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Quasi-continuous variation of the first premolars in the Polish population of the badger *Meles meles*

Elwira SZUMA

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The presence-absence polymorphism and the size of $P^1{}_1$ were studied in the Polish population of the badger *Meles meles* (Linnaeus, 1758) (n = 79). P^1 is more often absent than P_1. The lengths of $P^1{}_1$ range from 0.97 mm to 2.63 mm (V = 16.3–22.3). A breach in the continuous variation of the size of the teeth between their absence and the minimum length of the crown that is 0.97 mm suggests that a threshold mechanism, related to size, operates at an early stage of $P^1{}_1$ ontogeny. Such a mechanism would allow the development of a tooth only if it had reached the threshold size at the critical stage of its ontogeny. The correlation between the presence or absence of $P^1{}_1$ and the number of roots of $P^2{}_2$ confirms the existence of a gradient in shape and size within the morphogenetic field of cheek teeth. The frequent occurrence of $P^1{}_1$ in the Polish population of the badger (73%) corresponds to the clinal variation of the presence-absence polymorphism of the first premolars in Eurasia.

Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland

Key words: *Meles meles*, first premolars, quasi-continuous variation, threshold mechanism, Poland

Introduction

The presence-absence polymorphism of $P^1{}_1$ in the badger has been described many times before (Heptner *et al.* 1974, Spittler and Jansen 1985, Baryshnikov and Potapova 1990, Lüps 1990). A comparison of the frequency of occurrence of $P^1{}_1$ showed that P^1 is more often absent than P_1. It was also demonstrated that the length and width of $P^1{}_1$ are characterized by a coefficient of variation fluctuating between 10.2 and 15.0 (Lüps 1990).

Presence or absence of $P^1{}_1$ indicate a distinct clinal variation (Baryshnikov and Potapova 1990, Lüps 1990). Heptner *et al.* (1974) note that the lowest frequency of $P^1{}_1$ is characteristic of Far East populations of the badger. Moving from the east towards the west the frequency of the occurrence of $P^1{}_1$ gradually grows.

It has so far not been explained what mechanism is responsible for the presence--absence polymorphism and variation in size of $P^1{}_1$ in the badger. Thus, the aim of the present study is an attempt to find the answer to the question: what determines the presence or absence of $P^1{}_1$ in the badger's dentition, and when it is present, what determines its size? At the same time, the morphogenetical field theory was tested by examining the dependence of presence or absence of P^1_1 upon the number of roots and the size of P^2_2. Furthermore, the paper includes the comparison of the frequency of occurrence of P^1_1 in the dentition of the Polish badger in comparison with the populations from the neighbouring countries.

Material

The research was conducted on 79 skulls of the badger *Meles meles* (Linnaeus, 1758), including 16 females, 24 males and 39 specimens of an unknown sex. In six specimens the whole mandible was missing, and two lacked a dentary bone. Fourty-one badger's skulls came from the collection of the Mammal Research Institute of the Polish Academy of Sciences in Białowieża, 12 from the Institute of the Systematics and Evolution of Animals of the Polish Academy of Sciences in Cracow, seven from the Research Station of the Polish Hunters' Association in Czempiń, six from the Natural History Museum of Wrocław University, five from the Institute of Biology of Maria Curie-Skłodowska University in Lublin, three from the Institute of Biology of the Teachers Training College in Olsztyn, four from Dr A. Nowosad's private collection from Poznań and one from the private collection of Mr R. Miklaszewski from Toruń. All the above listed specimens were found in Poland between 1930 and 1992.

Methods

P^1_1 were considered present (+) when: (1) the teeth were embedded in their alveoli; (2) the teeth fell out but their alveoli remained, (3) the alveoli overgrown with a bony tissue were visible. P^1_1 were considered absent (0) when in the place where P^1_1 should occur there was no trace that they had been there before.

Measurements of left and right P^1_1 and P^2_2 were taken with the measuring microscope, type WILD, exact to 0.01 mm. Because there was no statistically significant difference in the frequency of occurrence of P^1_1 in males and females, the observations and measurements were analyzed jointly.

The following measurements were made: the length of P^1 and P_1 (LP^1 and LP_1): the greatest distance between the anteriormost and posteriormost points of the crown of P^1 and P_1; the length of alveolus of P^1 and P_1 (LAP^1 and LAP_1): the greatest diameter of the alveolar rim of P^1 and P_1; the length of P^2 and P_2 (LP^2 and LP_2): the greatest distance between the anteriormost and posteriormost points of the crown of P^2_2. The statistical analysis was based on the average of three repetitions of each measurement.

In order to describe the variation in number of roots of P^2_2 three morphotypes were distinguished: A, B and C. The definitions of morphotypes are given in the legend for Fig. 3.

