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Variation and correlation patterns in the dentition of the red fox from Poland

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Analysis of variation in tooth size in a population of red fox, *Vulpes vulpes* (Linnaeus, 1758) from Poland based on three indices (coefficient of variation CV, variation index V_{SD}, residual standard deviation R_{SD}) and its correlation with average tooth size revealed two contradictory patterns. The CV and V_{SD} were significantly correlated with average tooth sizes, while R_{SD} values was independent. It was, therefore, concluded that R_{SD} is the most reliable index for assessing population variation. The least variable position in the red fox dentition are M^1 and M_1, whereas the most variable is M_3. The strongest sexual dimorphism in tooth size in Polish red foxes is observed in the canines. The strongest between-tooth correlations were in the premolar region. Moreover, a strong correlation in both tooth length and tooth width was found between opposite canines. Both functional and developmental factors determine patterns of morphological variation in the dentition.

1. Introduction

Variation in mammalian dental characters has previously been analyzed using the coefficient of variation CV, where CV = SD × 100/*M* (e.g. Van Valen 1962, Yablokov 1974, Gould & Garwood 1969, Gingerich 1974, Gingerich & Schoeninger 1979, Gingerich & Winkler 1979, Pengilly 1984). Often a negative correlation between a tooth size and its coefficient of variation have been observed, usually explained by the influence of factors such as functional integration or developmental fields. Polly (1998) showed that the negative correlation may in fact be an artefact of the CV metric rather than a biological phenomenon. The author proposed alternative methods for assessing variation. Polly (1998) suggests that when comparing traits of significantly different sizes, assessment of differences in trait variation cannot be base solely on a single method. The traditional coefficient of variation CV and two other measures of variability proposed by Polly (1998) were used in this study to analyze dental variation patterns in the red fox from Poland.

Gingerich and Winkler (1979) and Pengilly (1984) in their studies of dental variation in red foxes showed that the most variable teeth are located at the boundaries of morphogenetic fields, whereas the least variable teeth (carnassials) are located more centrally. According to Gingerich and Winkler (1979), the pattern of dental variation reflects functional integration. Contrary to that, on the grounds of a statistically significant negative relationship between the CV and mean tooth size, Pengilly (1984) ascertained that the variation pattern was a direct consequence of a developmental process. Correlation patterns observed in two different red fox populations (Kurtén 1953, Gingerich & Winkler 1979) did not confirm the pattern of integration expected from the pattern of variation in this predator. The strongest correlations observed within the dentition were between non-occluding premolars rather than functionally integrated molars (Kurtén 1953, Gingerich & Winkler 1979).

In red foxes from Finland and Kökar Island, statistically significant *r* correlations were observed between teeth in the carnassial region (Kurtén 1953). The partial correlations of traits in the same region were only weakly correlated in foxes from the Upper Peninsula of Michigan (Gingerich & Winkler 1979). In Pengilly's opinion (1984) neither variation nor morphological integration are the direct result of functional integration, but rather the manifestation of developmental factors.

The aim of the present study was: (1) to determine patterns of dental variation and correlation in red foxes from Poland, and (2) to determine the factors responsible for those patterns.

2. Material and methods

In this study, the permanent dentitions of 1 453 specimens of the red fox *Vulpes vulpes* (Linnaeus, 1758) from Poland were examined. The sample included 637 males, 535 females, and 281 individuals of unknown sex. The red fox skulls are housed in the collections of the Mammal Research Institute of the Polish Academy of Sciences in Białowieża (MRI, 959 individuals) and the Institute of the Systematics and Evolution of Animals of the Polish Academy of Sciences in Cracow (ISEA, 494 individuals). Differences between total number of individuals and the number reported in tables and figures are due to various instances of skulls damage, missing teeth, or heavy wear.

2.1. Measurements

Teeth were measured with a Sylvac digital calliper and to the nearest 0.05 mm. The upper and lower teeth of both the left and right sides were measured (91 measurements were taken on each specimen). The length and width of each tooth and the heights of the canines were measured as follows (Fig. 1):

LI^1, LI^2, LI^3, LI_1, LI_2, LI_3 — length of the crown of I^1, I^2, I^3, I_1, I_2, I_3: the greatest mesio-distal distance on the tooth crown;

WI^1, WI^2, WI^3, WI_1, WI_2, WI_3 — width of the crown of I^1, I^2, I^3, I_1, I_2, I_3: the greatest labio-lingual distance on the tooth crown;

LC^1, LC_1 — length of the crown of C^1, C_1: the greatest mesio-distal distance at the base of the tooth crown;

WC^1, WC_1 — width of the crown of C^1, C_1: the greatest labio-lingual distance at the base of the tooth crown;

HC^1, HC_1 — height of the crown of C^1, C_1: the greatest distance between the occlusal tip and the distalmost (*i.e.*, posterior-most) point of the base of the tooth crown;

LP^1, LP^2, LP^3, LP_1, LP_2, LP_3, LP_4 — length of the crown of P^1, P^2, P^3, P_1, P_2, P_3, P_4: the greatest length between the anterior and posterior (mesial and distal) points of the tooth crown;

WP^1, WP^2, WP^3, WP_1, WP_2, WP_3, WP_4 — width of the crown of P^1, P^2, P^3, P_1, P_2, P_3, P_4: the greatest width between the lingual and buccal points of the tooth crown;

LP^4b — buccal length of the crown of P^4: the greatest length between the anteriormost point of the antero-buccal lobe of the tooth crown and the distalmost point;

LP^4l — lingual length of the crown of P^4: the greatest length between the anteriormost point of the antero-lingual lobe of the tooth crown and the distalmost point;

WP^4 — width of the crown of P^4: the greatest distance between the lingual and buccal points of the tooth crown measured perpendicular to LP^4b;

