyperbolic regression of coefficient of variation on mean for dental traits and cranial ones traits for wildcats (both sexes mixed).

the cranial characters is 1.04% ($n = 37$); the median measurement error of the dental characters is 8.84% ($n = 22$), more than eight times larger.

For the wolves measured repeatedly, the mean CV for cranial characters was 5.38% (± 1.621 , $n = 37$), and the median was quite

TABLE 4. Measurement errors for wolf traits as estimated by within-group variance component as percent of total variance in a single-classification ANOVA (see text). vaD indicates von den Dreisch 1976.

Character	Percent error
vdD ₁	0.84
vdD ₂	6.85
vdD ₄	1.73
vdD ₇	1.05
vdD ₈	0.56
vdD ₉	0.79
vdD ₁₀	6.21
vdD ₁₁	0.39
vdD ₁₂	0.54
vdD ₁₇	4.35
vdD ₁₈	0.27
vdD ₁₉	5.16
vdD ₂₀	3.09
P ₂₋₄	0.73
vdD ¹	0.07
vdD ²	0.08
vdD ⁸	0.24
vdD ¹⁵	1.05
vdD ¹⁶	8.14
vdD ¹⁷	0.37
vdD ²²	9.86
vdD ^{22a}	23.40
vdD ²³	0.63
vdD ²⁹	12.16
vdD ³⁰	0.09
vdD ³¹	0.91
vdD ³²	0.02
vdD ³³	0.39
vdD ³⁴	1.58
vdD ³⁵	1.04
vdD ³⁶	0.95
MAM	2.42
MAT	7.36
MFL	1.63
OCPH	2.42
TFL	0.48
TRL	3.12
C ^{sup} L	4.52
C ^{sup} W	13.59
P ¹ L	47.55
P ² L	11.53
P ³ L	5.20
P ⁴ Le	1.62
P ⁴ Li	11.69
P ⁴ Wa	33.25
P ⁴ Wb1	9.85
M ¹ L	4.60
M ¹ winc	26.66
M ² L	45.77
M ² W	12.02
C _{inf} L	7.82
C _{inf} W	26.38
P ₂ L	5.02
P ₃ L	7.13
P ₄ L	5.08
M ₁ L	6.62
M ₁ W	5.93
M ₂ L	7.23
M ₃ L	21.32

close to the mean, indicating a nearly symmetrical distribution. For dental characters, the mean CV was larger: 6.72% (± 1.57 , $n = 22$). The difference, although small, was significant ($t = 2.11$, $p = 0.05$). (A t -test was used because the variances did not differ significantly.) "Adjustment" of CV by character size as a covariate within the two groups did not reduce the difference among the groups, which remained significant.

Covariation between Dental and Cranial Characters.—For the wolves, the three components (Table 2) explain 81.2% of the total variation; 71.3% was explained by the first component alone. For wildcats (Table 3), the first three components explain 75.3% of the total variation; the first component alone accounted for 56.3%. These data are further illustrated in Figure 2. For both wolves and wildcats, all characters have high positive loadings on the first principal component but differ in response to the second principal component: they form two separate clusters, one composed largely of dental characters (with positive scores) and the other composed wholly of cranial (non-dental) characters (with negative scores). There is little overlap between these two groups. Precisely the same pattern arose for both wolves and wildcats in each of the principal component analyses of the randomly selected halves of the characters: on the second principal component, two distinct clusters arose, one largely of dental traits and one wholly of cranial traits. The same is true for wildcat measurement vdD_5 , the length of the lower tooth row. The few other exceptions (vdD_{20} for wolves, vdD_{10} , vdD_{17} , vdD_{18} , vdD_{19} , vdD_{20} , vdD_{21} , vdD_{22} , vdD_{28} for wildcats) are also cranial characters clustering with the dental characters. For wildcats, though positive on the second component, vdD_{10} , vdD_{17} , vdD_{18} , and vdD_{19} are close to the cluster of cranial traits.