Duncan's new multiple range test was used to estimate the differences between the average measurements (Duncan 1955). The correlation coefficient of Pearson (r) was also counted in order to estimate the asymmetry of P^1_1. The relation between the presence (absence) of P^1_1 and the number of roots of P^2_2 and between the presence (absence) of P^1_1 and the length of P^2_2 crowns were estimated by counting the correlation of quality traits.

Results

Taking 298 possible examples of P^1_1 (left and right P^1 plus left and right P_1) in 219 instances (73%) P^1_1 were present (Table 1). In the Polish population of the badger eight variants of dentition, considering the presence or absence of P^1_1, were found (Fig. 1).

The coefficients of variation (V) of LP^1_1 and LAP^1_1 are about three times greater than those for LP^2_2 (Table 2). The distribution of variability of left and right LP^1 and left and right LP_1 show the positive asymmetry. Measurements of LP^1 reach the highest frequency in the range from 1.15 mm to 1.90 mm (78% of measurements) whereas the characteristic measurements of LP_1 (78%) converge in the

Table 1. Frequency of occurrence of P^1_1 in the Polish population of the badger. *n*p – number of present P^1_1, *n*a – number of absent P^1_1.

	Left				Right				Total			
	*n*p	%	*n*a	%	*n*p	%	*n*a	%	*n*p	%	*n*a	%
P^1	46	59	32	41	46	59	31	41	92	59	63	41
P_1	64	89	8	11	63	90	7	10	127	89	15	11

Table 2. Descriptive statistics for the P^1_1 measurements (mm), according to body side. *n* – number of teeth, OR – observed range, *x* – average, SD – standard deviation, SE – standard error mean, V – coefficient of variation.

Measurement	Body side	*n*	OR	*x*	SD	SE	V
LAP^1	left	37	1.12–2.60	1.63	0.30	0.05	18.10
LAP^1	right	40	1.21–2.27	1.60	0.25	0.04	15.46
LAP_1	left	42	1.09–2.20	1.72	0.26	0.04	15.38
LAP_1	right	42	1.10–2.41	1.70	0.30	0.05	17.88
LP^1	left	17	1.15–2.55	1.62	0.36	0.09	22.31
LP^1	right	20	0.97–2.17	1.50	0.32	0.07	21.31
LP_1	left	22	1.31–2.37	1.67	0.27	0.06	16.34
LP_1	right	32	1.23–2.63	1.75	0.35	0.06	20.23
LP^2	left	41	3.94–5.37	4.78	0.30	0.05	6.28
LP^2	right	45	4.07–5.55	4.75	0.29	0.05	6.03
LP_2	left	60	4.39–5.82	5.14	0.30	0.04	5.74
LP_2	right	59	4.39–5.67	5.04	0.28	0.04	5.57

classes from 1.30 mm to 2.05 mm (Fig. 2A, B). The distribution of variation of LAP^1 and LAP_1 has a slight positive asymmetry. The characteristic measurements of LAP^1 comprise the class categories from 1.30 mm to 1.90 mm (80%) whereas 75% of measurements of LAP_1 fall into the category from 1.30 mm to 2.05 mm (Fig. 2C, D).

Correlations between LP^1 and LP_1 as well as between LAP^1 and LAP_1, for both left and right side of the body, turned out to be statistically insignificant ($p > 0.1$).

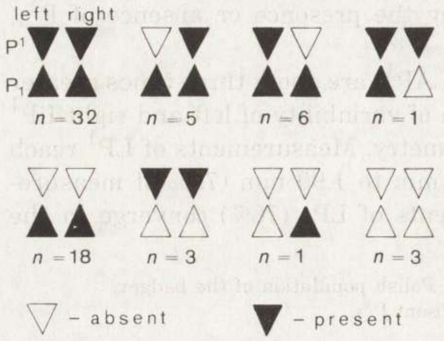

Fig. 1. Configurations of presence-absence of P^1_1 found in 69 skulls of the badger from Poland.