LM^1, LM^2, LM_1, LM_2, LM_3 — length of the crown

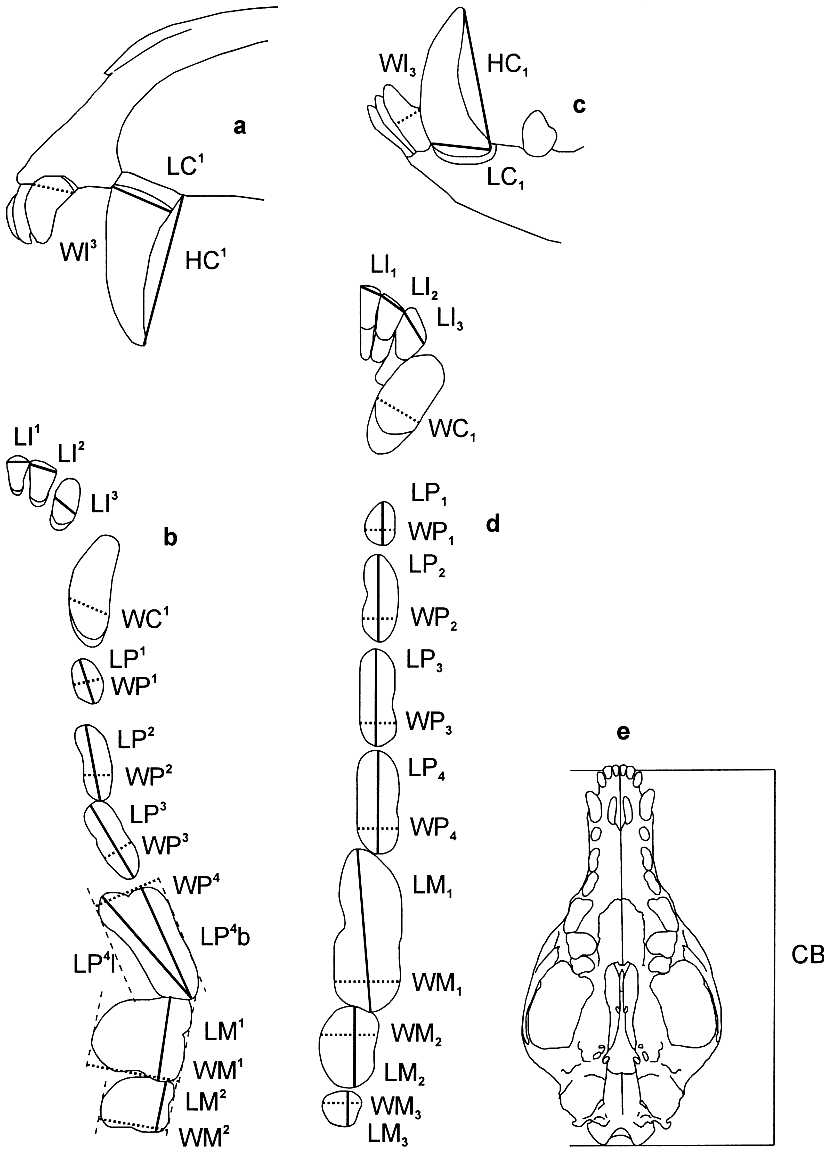

Fig. 1. The methods of measurements execution illustrate the following diagrams: the anterior part of the upper dental arch in lateral view (a), the upper dental arch in occlusal view (b), the anterior part of the lower tooth row in lateral view (c), the lower dental arch in occlusal view (d), and ventral view of the skull (e).

of M^1, M^2, M_1, M_2, M_3: the greatest distance between the anterior and posterior (mesial and distal) points of the tooth crown;

WM^1, WM^2, WM_1, WM_2, WM_3 — width of the crown of M^1, M^2, M_1, M_2, M_3: the greatest distance between the lingual and buccal points of the tooth crown;

CB — condylobasal length of the skull: the greatest distance between the line connecting the most distal points of the occipital condyles and the line connecting the anteriormost points of the premaxillary bones.

2.2. Statistical methods

Statistical analyses of the data were performed with Statgraphics (ver. 5.0) and Systat (ver. 5.0). The following tests were done: descriptive statistics, *t*-test, Duncan test, multifactorial analysis of variance (MANOVA), simple regression analysis, residual regression and the Pearson coefficient of correlation.

Descriptive statistics (arithmetic mean and standard deviation) and the analysis of variance were done using only measurements from the right

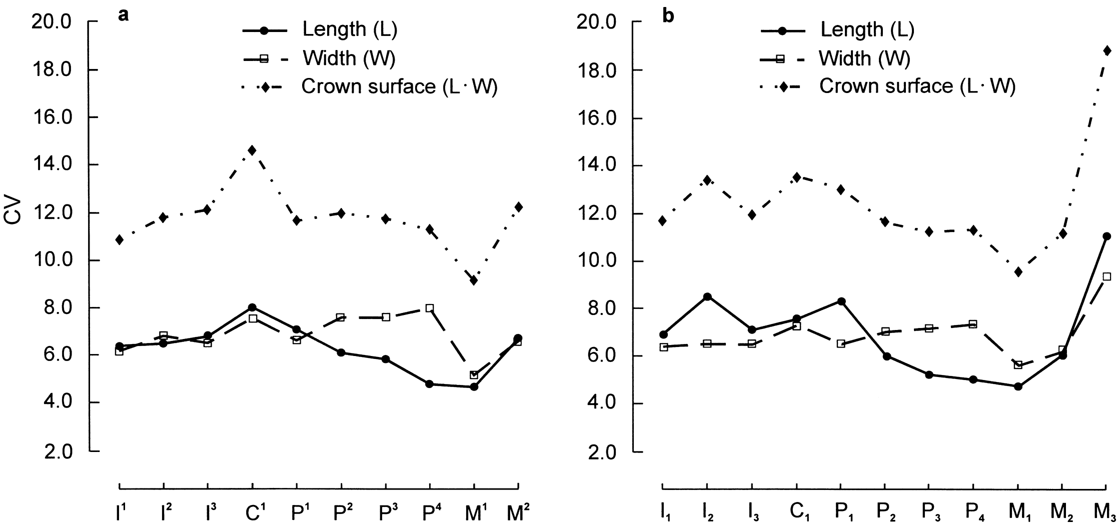

Fig. 2. Distribution of the coefficient of variability CV for tooth length, width and occlusal surface in the upper (a) and lower (b) dentition in the red fox (*Vulpes vulpes*) from Poland.

side of the dentition. In order to fully assess patterns of variation, three different indices were used following Polly (1998) — the coefficient of variation CV, the standard deviation of log transformed variables, and the residual standard deviation.

Occlusal surface variation was compared with the natural log of the product of length times width of each tooth (ln (L × W)). The coefficient of variation was estimated from the standard deviation of this metric (Lewontin 1966).

The relationships between mean tooth size and tooth variability and between variability and tooth eruption sequence were analysed using linear regression. The eruption sequence of permanent teeth determined by Linhart (1968) was used in the latter.

The following multivariate analyses were used to study patterns of correlation in the dentition: correlation between tooth lengths in the upper and in the lower tooth rows, correlation between tooth widths in the upper and in the lower tooth rows, correlation between tooth lengths from opposite tooth rows, correlation between tooth widths from opposite tooth rows. The correlation between all variables and condylobasal skull length was also studied.

2.3. Abbreviations

CV = coefficient of variation
F = the square root of the *t* statistics
M = the arithmetic mean
M_m/M_f = coefficient of dimorphism (division of the arithmetic mean for males by the homologous mean for females)
r = Pearson's correlation coefficient
r^2 = coefficient of determination (square root of *r*)
R_{SD} = residual standard deviation (the residual value for each variable after the standard deviation is regressed onto mean)
V_{SD} = variation index (the product of SD × 100 on log transformed data)

3. Results

3.1. Variation in tooth measurements

The CV for tooth measurements in red foxes from Poland ranged from 4.7 (LP^4l) to 11.1 (LM_3). The teeth with the lowest CV for both length and width were M^1 and M_1, whereas with the highest, M_3 (Table 1). The distribution of CV for the crown length and width measurement are presented in Fig. 2.

The CV for occlusal surfaces of maxillary teeth ranged from 9.2 (M^1) to 14.6 (C^1), while in mandibular teeth it ranged from 9.6 (M_1) to 18.9 (M_3) (Fig. 2). The pattern of variation indicated by V_{SD} was almost identical (Figs. 2 and 3).

The pattern of variation indicated by R_{SD} was quite different (Fig. 4). Among crown lengths in the upper dentition, C^1 showed the greatest variation and M^1 the lowest. The main differences in the patterns shown by R_{SD} *versus* CV and V_{SD} were in the incisor and premolar regions. According to the later two indices, the incisor region was more variable than the premolar one, but the residual SD analysis indicated that the premolar region was more variable.

Residual SD for tooth lengths in the mandible ranged from –0.114 (M_1) to 0.138 (M_3). A very high value of R_{SD} was also found for LC_1 (0.121).

In crown widths, the residual SD analysis also revealed a different pattern of variation than did either CV or V_{SD}. WP^4 had the highest variation and WM^1 the lowest. Comparatively high values were also found for WC^1 and WP^1, whereas the width of incisors was relatively low (ranging from 0.020 to –0.049). The range of R_{SD} values for tooth widths in the mandible was –0.043 (P_1) to 0.058 (M_3). According to this index, there were two points of heightened variability with the other two, WC_1 and WP_4 (if the hyper-variable WM_3 is excluded).

A regression of CV on the mean character size showed a significant inverse relationship ($r^2 = 0.30$, $F = 18.17$, $p < 0.001$; Fig. 5). A regression of V_{SD} on M for log transformed data also showed a significant inverse correlation ($r^2 = 0.28$; $F = 16.83$, $p < 0.001$). R_{SD} was necessarily uncorrelated with M since it is the residual of the regression on M ($r^2 = 7.11 \times 10^{-8}$, $F = 0.3 \times 10^{-5}$, $p > 0.05$; Fig. 6).