Variability of Vestigial Teeth.—Coefficients of variation taken on the putative vestigial teeth

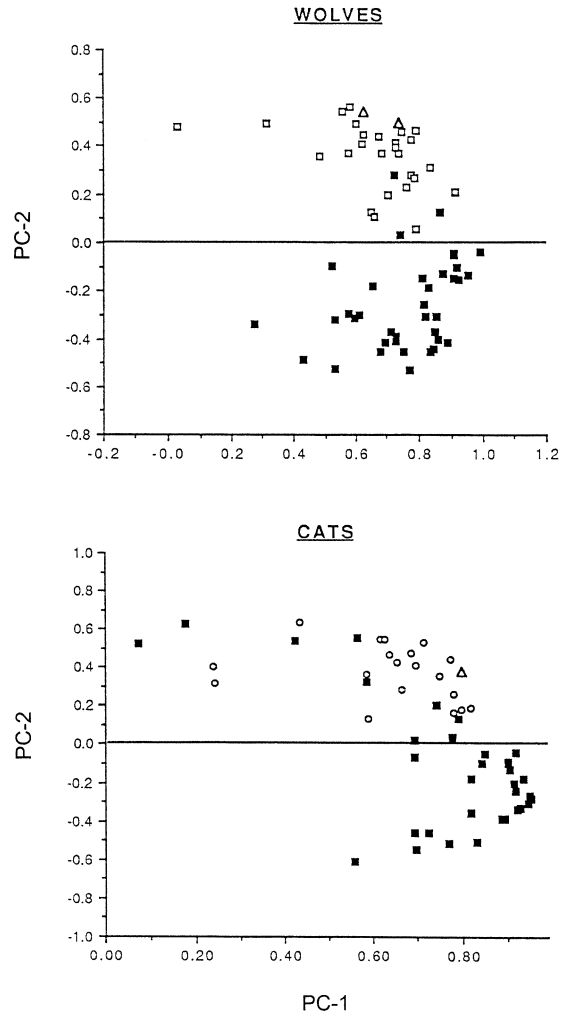


FIGURE 2. Top, character scores for dental (open squares) and cranial (closed squares) traits on first two principal components, for wolves of both sexes mixed. Open triangles represent two traits (lengths of upper and lower molar tooth rows) that, although cranial, are simply combined measures of dental traits because wolf molars have no spaces between them. Bottom, character scores for wildcat traits (symbols as for wolves) for both sexes mixed. Open triangle represents length of lower tooth row; there are no spaces between these teeth.

were larger than those of all other traits. Table 5 lists the five largest CVs, sorted from Tables 2 and 3. P^2L , P^2W , and M^1L lead the table for wildcat data; their CVs were twice the mean value. Among the wolf data, M_3L had the largest CV. Only two of these values were statistical outliers by Grubb's test. Dixon's test found no outliers, because the three top values, all very different from the others, were very similar and the test requires a large value

TABLE 5. Largest values of coefficients of variation (CV) for teeth, plus mean CV for all teeth, as well as character codes. M₃L for wolves and P²L, P²W, and M¹L for wildcats are considered vestigial and are marked by “v”.

Rank	Wolves			Wildcats		
	Males	Females	Both sexes	Males	Females	Both sexes
1	9.11 ^v	8.90	9.21	25.19 ^{*,v}	19.92 ^{*,v}	20.90 ^v
2	M ₃ L	C ^{sup} W	P ³ W	P ² L	M ¹ L	P ² L
	8.83	8.42	9.04 ^v	24.17 ^v	17.80 ^v	20.76 ^v
3	P ³ W	P ₄ W	M ₃ L	P ² W	P ² L	M ¹ L
	8.24	8.41 ^v	8.37	19.20 ^v	12.07	15.57 ^v
4	P ² W	M ₃ L	P ² W	M ¹ L	P ⁴ Wa	P ² W
	8.07	8.21	8.05	8.65	10.96	11.40
5	P ₄ W	P ³ W	C ^{sup} W	P ⁴ Wa	CinFL	CinFL
	7.34	7.88	8.03	7.60	10.91 ^v	10.51
Mean	P ⁴ Wa	P ² W	P ₄ W	CinFL	P ² W	P ⁴ Wa
	6.01	6.10	6.47	9.02	9.09	9.63