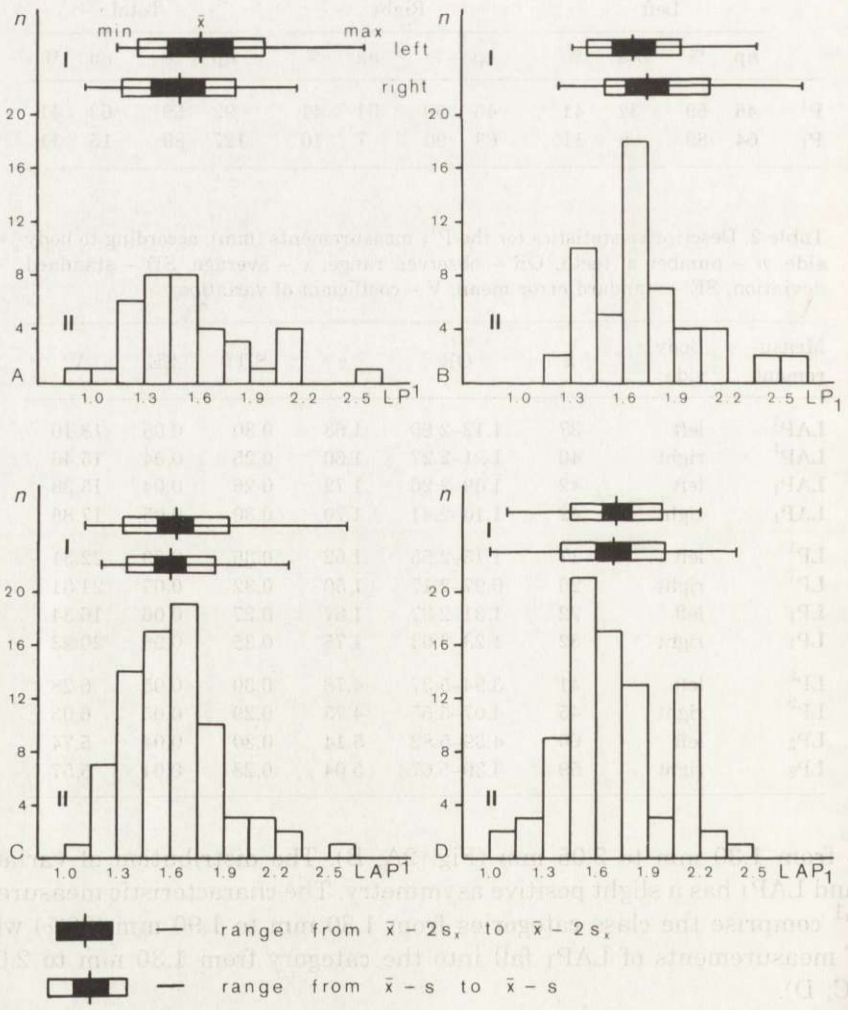

Fig 2. The range of variation (I) and the distribution of frequency (II) for: (A) left and right LP^1, (B) left and right LP_1, (C) left and right LAP^1, (D) left and right LAP_1. n – the number of teeth; the borders of classes for LP^1, LP_1, LAP^1 and LAP_1 are given in mm.

Statistically significant differences in the length of left and right alveoli of P^1 and P_1, as well as left and right crowns of P^1 and P_1, were not found ($p > 0.05$; Table 3). The correlation of the size of $P^1{}_1$ between left and right alveoli of P^1, left and right alveoli of P_1 as well as left and right P_1 are statistically significant (Table 4).

Table 3. Differences between the mean tooth measurements made, based on data from Table 2. – not significant, + $p < 0.05$.

	LP_2		LP^2
	right	left	right
LP^2 left	+	+	–
LP^2 right	+	+	
LP_2 left	–		

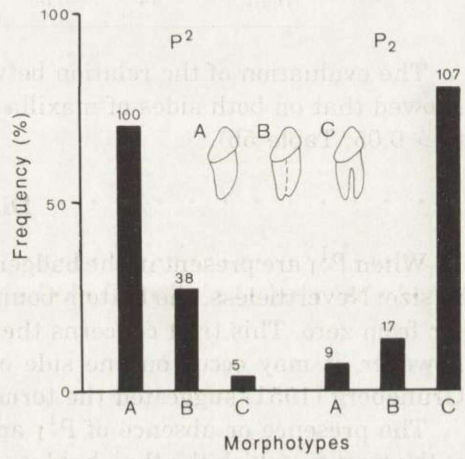

Fig. 3. Variation of P^2 and P_2 concerning the number of roots in 79 skulls of the badger. A – a tooth with one root: the lack of concavity on the top of the root or lack of bony septum at the bottom of the alvelous; B – a tooth with a partially divided root: in the outline of the root and along the root, one can see a channel or a hollow; the root divides into two parts at most up to the middle of its height; a bony septum is present down to the middle of the alveolus depth; C – a two-rooted tooth: it divides into two roots; the alveolus with a bony septum reaching more than a half of its depth. The numbers above the posts denote the number of P^2 and P_2 classified to each of the three morphotypes.

Table 4. Correlation coefficient of size of $P^1{}_1$ between left and right side for the crown and alveolus in the upper and lower jaw.

	Alveolus			Crown		
	n	*r*	%	*n*	*r*	%
P^1	30	0.56 $p < 0.005$	31.3	10	0.37 $p > 0.1$	13.4
P_1	34	0.76 $p < 0.001$	57.3	18	0.91 $p < 0.001$	83.0

The statistically significant negative correlation ($p < 0.001$) between the frequency of occurrence of P^1 and the number of roots of P^2 was noted. The same relation in mandible appeared to be statistically insignificant ($p > 0.1$; Table 5a). P_1 was present in about 90% of specimens and the predominant morphotype in P_2, as far as the number of roots is concerned, was a two-rooted tooth (morphotype C, 80%; Fig. 3).