There was a linear relationship between the tooth eruption time and CV for the occlusal surface, which is described by the equation $y = 0.44x + 4.34$ ($r^2 = 0.31$, $F = 8.62$, $p < 0.001$; Fig. 7). A regression of V_{SD} of tooth lengths onto the eruption time did not indicate a correlation, however $y = 0.16x + 3.72$, $r^2 = 0.07$, $F = 1.53$, $p > 0.05$. Residual SDs for tooth lengths were also not cor-

Table 1. Descriptive statistics for measurements (mm) of the dentition and skulls of the red fox (*Vulpes vulpes*) from Poland; *n* = number of specimens, *M* = average of measurement, SD = standard deviation, CV = coefficient of variation.

Measure	*n*	min.–max.	*M*	SD	CV
LI^1	949	2.06–3.26	2.69	0.17	6.4
WI^1	1180	2.14–3.40	2.82	0.17	6.2
LI^2	948	2.37–3.96	3.01	0.20	6.5
WI^2	1225	2.46–4.06	3.24	0.22	6.8
LI^3	1190	2.75–4.67	3.65	0.25	6.8
WI^3	1311	2.63–4.85	3.91	0.25	6.5
LC^1	1052	5.22–9.85	6.71	0.53	8.0
WC^1	1166	3.29–5.57	4.32	0.33	7.6
HC^1	733	13.38–20.20	17.02	1.08	6.4
LP^1	1199	3.62–6.05	4.75	0.34	7.1
WP^1	1248	2.09–3.73	2.76	0.18	6.6
LP^2	1319	6.73–10.41	8.70	0.53	6.1
WP^2	1348	2.33–3.82	3.10	0.24	7.6
LP^3	1334	7.16–11.69	9.38	0.54	5.8
WP^3	1359	2.55–4.13	3.28	0.25	7.6
LP^4b	1339	11.41–16.02	13.54	0.67	4.9
WP^4	1363	4.98–9.64	6.79	0.54	8.0
LP^4l	1305	12.36–17.80	15.09	0.72	4.7
LM^1	1314	8.21–11.37	9.78	0.46	4.8
WM^1	1352	9.12–13.73	11.55	0.61	5.3
LM^2	1287	4.02–7.27	5.78	0.39	6.7
WM^2	1364	6.26–11.36	8.72	0.58	6.6
LI_1	831	1.50–2.25	1.87	0.13	6.9
WI_1	1194	1.91–2.99	2.40	0.15	6.4
LI_2	751	2.01–3.24	2.56	0.22	8.5
WI_2	1246	2.25–3.70	2.95	0.19	6.5
LI_3	646	2.69–4.44	3.61	0.25	7.1
WI_3	1285	2.41–4.08	3.38	0.22	6.5
LC_1	1155	6.00–9.77	7.79	0.59	7.6
WC_1	1178	3.35–5.66	4.51	0.33	7.3
HC_1	828	12.52–18.30	15.51	0.99	6.4
LP_1	1122	2.87–5.18	3.92	0.32	8.3
WP_1	1219	1.95–3.06	2.51	0.16	6.5
LP_2	1273	6.50–10.01	8.36	0.50	6.0
WP_2	1335	2.48–4.34	3.15	0.22	7.0
LP_3	1329	7.33–10.77	9.09	0.48	5.3
WP_3	1356	2.55–4.37	3.30	0.24	7.2
LP_4	1357	7.94–11.06	9.58	0.48	5.1
WP_4	1381	3.01–5.03	4.05	0.30	7.4
LM_1	1303	12.87–18.03	15.42	0.74	4.8
WM_1	1303	4.87–7.51	5.98	0.34	5.6
LM_2	1271	5.57–8.68	7.35	0.44	6.1
WM_2	1301	4.14–6.79	5.48	0.34	6.3
LM_3	1131	2.11–4.91	3.47	0.39	11.1
WM_3	1178	2.15–4.46	3.08	0.29	9.4
CB	1223	116.70–160.54	141.32	6.31	4.5

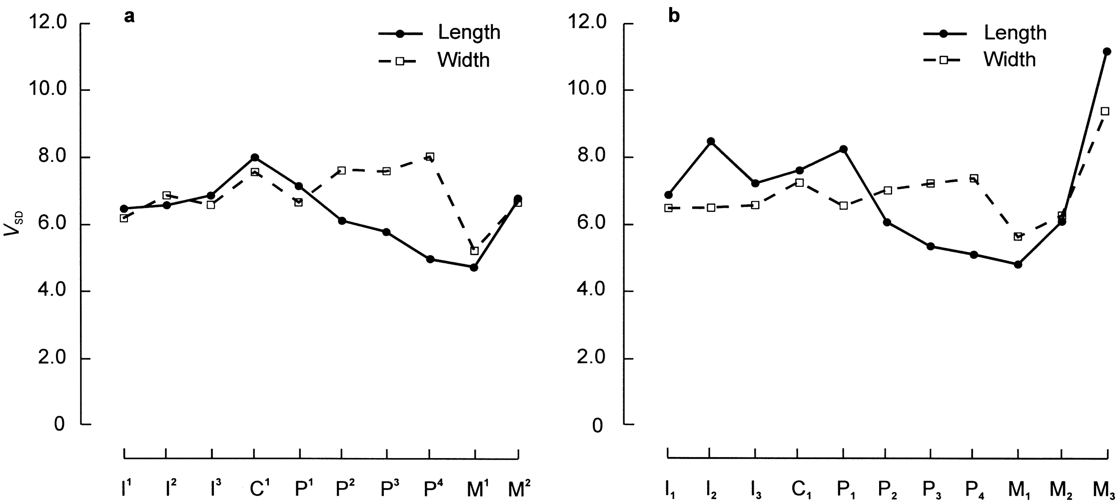

Fig. 3. Distribution of the V_{SD} index for tooth length and width in the upper (a) and lower (b) dentition in the red fox (*Vulpes vulpes*) from Poland.

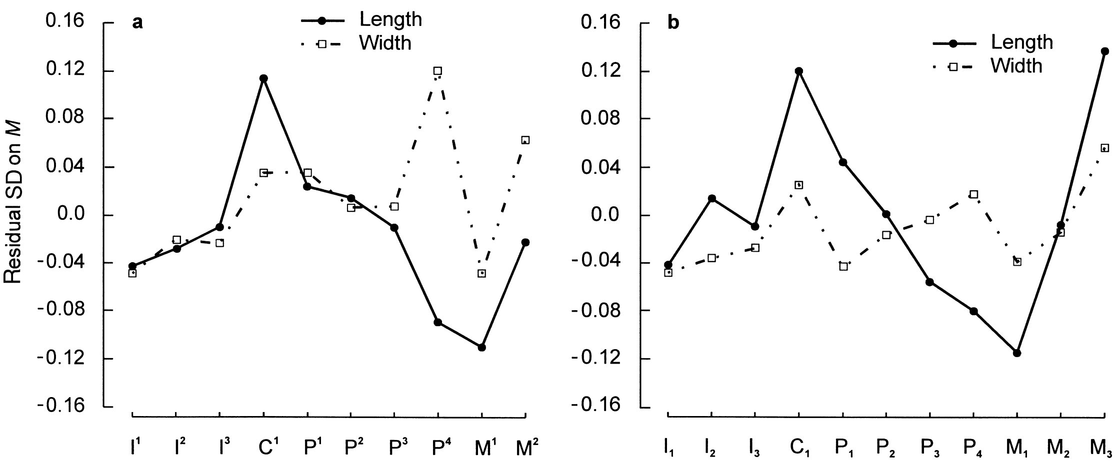

Fig. 4. Distribution of the R_{SD} index for tooth length and width in the upper (a) and lower (b) dentition in the red fox (*Vulpes vulpes*) from Poland.

related with the eruption sequence ($r^2 = 0.14$, $F = 3.0$, $p > 0.05$; Fig. 8).

3.2. Sexual dimorphism

In males and females the size ranges of each teeth overlap extensively, sometimes with identical means. Usually, however, the female mean was lower than the male one with a significance of $p < 0.001$. The only exceptions were LP_1 and LM_3 which were not significantly larger in males ($p > 0.1$), although the width of M_3 were smaller in females ($p < 0.01$; Table 2).