* $p < 0.05$, one-tailed Grubb's test.

of $y_3 - y_1$. However, the qualitative order of the CVs supports the conclusion that vestigial teeth are, in fact, the most variable.

Discussion

Variability of Dental and Cranial Characters.—Our results demonstrate a negative nonlinear relationship between the means and the coefficients of variation of the dental and cranial characters studied in wolves and wildcats. Teeth are generally smaller than cranial traits and are more variable on average. Exactly the same relationship obtains for the two weasel species.

If the difference in magnitude of CV between dental and cranial traits results from measurement error, then the mean CV among individuals within the two groups, particularly for dental characters, should be smaller in the repeated-measurements study. Using the mean of five measurements, rather than a single one, reduces random measurement variations among skulls. This should have had the effect of reducing the difference in mean CV between the two groups.

This reduction did not happen: both mean values of CV were larger in the measurement error study than in the previous one. (The difference may be due to the fact that a different person made the measurements, or to the particular selection of skulls for this study.) Thus dental characters are inherently more variable among individuals than cranial characters are (a pattern that would have been exacerbated

had we not omitted repeated measurements of seven traits), not only because of measurement error associated with their smaller size. Measurement error in the systems we studied seemed to us to be less a product of measurement size, and more a result of the particular structure of a morphological trait, the clearcut landmarks for measurement, its proximity to other characters (such as other teeth), the ease with which calipers can be placed, etc.

Moreover, the phenomenon of higher variability in teeth occurs in carnivores in a very wide spectrum of sizes. Wolf upper carnassials are three-fourths as long as the least weasel (*Mustela nivalis*) skull, yet within species (and sex) this general phenomenon obtains. Coefficients of variation of least weasel skull lengths (from Holmes 1987) resemble those of wolf and wildcat skull lengths and are much lower than those for wolf dental measurements of similar size. The range of variability for all traits of the different sexes and species is similar in spite of order-of-magnitude differences in absolute size.

An inverse relationship between mean and coefficient of variation has occasionally been noted in various studies for many years (e.g., Alpatov and Boschko-Stepanenko 1928; Bader and Hall 1960). Yablokov (1974) proposed as an empirical rule that, within one organ system of a population, characters of the same dimensionality tend to show a negative correlation between the mean and the CV. He demonstrated this phenomenon for a variety of lin-

ear dimensions of pinniped skulls, among other traits.

Pearson and Davin (1924) suggested a reason for this inverse hyperbolic relationship that was later developed by Lande (1977). Lande noted that for both bats (Bader and Hall 1960) and pinnipeds (Yablokov 1974) the CVs of composite measures are among the smallest. He suggested that this fact may result from a mathematical constraint when one compares the variation of a whole to that of its parts. The more parts in a morphological feature, the lower should be the CV (Lande 1977). Soulé (1982) suggested the term "allometric variation" for trends of variation attributable to changing numbers of components; his principle of allometric variation predicts an inverse relationship between the CV and the square root of size. In this formulation, Soulé (1982) equated greater size of the mean with higher complexity.

The mammalian jaw and skull result from the consolidation of a number of different parts with different embryological origins, controlling factors, and rates of growth (Atchley et al. 1985a,b). Viewing each such developmental unit as a part from which the whole is composed may explain the decrease of CV with size (increased size is usually equivalent to a greater number of developmental units). After all, Lande's (1977) explanation for this phenomenon rests on the fact that parts are correlated to some extent with one another; in the mammalian skull and jaw it is clear that the developmental trajectories of the various component parts have been extensively integrated during ontogeny (Atchley 1987), and this integration necessitates some correlation between them.