Table 5. Correlation coefficient between: (a) number of roots in $P^2{}_2$ and presence of the adjacent $P^1{}_1$, (b) size of $P^2{}_2$ and presence of the adjacent $P^1{}_1$. n – sample size, r – correlations coefficient, t – statistical significance, * $p < 0.01$.

Body side	Maxilla			Mandible		
	n	r	t	n	r	t
(a) left	71	−1.98	5.67*	68	−4.38	1.97
right	72	−2.00	5.62*	65	−4.59	1.83
(b) left	40	−0.29	1.96	59	0.11	0.85
right	44	−0.33	2.42	58	0.10	0.79

The evaluation of the relation between the presence of $P^1{}_1$ and the size of $P^2{}_2$ showed that on both sides of maxilla and mandible it is statistically insignificant ($p > 0.05$; Table 5b).

Discussion

When $P^1{}_1$ are present in the badger's dentition they show a continuous variation in size. Nevertheless, the bottom boundary of the size of the teeth is always moved far from zero. This trait concerns the specimens of either sex to the same degree, however, it may occur on one side or on both sides. For this type of variation, Grüneberg (1951) suggested the term "quasi-continuous variation".

The presence or absence of $P^1{}_1$ and the variability in size and shape of teeth is the trait for which the threshold mechanism is most probably responsible (Searle 1958). According to the threshold mechanism theory the germs of $P^1{}_1$ that at the critical stage reached the required threshold size, can continue further development, while the smaller structures undergo the atrophy. The action of thresholds consists in allowing or hindering the further development of the structures – in this case, tooth germs. Whether a tooth at the threshold stage will or will not reach the dimensions necessary for further development may be conditioned by both genetic or environmental factors (Grüneberg 1951, Searle 1958, Wolsan 1989). The genetical information accounts for the antethreshold morphological pattern as well as the threshold height and the duration of action in course of the ontogeny. The environmental factors can modify the final morphological pattern. Nevertheless, it seems that non-genetic factors cause only a slight shifting of the threshold level and threshold stage (Wolsan 1989).

The dentition of mammals may be morphologically varied along the mesial--distal axis, within three morphogenetical fields, which correspond to a group of incisors, canines, and a group of cheek teeth (Butler 1939). Each field includes a gradient of size and shape of the structures that constitute the field. The teeth that are most stable in size and shape form the centre of the field, while more variable teeth move towards its verges (Lombardi 1978).

The studies on the badger in Switzerland (n = 40) indicate that the teeth that are most stable in size and shape are I^1_2, C^1_1, P^4, M_1 (Lüps and Roper 1988).

P^1_1 is situated in the most peripheral position in the morphogenetical field of cheek teeth. Quite often P^1_1 does not erupt, which is characteristic of the badger, and when it is present it frequently falls out early in animal's life. The coefficient of variation of LP^1_1 is about three times greater than those for LP^2_2 (Table 2). P^1 is more often absent than P_1. Furthermore, on both sides of the maxilla the frequency of P^1 tends to be lower and the number of roots of P^2 gets smaller, whereas in the mandible, the two-rooted P_2 is almost permanently accompanied by P_1. It seems that the direction of changes taking place at the verge of the row of cheek teeth in maxilla is more progressive than the changes affecting P_1 and P_2. Lüps and Roper (1988) note that P^1 undergoes a stronger reduction in size and it more often does not erupt than P_1. Similar directions of reducing the size and losing peripheral teeth are known in other mammals, for example *Vulpes vulpes* (Ratcliffe 1970), *Felis bengalensis* (Glass and Todd 1977), *Martes martes*, *M. foina* (Wolsan *et al.* 1985). In accordance with the findings of the morphogenetical field theory (Butler 1939, Osborn 1978) and on the basis of my own data as well as those of Lüps and Roper (1988), one can assume that P^1_1 are the most variable teeth within the premolars just as in the whole badger's dentition.

Polymorphism of P^1_1 occurs within the whole Eurasian range of the badger. In the specimens from the populations living farthest to the east P^1_1 occur very rarely, for example in the badgers from Kazakhstan the percent of present P^1_1 approaches 2% (Heptner *et al.* 1974). In the badgers from central Asia the frequency of P^1_1 reache 30% (n = 23, Lüps 1990). In the Polish population of the species, P^1_1 are present in 73% (n = 79). Lüps (1990) notes that the frequency of P^1_1 for the badger from central Switzerland equals 71 % (n = 315), while for Denmark it is 70% (n = 100). The tooth reached the highest frequency of occurrence in Romania (about 80%, n = 47). These data suggest that in the central Europe the frequency of occurrence of P^1_1 is similar and ranges from 70% to 75%.

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