The M_m/M_f index ranged from 1.01 to 1.08. The largest difference between males and females was in the canines (from 1.06 to 1.08; Table 2).

In both groups, the patterns of tooth size variation as indicated by CV were similar (Fig. 9). It was ascertained that the average CV for all dental traits was insignificantly higher in females (6.56) than in males (6.49; $p > 0.05$).

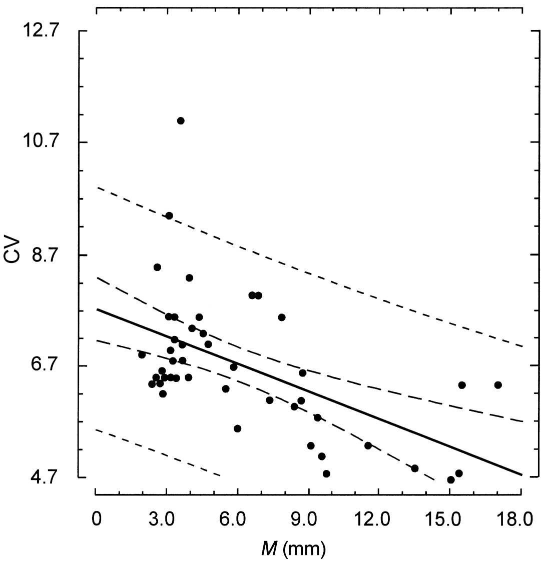

Fig. 5. Linear regression of the coefficient of variability (CV) on the mean tooth measurements (*M*) in the red fox (*Vulpes vulpes*) from Poland. Regression line is described by the following equation: $y = -0.16x + 7.73$. The broken lines indicate 99% and 95% confidence intervals.

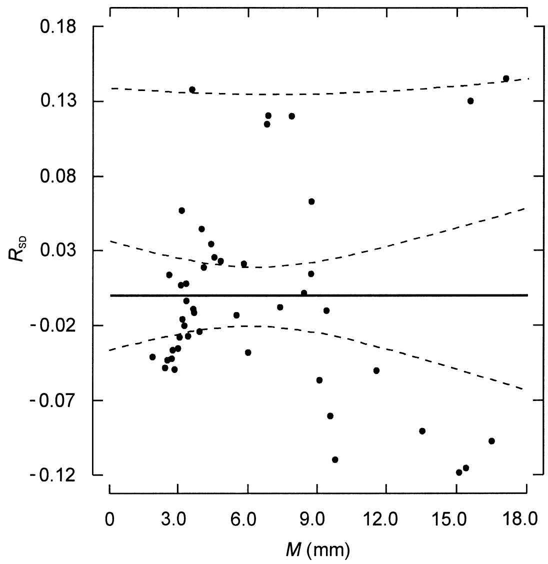

Fig. 6. Linear regression of the residual SD (R_{SD}) on the mean tooth measurements (*M*) in the red fox (*Vulpes vulpes*) from Poland. Regression line is described by the following equation: $y = -4.27 \times 10^{-6}x + 7.10 \times 10^{-5}$. The broken lines indicate 99% and 95% confidence intervals.

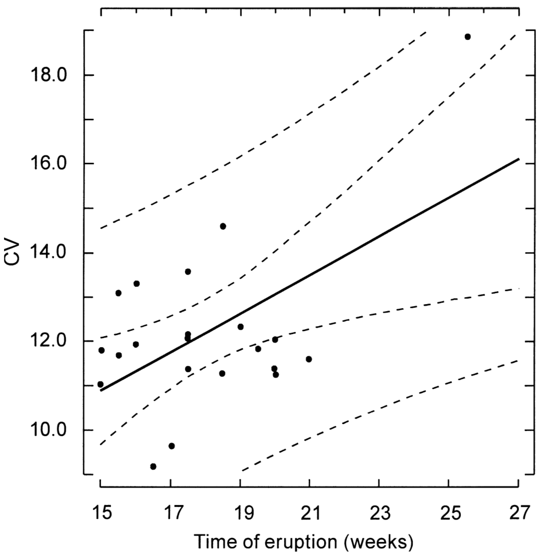

Fig. 7. Linear regression of the coefficient of variability (CV) for occlusal crown surfaces (natural logarithm of the tooth length and width product) on the dental eruption time in the red fox (*Vulpes vulpes*) from Poland. Regression line is described by the following equation: $y = 0.44x + 4.34$. The broken lines indicate 99% and 95% confidence intervals.

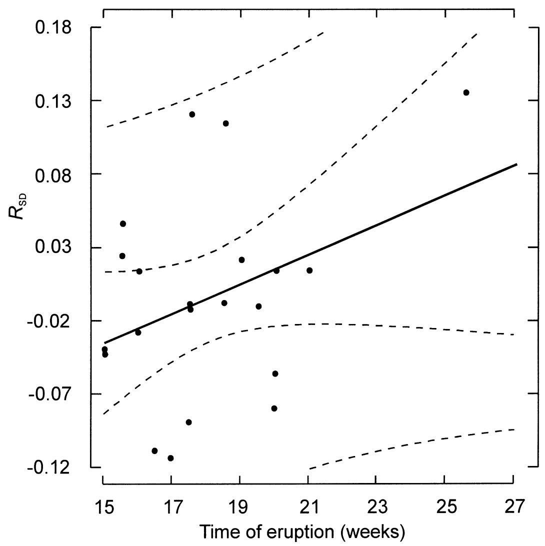

Fig. 8. Linear regression of the residual SD (R_{SD}) for averages of tooth lengths on the dental eruption time in the red fox (*Vulpes vulpes*) from Poland. Regression line is described by the following equation: $y = 0.01x - 0.19$. The broken lines indicate 99% and 95% confidence intervals.

3.3. Correlation

In the upper dental arch the strongest correlation of crown lengths was observed in the following pairs: P^2-P^3 ($r = 0.83$) and P^3-P^4 ($r = 0.71$) (Table 3). In the lower dental arch the most highly correlated lengths were in the premolar region, i.e.: P_2-P_3 ($r = 0.85$), P_3-P_4 ($r = 0.85$) and P_2-P_4 ($r = 0.81$)

Table 2. Descriptive statistics for tooth length and width (mm) in females and males of the red fox (*Vulpes vulpes*) from Poland.