Pengilly (1984) ascribed the negative relationship between size and CV in fox dental measurements to the higher complexity of larger teeth. If larger and more complex teeth (with more roots and cusps) are indeed composed of a greater number of developmental units regulated perhaps by a greater number of genes, then they too may be expected to have reduced variability as compared with simple teeth. The developmental process of tooth formation is currently being unraveled (e.g., Jernvall 2000; Jernvall and Thesleff 2000;

Jernvall et al. 2000), and although analyses of gene expression patterns have revealed associations of many genes with tooth morphogenesis, it appears that genes involved in cusp development are the same among all individual cusps, and that, at the level of molecular signaling, all cusps are alike (Jernvall and Thesleff 2000). Jernvall (2000) concludes that the generation of mammalian cheek-tooth complexity may have required very little increase in developmental complexity. Species-specific cusp patterns form through reiterative addition of new secondary enamel knots within an existing tooth-crown base (Jernvall and Thesleff 2000), but it is difficult to see if the developmental process implies the kind of complexity that can be ascribed to cranial features.

Studying dental traits of the American marten (*Martes americana*) and the gray fox (*Urocyon cinereoargenteus*), Polly (1998a) argues that CV is likely to be strongly negatively correlated with size. This correlation, in his view, reflects a combination of the fact that CV is a ratio and the fact that measurement error is inevitable. Thus, as the mean size of a trait approaches zero, even if the standard deviation of that size were to approach zero, the measured standard deviation would not because it would include the omnipresent measurement error. This would be true even if measurement error were not a function of size. Because size, approaching zero, is in the denominator of CV, whereas SD, which does not approach zero, is in the numerator, at some point as size decreases, CV must increase. In short, Polly (1998a,b) saw the relationship of size and CV as artifactual, rather than as an indication of greater variability for smaller traits, and he believed that the artifact is particularly misleading in comparisons of variables differing in size by an order of magnitude (as teeth and cranial traits often do).

By inspection of the plots of his data, Polly (1998a) concluded that CVs can be used without fear of the artifactual relationship with size if the measurement error is less than 0.10. For the wolf skulls, all but two of the 36 cranial characters pass this test, but 11 of the 24 dental traits fail it. Thus, it is certainly possible that at least part of the generally greater variability

for teeth than for skulls in our study is an artifact of measurement error. However, we cannot conclude that this entire pattern reflects measurement error. Further, none of the alternative measures of variability suggested by Polly (1998a) solves the problem, because they all reside in his attempt to produce an ad hoc index that, with his data, shows no relationship of the index with size. But this approach is paradoxical. There may be a real relationship between size and variability, unrelated to measurement error, and our goal should be to reveal it rather than to obliterate it. Thus, *faute de mieux*, we follow many others (e.g., Hilborn and Mangel 1997) in continuing to use CVs, albeit with caution. As noted above, our regressions of CV on mean size left much variation in CV unexplained, and, over the joint size domain, there was no systematic tendency for residuals of the two sorts of traits to fall on different sides of the regression line or to differ in magnitude.

Teeth may still be extremely valuable in paleontology but not because they have low variability. In general, teeth are relatively more variable than cranial characters and in this respect are not the best diagnostic traits for distinguishing between closely related taxa. This pattern contradicts that implied in some of the paleontological literature. Moreover, the higher relative variability of teeth renders the prediction of population means on the basis of one or few dental measurements less accurate than a prediction based on one or few cranial characters.

