

Variation and Asymmetry in the Dentition of the Pine and Stone Martens (*Martes martes* and *M. foina*) from Poland

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To describe the variation and asymmetry patterns in 220 pine martens, *Martes martes* (Linnaeus, 1758), and 43 stone martens, *Martes foina* (Erxleben, 1777), from Poland, some teeth were measured, five groups of morphotypes were distinguished, and congenital oligodonties were counted. Dental characteristics for distinction between *M. martes* and *M. foina*, including a few originally described ones, are presented. All the characteristics show the overlapping ranges of variation in more numerous samples. Hence, as many traits as possible should simultaneously be taken into consideration to increase the probability of correct species determination. Sexual dimorphism is involved not only in tooth size, with males being generally larger than females, but also it affects both tooth shape and the ability for congenital tooth loss. Both variation and asymmetry are generally lower for the central cheek teeth than for the peripheral ones, which is related to the gradient of tooth shape and size. In addition, there is a relationship between the frequencies of the morphotypes and the asymmetry in their occurrence: the more frequent a morphotype is the less asymmetry there is in its occurrence. The tooth variation reflects the evolutionary trends in the lineage of the species, throwing light on their ancestry and on the potential direction of microevolutionary changes.

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1. INTRODUCTION

An anatomical system yielding the most information about mammals is undoubtedly their dentition (Gingerich, 1976, 1977; Gingerich & Simons, 1977; Gingerich & Winkler, 1979). The study of variation and bilateral asymmetry in mammalian dentitions is of great importance to systematic identification and may throw light on the evolution of a given taxon as well as on the ontogeny of mammalian heterodonty.

The present paper gives a description of variation and asymmetry patterns in some teeth of the pine and stone martens from Poland according to sex, and a comparison of the patterns between the two morphologically similar species with extensively overlapping geographic ranges (e.g. Anderson, 1970) to find the differences of taxonomic importance. In addition, paleontological data are adduced to show evolutionary importance of tooth variation in the species.

2. MATERIAL AND METHODS

2.1. Characteristics of the Material

The study is based on the examination of the permanent dentitions in 220 (126 males and 94 females) specimens of the pine marten, *Martes martes* (Linnaeus, 1758), and 43 (30 males and 13 females) specimens of the stone marten, *Martes foina* (Erxleben, 1777), caught in Poland. The differences between the numbers mentioned above and the numbers of skulls and teeth given in tables and figures are caused by missing teeth as well as by teeth showing some wear which makes unmistakable determination of a morphotype or taking a reliable measurement impossible. Dental anomalies (Wolsan, 1984a) were not taken into consideration in this respect as well.

The sex of the examined specimens was recorded from the collection data, corrected in evident cases of misidentification, while the age classes (1=infants, 2=juveniles, 3=subadults, 4=adults, 5=old adults) were distinguished on the basis of the definitions proposed by Buchalczyk & Ruprecht (1977) for the polecat.

2.2. Measurements and Indexes

All the measurements were taken with a slide caliper to the nearest 0.05 mm. They are:

LP³: Length of P³ or the greatest distance between the anterior and posterior points of the crown of the tooth (Fig. 1a).

WP³: Width of P³ or the greatest distance between the lingual and buccal points of the crown of the tooth perpendicular to its length (Fig. 1a).

LM¹: Length of M¹ or the greatest distance between the anterior and posterior points of the inner lobe of the tooth perpendicular to its width (Fig. 1a).

WM¹: Width of M¹ or the greatest distance between the lingual and buccal points of the crown of the tooth measured along its long axis (Fig. 1a).

WM₁: Width of M₁ or the greatest distance between the lingual and buccal points of the talonid of the tooth perpendicular to its long axis (Fig. 1b).

DM₂: Greatest diameter of M₂ or the greatest distance between two distal points of the crown of the tooth measured across its center (Fig. 1b).

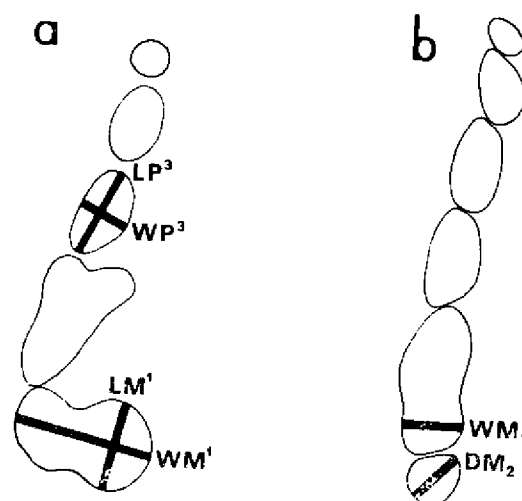


Fig. 1. Diagrams of the upper (a) and lower (b) marten postcanine dentitions, showing the manner of taking the measurements used.

Three indexes: $(WP^3 \times 100)/LP^3$, $(LM^1 \times 100)/WM^1$, and $(DM_2 \times 100)/WM_1$ were calculated basing on these measurements, in order to show the patterns of variation in the relative width of P³, the relative antero-posterior dimension of the inner lobe of M¹, and the relative size of M₂, respectively.