Measure	Males					Females					M_m/M_f
	n	min.–max.	*M*	SD	CV	*n*	min.–max.	*M*	SD	CV	
LI^1	447	2.06–3.26	2.72	0.17	6.4	331	2.16–3.06	2.65	0.17	6.4	1.03
WI^1	534	2.29–3.35	2.86	0.17	6.0	427	2.14–3.28	2.77	0.16	5.8	1.03
LI^2	446	2.42–3.96	3.05	0.19	6.2	326	2.37–3.73	2.96	0.19	6.5	1.03
WI^2	555	2.63–4.06	3.30	0.21	6.4	444	2.46–3.76	3.15	0.20	6.2	1.05
LI^3	541	2.83–4.67	3.70	0.24	6.6	432	2.75–4.44	3.58	0.25	6.9	1.03
WI^3	585	3.13–4.85	3.99	0.24	6.0	481	3.07–4.65	3.82	0.24	6.3	1.04
LC^1	468	5.44–9.85	6.92	0.52	7.5	396	5.22–8.24	6.46	0.47	7.3	1.07
WC^1	528	3.60–5.57	4.47	0.30	6.7	428	3.29–5.10	4.15	0.27	6.6	1.08
HC^1	341	14.87–20.20	17.43	0.98	5.6	260	13.38–19.57	16.51	0.98	5.9	1.06
LP^1	527	3.85–5.80	4.81	0.34	7.1	450	3.62–6.02	4.68	0.33	7.0	1.03
WP^1	554	2.33–3.73	2.81	0.18	6.4	465	2.09–3.24	2.71	0.17	6.3	1.04
LP^2	584	7.47–10.41	8.84	0.51	5.8	486	6.73–10.07	8.54	0.51	5.9	1.03
WP^2	598	2.51–3.82	3.16	0.23	7.3	498	2.33–3.77	3.03	0.22	7.4	1.03
LP^3	581	7.16–11.69	9.54	0.52	5.5	502	7.61–10.98	9.20	0.51	5.5	1.04
WP^3	600	2.75–4.13	3.35	0.24	7.3	506	2.55–4.09	3.20	0.24	7.4	1.05
LP^4b	593	11.93–16.02	13.77	0.66	4.8	488	11.41–14.93	13.28	0.58	4.4	1.04
WP^4	602	5.08–8.87	6.96	0.53	7.6	504	4.98–8.26	6.61	0.50	7.5	1.05
LP^4l	580	13.32–17.80	15.36	0.69	4.5	478	12.36–16.96	14.80	0.64	4.3	1.04
LM^1	571	8.68–11.27	9.90	0.46	4.7	483	8.21–11.37	9.63	0.42	4.4	1.03
WM^1	582	9.88–13.73	11.75	0.58	4.9	506	9.84–13.58	11.35	0.56	4.9	1.03
LM^2	560	4.66–7.27	5.85	0.39	6.7	480	4.02–6.72	5.70	0.37	6.6	1.03
WM^2	595	7.20–11.36	8.84	0.57	6.5	510	6.96–10.50	8.57	0.55	6.5	1.03
LI_1	386	1.52–2.25	1.89	0.13	6.7	292	1.50–2.21	1.83	0.12	6.8	1.03
WI_1	533	1.92–2.99	2.44	0.15	6.1	439	1.91–2.80	2.35	0.15	6.2	1.04
LI_2	339	2.12–3.17	2.60	0.22	8.4	268	2.01–3.17	2.54	0.22	8.9	1.02
WI_2	548	2.36–3.70	2.98	0.19	6.5	459	2.25–3.70	2.91	0.19	6.5	1.02
LI_3	305	2.84–4.44	3.66	0.24	6.5	223	2.69–4.18	3.55	0.27	7.6	1.03
WI_3	564	2.84–4.06	3.44	0.21	6.0	478	2.65–3.91	3.31	0.21	6.2	1.04
LC_1	524	6.23–9.77	7.97	0.55	6.9	415	6.00–9.23	7.54	0.56	7.4	1.06
WC_1	528	3.81–5.66	4.64	0.30	6.4	428	3.35–5.27	4.34	0.27	6.2	1.07
HC_1	389	13.36–18.30	15.91	0.88	5.5	287	12.52–17.75	15.01	0.87	5.8	1.06
LP_1	504	3.11–4.92	3.94	0.31	7.9	420	2.87–5.18	3.91	0.34	8.6	1.01
WP_1	549	1.99–3.06	2.55	0.16	6.4	452	1.95–2.91	2.47	0.15	6.3	1.03
LP_2	570	6.84–10.01	8.49	0.49	5.7	470	6.50–9.34	8.18	0.47	5.8	1.04
WP_2	598	2.63–4.34	3.22	0.21	6.7	495	2.48–3.85	3.08	0.21	6.8	1.04
LP_3	587	7.67–10.77	9.24	0.46	5.0	495	7.33–10.19	8.91	0.44	5.0	1.04
WP_3	603	2.78–4.20	3.37	0.23	6.8	500	2.55–4.37	3.23	0.23	7.2	1.04
LP_4	602	8.40–11.06	9.73	0.46	4.8	498	7.94–10.62	9.39	0.44	4.7	1.04
WP_4	611	3.33–5.03	4.13	0.29	6.9	510	3.01–4.78	3.96	0.29	7.4	1.04
LM_1	574	13.69–18.03	15.67	0.69	4.4	483	12.87–17.94	15.15	0.68	4.5	1.03
WM_1	573	5.12–7.51	6.08	0.34	5.5	488	4.87–6.84	5.88	0.31	5.4	1.03
LM_2	564	5.57–8.68	7.41	0.46	6.3	466	5.61–8.34	7.27	0.42	5.8	1.02
WM_2	572	4.62–6.79	5.53	0.36	6.5	477	4.14–6.42	5.40	0.32	5.9	1.02
LM_3	506	2.11–4.83	3.50	0.39	11.1	419	2.58–4.91	3.46	0.38	11.1	1.01
WM_3	523	2.23–4.46	3.12	0.29	9.3	440	2.15–4.13	3.06	0.29	9.6	1.02
CB	562	122.90–160.54	144.66	5.42	3.7	445	116.70–154.94	137.83	5.38	3.9	1.05

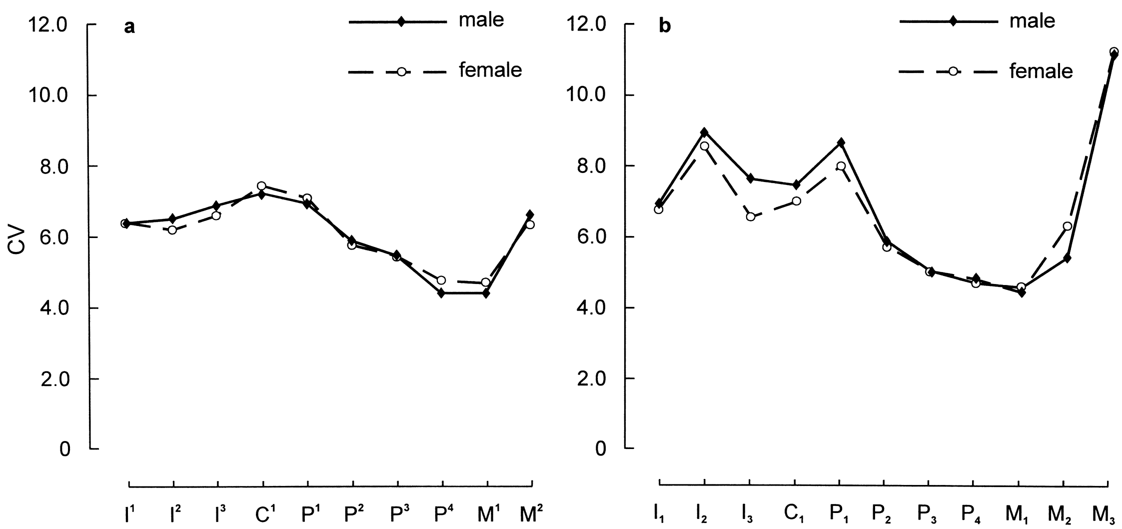

Fig. 9. Distribution of the coefficient of variability CV for tooth lengths in the upper (a) and lower (b) dentition in females and males of the red fox (*Vulpes vulpes*) from Poland.

(Table 3).

In the maxillary tooth row the crown widths were strongly correlated in pairs: P^2-P^3 ($r = 0.85$), I^1-I^2 ($r = 0.78$) and I^2-I^3 ($r = 0.75$) (Table 4). The strongest correlations between tooth widths in the mandibular tooth row were: P_2-P_3 ($r = 0.87$), P_3-P_4 ($r = 0.82$), P_2-P_4 ($r = 0.78$), I_1-I_2 ($r = 0.73$) (Table 4).

The strongest relationships were observed in occluding tooth pairs. Among those, the strongest correlations of lengths were: P^3-P_3 ($r = 0.85$), P^2-P_2, P^3-P_2 ($r = 0.82$), P^2-P_3 ($r = 0.81$), P^3-P_4 ($r = 0.80$), C^1-C_1, P^4-M_1 ($r = 0.76$), M^1-M_1 ($r = 0.75$), P^4-P_4 ($r = 0.73$) and P^4-P_3 ($r = 0.72$) (Table 5). In the remaining pairs of occluding teeth the power of reciprocal correlations of tooth lengths was considerable ($0.51 < r < 0.70$) or moderate ($0.31 < r < 0.50$) (Table 5). The r coefficient for crown lengths in opposite but non-occluding tooth pairs had a very broad range (0.74–0.10). The strongest correlations were found in pairs LP^4-LP_2 and LP_4-LP^2, while extremely low in pairs LM_3-LP^2 and LM_3-LI^3 (Table 5).