Covariation between Dental and Cranial Characters.—For both wolves and wildcats, all cranial and dental characters score positively on PC1. The first principal component is often viewed as a size component, an interpretation that is rational if all loadings are positive and if they do not differ tremendously in magnitude (Jolicœur and Mosimann 1960; Bookstein 1989). These conditions are met by our data sets. Both data sets separate into two clusters on PC2, which can be interpreted as a “shape component” (Jolicœur and Mosimann 1960; Bookstein 1989). Such clustering is commonly interpreted as resulting from a functional linkage (e.g., Neff and Marcus 1980), or a genetic/developmental constraint within

each cluster. The facts that both wolf and wildcat data produced the same dichotomy, between most cranial traits on the one hand and all dental traits plus a few cranial ones on the other, and that each half of each data set produced the same dichotomy when analyzed alone, argue strongly that this pattern is not an artifact of having very many traits measured on relatively few specimens.

There is a growing number of multivariate morphological analyses of the developmental trajectories and morphological integration of the mammalian skull and jaw (e.g., Cheverud 1982, 1989, 1995, 1996; Atchley 1987; Zelditch 1988; Roth 1996; Cheverud et al. 1997). Studies of the interrelationships of dental characters and morphogenetic fields in mammalian dentitions have been common for many years (e.g., Butler 1939; Lombardi 1975; Osborn 1978), but the interface between mammalian teeth and skulls has received less attention. The notion that teeth and crania are under different genetic control is in no way heretical (Kieser and Groenvelde 1988, 1990; Shea and Gomez 1988; Kieser 1990). Also, the clustering of most cranial characters is not surprising. After all, although the mammalian skull and jaw result from the consolidation of a number of different parts with different embryological origins, controlling factors, and rates of growth (Atchley et al. 1985a,b), the developmental trajectories of the various component parts have been extensively integrated during ontogeny (Atchley 1987).

Teeth, on the other hand, may well be controlled by genetic factors other than those governing the cranium (cf. Shea and Gomez 1988). Teeth form spatially separate units, so an integration of dental characters similar to that for cranial characters is unnecessary. Nevertheless, we see here that dental traits do cluster. For adaptive evolution to proceed efficiently, traits that develop and function together should be morphologically integrated and inherited together (Cheverud 1982, 1995, 1996). This clustering could conceivably be ascribed to functional constraints: one might view the teeth as a functionally linked set of characters used for capturing, handling, and processing prey. If the issue were only functional integration, however, one might expect

a more complex relationship, in which cranial characters related to jaw musculature of mastication (such as temporal fossa length and the width of the zygomatic arch) cluster with the dentitions. We see no such clustering, so it appears that the functional link is outweighed by genetic correlations among dental characters and separate genetic correlations among cranial characters. The few cranial traits that cluster with the dental ones have no functional significance that explains this pattern.

Wolves and wildcats differ considerably in cranial morphology and killing behavior. The similarity in the results of our present analysis of these two species suggests the generality of the cranial and dental dichotomy outlined above. Similarly, Voss (1988), who carried out a PCA of 15 populations of ichthyomine rodents, found that the variables with the highest loadings on the principal shape component were teeth or measurements of interdental spaces. He suggested that this factor might represent a system of morphological integration within the masticatory apparatus, although he considered the possible participation of other functional influences. High loadings on the principal shape component can also be seen for cheek-tooth row lengths in muskrats (*Ondatra zibethicus*) (Pankakoski et al. 1987) and pocket gophers (*Thomomys bottae*) (Smith and Patton 1988).

Various studies have interpreted different patterns depicted by cranial and dental characters as resulting from differences in evolutionary rates (e.g., Marshall and Corruccini 1978; Van Valkenburgh 1988). Dental allometry in dwarfed lineages differs from the expected allometric relationship in some cases but not in others (e.g., Gould 1975; Prothero and Sereno 1982; Shea and Gomez 1988; Roth 1990), perhaps reflecting an extreme case of differences in evolutionary rates between dental and cranial traits. Other studies (Dayan et al. 1989a,b, 1990, 1992; Dayan and Simberloff 1994a,b) suggested the operation of different selective pressures on teeth and skulls. The separation of these two character sets on the second component is consistent with different selective regimes and different evolutionary rates for teeth and crania. Thus the relationship between tooth size and body size might

change both within and between species, depending on selective regimes, although a functional relationship between the two must be maintained.