The correlation for widths of the teeth from opposite tooth rows was strongest in the following pairs: C^1-C_1, P^2-P_2 ($r = 0.84$), P^2-P_3 ($r = 0.81$), P^3-P_2 ($r = 0.80$), P^3-P_3 ($r = 0.79$), P^1-P_1 ($r = 0.74$), P^3-P_4 ($r = 0.73$), P^2-P_4 ($r = 0.71$) (Table 6). The

Table 3. Correlations (r) of tooth length for each pair of teeth within the upper dentition (upper triangular matrix) and lower dentition (lower triangular matrix) in the red fox (*Vulpes vulpes*) from Poland.

			I^1	I^2	I^3	C^1	P^1	P^2	P^3	P^4	M^1	M^2	CB	
I_1	0.47			0.62	0.44	0.35	0.44	0.43	0.42	0.46	0.39	0.29	0.44	I^1
I_2	0.22	0.49			0.57	0.49	0.50	0.42	0.46	0.51	0.49	0.34	0.48	I^2
I_3	0.42	0.43	0.39			0.58	0.54	0.49	0.55	0.50	0.50	0.35	0.46	I^3
C_1	0.62	0.40	0.21	0.45			0.54	0.64	0.66	0.59	0.52	0.40	0.68	C^1
P_1	0.33	0.39	0.34	0.39	0.41			0.60	0.68	0.53	0.54	0.38	0.51	P^1
P_2	0.69	0.43	0.24	0.49	0.63	0.49			0.83	0.70	0.54	0.35	0.64	P^2
P_3	0.72	0.42	0.25	0.41	0.63	0.43	0.85			0.71	0.55	0.40	0.69	P^3
P_4	0.66	0.41	0.23	0.50	0.61	0.42	0.81	0.85			0.66	0.40	0.66	P^4
M_1	0.60	0.45	0.26	0.45	0.60	0.42	0.65	0.67	0.70			0.60	0.58	M^1
M_2	0.48	0.21	0.16	0.25	0.30	0.23	0.40	0.41	0.40	0.43			0.46	M^2
M_3	0.28	0.22	0.22	0.17	0.17	0.19	0.12	0.15	0.10	0.13	0.40			
	CB	I_1	I_2	I_3	C_1	P_1	P_2	P_3	P_4	M_1	M_2	M_3		

range of *r* for crown widths in non-occluding tooth pairs was also broad (0.71–0.10). The highest value in this range was found in pair WP^2-WP_4, whereas the lowest was found in WP^2-WM_3 (Table 6).

LP_3 had the strongest correlation with CB (*r* =

Table 4. Correlations (*r*) of tooth width for each pair of teeth within the upper dentition (upper triangular matrix) and lower dentition (lower triangular matrix) in the red fox (*Vulpes vulpes*) from Poland.

			I^1	I^2	I^3	C^1	P^1	P^2	P^3	P^4	M^1	M^2	CB	
I_1	0.42			0.78	0.66	0.57	0.56	0.50	0.48	0.46	0.57	0.43	0.51	I^1
I_2	0.31	0.73			0.75	0.62	0.56	0.50	0.48	0.48	0.54	0.46	0.55	I^2
I_3	0.48	0.65	0.62			0.67	0.59	0.58	0.57	0.58	0.54	0.46	0.53	I^3
C_1	0.61	0.47	0.37	0.58			0.55	0.60	0.58	0.60	0.61	0.44	0.66	C^1
P_1	0.40	0.51	0.43	0.54	0.50			0.64	0.62	0.51	0.48	0.34	0.43	P^1
P_2	0.56	0.47	0.39	0.62	0.63	0.64			0.85	0.61	0.51	0.41	0.47	P^2
P_3	0.51	0.46	0.38	0.58	0.58	0.61	0.87			0.59	0.47	0.41	0.47	P^3
P_4	0.48	0.45	0.34	0.57	0.56	0.56	0.78	0.82			0.52	0.42	0.46	P^4
M_1	0.48	0.51	0.42	0.56	0.59	0.53	0.61	0.59	0.63			0.66	0.51	M^1
M_2	0.40	0.34	0.30	0.46	0.46	0.37	0.45	0.39	0.38	0.51			0.42	M^2
M_3	0.21	0.16	0.14	0.21	0.23	0.14	0.17	0.14	0.12	0.19	0.46			
	CB	I_1	I_2	I_3	C_1	P_1	P_2	P_3	P_4	M_1	M_2	M_3		

Table 5. Correlations (*r*) of tooth length for teeth from opposite tooth rows (left and right side together) in the red fox (*Vulpes vulpes*) from Poland.

	I_1	I_2	I_3	C_1	P_1	P_2	P_3	P_4	M_1	M_2	M_3	
I^1	0.58	0.48	0.43	0.35	0.35	0.39	0.43	0.44	0.43	0.26	0.20	I^1
I^2	0.50	0.45	0.49	0.46	0.41	0.42	0.46	0.47	0.52	0.28	0.17	I^2
I^3	0.43	0.34	0.52	0.51	0.46	0.54	0.53	0.53	0.53	0.32	0.10	I^3
C^1	0.43	0.29	0.51	0.76	0.41	0.67	0.64	0.65	0.59	0.35	0.18	C^1
P^1	0.41	0.32	0.46	0.56	0.65	0.58	0.58	0.55	0.56	0.31	0.18	P^1
P^2	0.45	0.30	0.44	0.61	0.45	0.82	0.81	0.74	0.65	0.34	0.10	P^2
P^3	0.44	0.27	0.47	0.63	0.47	0.82	0.85	0.80	0.64	0.40	0.14	P^3
P^4	0.46	0.30	0.43	0.59	0.40	0.71	0.72	0.73	0.76	0.39	0.18	P^4
M^1	0.37	0.27	0.39	0.54	0.37	0.56	0.55	0.54	0.75	0.59	0.31	M^1
M^2	0.25	0.19	0.26	0.38	0.27	0.40	0.43	0.40	0.42	0.64	0.38	M^2
	I_1	I_2	I_3	C_1	P_1	P_2	P_3	P_4	M_1	M_2	M_3	

Table 6. Correlations (*r*) of tooth width for teeth from opposite tooth rows (left and right side together) in the red fox (*Vulpes vulpes*) from Poland.

	I_1	I_2	I_3	C_1	P_1	P_2	P_3	P_4	M_1	M_2	M_3	
I^1	0.69	0.60	0.62	0.53	0.56	0.55	0.52	0.46	0.51	0.40	0.14	I^1
I^2	0.65	0.57	0.65	0.57	0.56	0.56	0.55	0.51	0.52	0.41	0.16	I^2
I^3	0.56	0.48	0.68	0.61	0.61	0.64	0.64	0.59	0.58	0.45	0.16	I^3
C^1	0.49	0.37	0.58	0.84	0.52	0.66	0.61	0.59	0.62	0.45	0.21	C^1
P^1	0.49	0.38	0.53	0.51	0.74	0.66	0.64	0.57	0.53	0.37	0.13	P^1
P^2	0.44	0.36	0.55	0.57	0.58	0.84	0.81	0.71	0.54	0.35	0.10	P^2
P^3	0.43	0.36	0.53	0.54	0.57	0.80	0.79	0.73	0.52	0.38	0.15	P^3
P^4	0.44	0.32	0.52	0.53	0.45	0.62	0.61	0.60	0.53	0.40	0.13	P^4
M^1	0.50	0.38	0.54	0.60	0.46	0.54	0.51	0.47	0.65	0.53	0.18	M^1
M^2	0.38	0.29	0.46	0.42	0.33	0.46	0.42	0.38	0.43	0.60	0.29	M^2
	I_1	I_2	I_3	C_1	P_1	P_2	P_3	P_4	M_1	M_2	M_3	

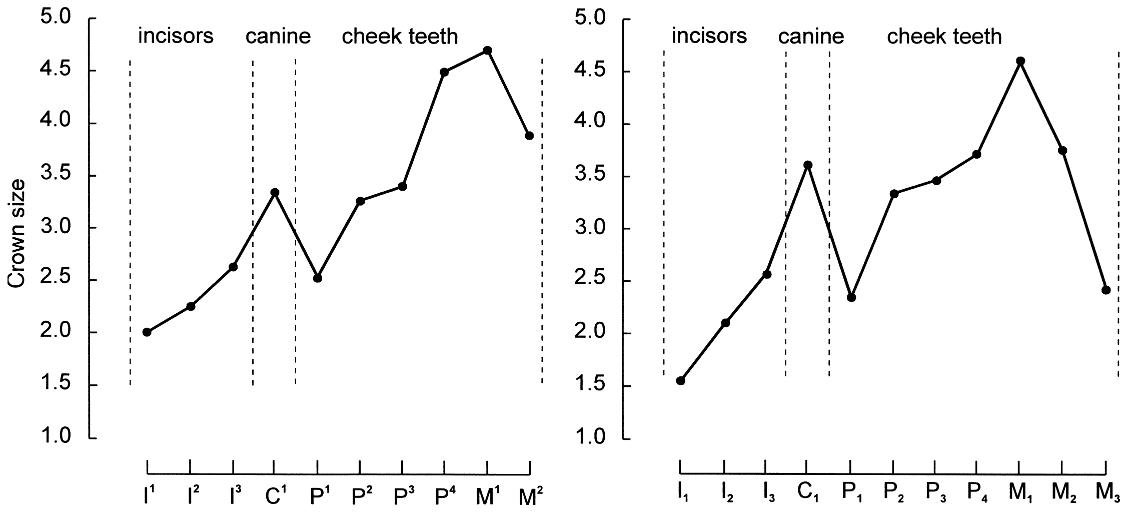

Fig. 10. Occlusal crown size [ln (length × width)] in upper and lower dental arches in the red fox (*Vulpes vulpes*) from Poland.

0.72). A considerable power of correlation relationships ($0.51 < r < 0.70$) with CB was revealed by LC^1, LP^1, LP^2, LP^3, LP^4, LM^1 and LC_1, LP_2, LP_4, LM_1. The LI_2 and LM_3 were weakly correlated with CB ($r < 0.30$; Table 3).

The crown widths were generally less correlated with CB than the crown lengths in the red fox dentition. Within the upper tooth row, however a considerable correlation with CB ($0.51 < r < 0.70$) was manifested by WC^1, WI^2, WI^3 and WI^1, and in the lower tooth row by WC_1, WP_2 and WP_3 (Table 4).

4. Discussion

4.1. Variation pattern

In the dentition of carnivoran mammals a morphological gradient of tooth size and shape is observed. Extreme variation in size and shape occurs in the premolar region. In the upper tooth row P^4 and M^1 have the largest measures of size and complexity. Anteriorly and posteriorly from these points a gradual size reduction and tooth simplification are observed. The central point in the lower tooth row is M_1. In the anterior region of the upper and lower tooth rows an unilateral decrease of tooth size is observed from posterior to anterior, i.e. from C^1 to I^1 and from C_1 to I_1 (Fig. 10). In dental profiles of mammals the gradient of size and complication of tooth characters is accompanied by definite trends in variability.

The variability analyses based on CV show a similar variability pattern to that found in many mammal species. The least variable teeth are present in the center of the tooth row and the most variable ones lie on its borders (Gingerich 1974, Gingerich & Schoeninger 1979, Gingerich & Winkler 1979, Pengilly 1984). Both CV and V_{SD} indices showed a pattern of dental variation in the red fox from Poland that was very similar to the dental pattern found by Gingerich and Winkler (1979) in the red fox from the Upper Peninsula of Michigan. In both populations the least variability was observed in the central region of the cheek tooth row (M^1 and M_1). The upper carnassial showed low variability in length and high variability in width. In both the upper and lower tooth rows an increase in size variation was observed from the central region (carnassial region) towards the anterior and posterior ends of the tooth row. The highest values of CV and V_{SD} for crown length and width were found in M_3. In Gingerich and Winkler's (1979) opinion M^2 was the most variable tooth in the upper dentition. However, this analysis of red foxes from Poland shows that the size of the M^2 is quite a stable character. Contrary to the red foxes from the Upper Peninsula of Michigan, red foxes from Poland have great variation in C^1 and C_1. In both these samples the premolar region has an intermediate level of variability.

In the red fox dentition, all teeth have differences in the CV of crown lengths *versus* widths. In the upper tooth row, in the incisor and canine regions, the differences between CV of these measurements are not great. The differences increase toward the P^4 but in the molar region they are small again. In the mandibular tooth row the pattern of variation of tooth lengths and widths looks quite different than in the maxillary tooth row. In the anterior part of the mandible (from I_1 to P_1) the tooth lengths are more variable than the widths, whereas in the tooth row from P_2 to M_2 the situation is the opposite.

The large differences between CV for tooth lengths and widths in the premolar region is probably the result of the specific, distinctly elongate shape of the teeth, where the tooth lengths are two or three times longer than tooth widths. The average value of the variation of tooth widths is slightly higher than the average value of the variation of tooth lengths in red foxes from Poland. The foregoing observations confirm an earlier assertion by Yablokov (1974) that the CV is determined by a character's size. The smaller a measurement, the higher the CV, and *vice versa*.

Analyses of the averages of tooth lengths and CV suggest that there should be an inverse relationship between tooth size and the coefficient of variability (CV). Negative relationships between CV and measurements of cheek teeth were previously found in a sample of the red fox *Vulpes vulpes* (Gingerich & Winkler 1979), in the arctic fox *Alopex lagopus* (Pengilly 1984), as well as in samples of the American marten *Martes americana* and the Eastern grey fox *Urocyon cinereoargenteus* (Polly 1998). The regression of the R_{SD} index in relation to averages of tooth size carried out in the sample of red foxes from Poland showed complete absence of the influence of character size on its variation level, and thus Polly's observations (1998) were confirmed.

The R_{SD} regression used in the studies of dental variation in the red fox from Poland showed total absence of the relation between character size and the variation level. Contrary to the variability pattern based on CV and V_{SD}, in the pattern constructed on the R_{SD} for P^2, P^3, P_2, and P_3 no significant differences have been observed between variation in tooth lengths and widths. Moreover, in the case of P^2 and P_2 the crown lengths are slightly more variable than the widths.

Regression of the CV of the occlusal crown surface on the eruption sequence of the permanent teeth showed a trend of increasing tooth size variability with later eruption times. The analysis of the dental variation pattern in the sample of the red fox from the Upper Peninsula of Michigan showed no influence of the eruption time on tooth variation (Gingerich & Winkler 1979). The relationship between the eruption sequence and variation of crown lengths in the sample of the red fox from Poland based on V_{SD} and R_{SD} showed a positive but statistically insignificant relationship. It seems that the relationship between eruption time and variation in tooth size in the population of the red fox in Poland reveals one of many factors determining dental variation patterns, viz. development.

Gingerich and Winkler (1979) said that the pattern of variation is a good measure of functional integration in particular regions of the dental apparatus. They observed that in the red fox dentition the most precise occlusion is in the carnassial region, whereas more simple occlusion is present in the incisor and canine regions. Opposite premolars are characterised by the complete absence of contact during occlusion of the upper and lower jaws. The pattern of variation in the dentition of the red fox from Poland partially agrees with that proposed by Gingerich and Winkler (1979). The hypothesis offered by these authors explains and affirms that the occlusal complexity also partially explains the variation pattern of tooth dimensions.