Mammalian systematists base specific and subspecific designations, reflecting probable phylogenetic relationships, on various morphological characters, few of which are dental. On the other hand, the systematics and phylogenetic relationships of fossil mammals are largely based on dental material (e.g., Hussain 1971; West 1979; Schoch and Lucas 1981; Legendre 1982). Using different groups of characters that might be under different selective pressures may yield different results.

A clear resolution of the genetics of morphological integration is required (e.g., Kieser 1990; Hillson 1996). At this stage we simply suggest that variation in tooth size best estimates variation of size and shape of all teeth but provides a poorer estimate of the variation of cranial size. This observation accords well with the fact that, within species, although cranial size is apparently a good estimator of body weight (see Gould 1975; Janis 1990), tooth size sometimes is not (e.g., Damuth and MacFadden 1990; Fortelius 1990; Janis 1990).

Variability of Vestigial Teeth.—CV of the third lower molar of Israeli wolves, although high, is what would be expected on the basis of the general relationship between size and CV. Thus in terms of variability, there is no support for viewing this tooth as vestigial. Although its occlusion with the second upper molar may be simple (Gingerich and Winkler 1979), it does occlude with this tooth in what appears to be a fully functional manner, and it retains the pattern of its cusps.

By contrast, the high CVs of the second upper premolar and first upper molar of the wildcat are indeed outliers to the regression. These teeth are very small and are often missing entirely. The second upper premolar is especially small and is absent altogether in some felid species (Glass and Todd 1977). Even in species where this tooth occurs, an appreciable portion of the population lacks it (*Felis catus* [Searle 1959; Todd et al. 1974; Bateson 1894; cited in Glass and Todd 1977] and *Felis bengalensis* [Glass and Todd 1977]). Moreover, Glass and Todd (1977), who did not measure

sizes of second upper premolars in their study of *Felis bengalensis*, ranked them into four categories: rudimentary (present as a disorganized piece of enamel), through very small (single root and simple crown), small (suggestion of double root or crown), and medium sized (double root and/or double cusp). These observations suggest that this non-occluding tooth is indeed vestigial in wildcats.

Additionally, cats do not masticate meat (Romer 1953), and the peglike first upper molar does not occlude with any tooth of the lower jaw, so it serves no clear function. The extreme variability of these teeth conforms well to their apparent lack of (or extremely reduced) function.

The importance of understanding the relationships between size and variability prior to drawing evolutionary or selective inferences is obvious. In particular, one should bear in mind that vestigial teeth are reduced (e.g., Kurtén 1953) and therefore also may be the most variable on size grounds alone. It is essential to separate these two effects.

Conclusions

Teeth are usually the best-preserved element of fossil vertebrate remains and are highly diagnostic in mammals, so their importance to paleontological, systematic, and evolutionary research cannot be overemphasized. Because of their central role, the study of teeth must be conducted with a clear understanding of their variability and relationships to other characters.

Teeth are generally more variable than cranial characters in carnivores; this is not just a reflection of measurement error. Thus, although teeth are extremely valuable for paleontological research, their value does not reside in low variability. In terms of their variability, teeth are not the best taxonomically diagnostic character at the species level. Nevertheless, studying the extreme case of vestigial teeth clearly confirms that natural selection affects patterns of variability. Results of the principal components analysis show that dental and non-dental traits largely separate on the shape factor. This separation may well reflect the different selective pressures operating on skulls and teeth, as well as dif-

ferent genetic constraints. Thus the functional/developmental integration of teeth and skulls may be loose enough to allow different patterns of covariation in different conspecific populations, as well as among ecologically similar species.

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