In both populations the most tightly occluding, and the most complicated teeth of the carnassial region show the lowest variability. The variability increases gradually from the centre to the anterior and posterior ends of the cheek tooth row, and on M_3, P^1 and P_1 it reaches the highest values. The incisor region is characterised by a simple occlusion and rather low variation. The variation level is a little lower in I^1 and I_1, and increases posteriorly. A simple occlusion of the canines is not confirmed by its CV value. In the maxilla, the highest variation of the occlusal surface of the crown was shown by C^1. The size variation of C_1 was also high but it was lower than C^1. Trends in variability based on R_{SD} and occlusal complication of tooth crowns were similar to those which were obtained for CV. High variation was found in LC^1, LC_1 and WP^4. The analysis of variation in females and males individually showed that values of CV for occlusal surfaces of C^1 and C_1 were lower than in the sample of both sexes together.

These results suggest that sexual dimorphism is responsible for higher variation of the canines. In the dentition of the red fox from Poland, the values (except P^1, P_1 and M_3) are significantly higher in males than in females. A similar picture of sexual dimorphism of dental characters was found by Ansorge (1994) in the population of the red fox from Oberlausitz. He observed that sexual dimorphism in the canine region was higher than in the carnassial region. Dayan *et al.* (1989, 1991) stated that in most canids sexual dimorphism of the canine lengths is not greater than the dimorphism of the carnassial lengths. On the contrary, Gittleman and Van Valkenburgh (1997) demonstrated that in the canid family the highest sexual dimorphism of measurements occurred on C^1 and C_1, and it was higher than the sexual differences in the carnassial region. Alvesalo (1970) indicated that in all earlier odontometric studies of human populations the largest differences between sexes appeared in the length and width of C^1 and C_1. In the dentition of the red fox from Poland the highest values of the M_m/M_f index were found in the length, width and height of C^1 and C_1. It seems that sexual dimorphism is one of the more important factors contributing to the higher variation of canines.

The completion of the eruption of the permanent dentition in the red fox occurs at the end of the sixth month of life (Linhart 1968). Studies of tooth development in dogs showed that the enclosing and filling of the roots of C^1 and C_1 was a process which lasted into the eighth month of life. By that time, canines undergo heavy hormonal changes typical for a young organism. Active changes in the root size have their reflection in active transformations in the oval crown outline of the cross-section of canines, especially in their lower part (Lorber *et al.* 1979). Measurements of the canine lengths and widths in the sample of the red fox from Poland were taken just over the junction of the enamel and cement. Moreover, a relatively great part of this sample was composed of young specimens (about seven or eight months of age). It seems that a higher variation of canines in foxes may be another proof of a significant influence of the developmental process on the dental variation pattern.

4.2. Correlation pattern

The general pattern of correlations in the dentition of the red fox from Poland is concordant with that found in other mammals. Inside of each morphological region, homologous teeth have stronger correlations than between teeth from different regions (Garn *et al.* 1965, Polly 1997). However, Garn *et al.* (1965) already remarked that the neighbouring teeth in two different morphological fields often have higher correlations than more distant teeth in the same field. In the dentition of the red fox from Poland neighbouring teeth lying in different regions, such as: I^3 and C^1, C_1 and P^1, are more strongly correlated with each other than tooth pairs that are more distant but lying in the same region, e.g. I^1 and I^3. In accordance with the neighbourhood rule (Kurtén 1953, Van Valen 1970), more significant correlations in a single region are found between neighbouring teeth, the strongest being in the central region of the field. Though the upper and lower tooth rows are composed of two different morphological units, the general pattern of relations is identical with correlations in a single tooth row.

The correlation pattern of tooth lengths found in red foxes from Poland resembles the correlation patterns found for red foxes from Finland and the Kökar Island (Kurtén 1953) and the Upper Peninsula of Michigan (Gingerich & Winkler 1979), as well as for the population of arctic foxes from Alaska and Canada (Pengilly 1984). The highest level of correlation both for crown length and width in the sample of red foxes from Poland was found in the premolar region. This observation confirmed earlier suggestions about the highest morphological integration in the premolar region. Pengilly (1984) stated that the absence of precise occlusion between opposite premolars excludes the functional explanation of such a high level of morphological integration of the teeth. In his opinion the only explanation of the strong relationships is a common developmental factor. It

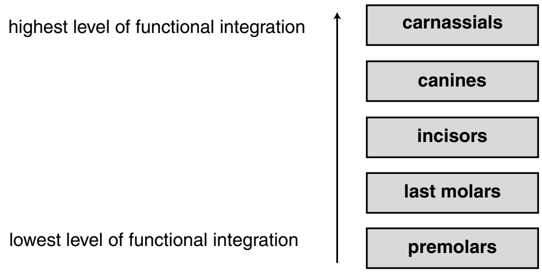

Fig. 11. Hypothetical pattern of functional integration in the red fox dentition.

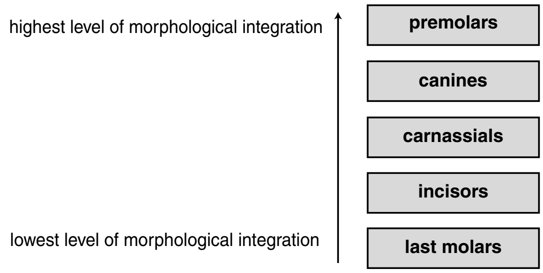

Fig. 12. Pattern of morphological integration in the red fox dentition.

seems that the premolars create a distinct, morphogenetic field which is subject to the influence of the same developmental factors.

Important traits of the correlation pattern in the red fox dentition from Poland are the close relationships between lengths and widths in pair C^1 and C_1, and also the precise correlation between the widths in neighbouring incisors. Unlike the variability indices, the coefficient of correlation r reflects the functional significance of pairs of opposite canines. Mellett (1984) emphasised that the frequently forgotten but very important function of canines is to guide occlusion in the upper and lower tooth rows. This function requires a high level of integration in the canine region. High values of the r coefficient for C^1 and C_1 are evidence of that. The strong correlation of the widths between neighbouring incisors can be explained both by the influence of the functional factor (simple occlusion) and of the common developmental factor (morphogenetic field of incisors).

In any particular dental system particular tooth groups or pairs have different functions. In predators, the most important are the carnassials (performing both grinding and cutting functions). The canines are used to kill and play a significant role in social interactions. The incisors function in catching and holding a prey. Premolars and posterior molars have a secondary functional value in respect to catching and grinding of the food. The premolars help to hold the prey, while it is carried, whereas the last molars are helpful in grinding food. The most probable pattern of functional integration in the red fox dentition is presented in Fig. 11. The necessity of correct and effective function in particular regions and of the whole dental system requires at least a minimal integration level. Dental regions performing significant functions in life should be characterised by a considerable character correlation. Therefore, one would expect that the correlation pattern in the red fox dentition is a reflection of the functional integration pattern. However, multivariate correlations of dental features showed that something other than the functional integration explains the correlation pattern in the dentition of the red fox from Poland (Fig. 12). The highest level of tooth measurement correlations was found in the region of neighbouring as well as opposite and occluding premolars. A high correlation in respect to all dimensions was found between C^1 and C_1. The carnassials showed a strong relationships only in crown length. In the incisor field I observed mainly moderate levels of correlation, though as for tooth width strong correlations were found in the following pairs: I^1-I^2, I^2-I^3 and I_1-I_2. The lowest correlation values were noted in the posterior molars.

The overall pattern of variation and correlation in the red fox dentition is created by complicated scheme of functional and developmental factors. Eruption time, hormonal regulation during development, sexual dimorphism and functional significance of particular regions determine the variation level of tooth size. Yet the correlation pattern is not a direct reflection of the functional importance of the dental system. This pattern is a result of some factors operating during development, such as: factors of morphogenetic field, hormonal environment, and also external environment of the system.

5. Conclusions

1. Analysis of size variation in the red fox dentition showed that the first molars (M^1 and M_1) are the most stable, whereas M_3 is the most variable tooth. The overall dental variation pattern is a result of both functional and developmental factors.
2. Sexual dimorphism in the canine region was higher than in the carnassial region. It seems to be a consequence of the significant social role of the canines.
3. The highest correlations in both crown length and width in the premolar region are a consequence of common morphogenetic influences, whereas the strong correlations in pair C^1-C_1 are a result of the very important function of canines, namely guiding occlusion between upper and lower tooth rows.

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