2.3. Morphotypes

The morphotypes of group A (Fig. 5) describe variation in the morphology of P³ consisting in the occurrence of the teeth representing successive stages in the transition from the three-rooted to the two-rooted tooth accompanied by gradual morphological changes in the base of the crown:

A 1: Two roots. No concavity in the outline of the crown.

A 2: Two roots. The postero-lingual part of the crown slightly concave in outline.

A 3: Two roots but the posterior one shows, lingually and/or buccally, the presence of an occluso-basal groove. A distinct concavity in the outline of the postero-lingual part of the crown accompanied anteriorly by a convexity followed by a slight concavity in the antero-lingual part of the cingulum. The buccal part of the crown may show a slight concavity in outline.

A 4: Three roots, with the smallest one placed lingually. Both the buccal and the two lingual concavities as well as the lingual convexity, mentioned above, are distinct.

The morphotypes of group B (Fig. 7) describe variation in the morphology of P₃ and P₄ consisting in the occurrence of the teeth representing successive stages in the transition from the tooth with the presence of a small accessory cusp on the posterior ridge of the protoconid to that without any sign of the cusp:

B 1: The posterior ridge of the protoconid without any sign of convexity.

B 2: The presence of a small elevation passing smoothly into the posterior ridge of the protoconid.

B 3: The presence of an elevation passing anteriorly into the posterior ridge of the protoconid on the square.

B 4: The presence of a cusp-like elevation separated anteriorly from the posterior ridge of the protoconid by a shallow occluso-basal V-shaped indentation.

B 5: The presence of a small but distinct cusp separated anteriorly from the posterior ridge of the protoconid by a clear V-shaped or nearly U-shaped valley.

The morphotypes of group C (Fig. 9) describe variation in the morphology of M¹ consisting in the occurrence of the teeth representing successive stages in the transition from the tooth with the presence of a V-shaped indentation in the outline of the postero-buccal part of the crown to that without any sign of concavity:

C 1: The postero-buccal part of the crown without any sign of concavity in outline.

C 2: The presence of a slight concavity in the outline of the postero-buccal part of the crown.

C 3: The presence of a distinct V-shaped indentation in the outline of the postero-buccal part of the crown.

The morphotypes of group D (Fig. 11) describe variation in the morphology of M¹ consisting in the occurrence of the teeth with absence (morphotype D 1) or presence (morphotypes D 2—D 10) of accessory structures on the occlusal surface of the inner lobe of the tooth.

The morphotypes of group E (Fig. 12) describe variation in the morphology of M¹ consisting in the occurrence of the teeth representing successive stages in the transition from the tooth with the presence of a shallow occluso-basal V-shaped indentation in some half of the length of the crista running postero-lingually from the anterior cingulum to that without any sign of concavity in the crista:

E 1: The crista without any sign of concavity.

E 2: The presence of a concavity in the crista.

2.4. Oligodonty

The authors have been interested only in congenital deficiencies in dentition, therefore the absence of a tooth was noted only when there was no sign of its prior presence in dentition, that is when there was no alveolus nor any trace of its overgrowing. Tooth deficiencies clearly resulting from development disturbances in the embryogeny caused by the influence of environmental factors were

not taken into consideration in this respect as well. The teeth in the *Carnivora*, especially the smallest ones, tend to be lost in the course of the animal's life and their alveoli to be overgrown, hence the older an animal is the more probable it becomes to recognize a tooth lack incorrectly as congenital. Therefore, the data on oligodontics have been presented according to age classes.

2.5. Statistical Methods

The new multiple range test (Duncan, 1955) has been used for testing the differences between means, while the significance of the differences between frequency distributions has been discovered using the χ^2 test. The Pearson product-moment correlation coefficient r has been used to express left-right dental asymmetry.

2.6. Abbreviations

F	females	N	number of teeth
M	males	O.R.	observed range
l	left body side	\bar{x}	mean
r	right body side	s	standard deviation
n	number of skulls	V	coefficient of variation

Other abbreviations are defined where used.

3. RESULTS

3.1. Quantitative Variation

3.1.1. Variation in Measurements

Table 1 shows variation in the tooth measurements. The coefficients of variation (V) range from 3.9 to 7.7 for *M. martes* and from 2.7 to 10.0 for *M. foina*. In both the species, they reach the lowest values for WM¹ and the highest ones for DM₂. For P³ the width is distinctly more variable than the length, with the ranges of the coefficients of variation being respectively 5.7—7.3 and 3.9—4.8, in *M. martes*, while in *M. foina* both the dimensions are practically equally variable, with the ranges being 4.0—5.5 and 4.1—6.2 respectively. For M¹ the length distinctly exceeds the width in variability in both the species, with the ranges of the coefficients of variation being respectively 5.8—6.3 and 3.9—4.1 in *M. martes*, and 6.4—7.0 and 2.7—4.3 in *M. foina*. The ranges of the coefficient of variation for WM₂ are 4.5—4.9 in *M. martes* and 4.5—5.4 in *M. foina*, while for DM₂ they are 7.0—7.7 and 7.8—10.0 respectively.

Table 2 shows a statistical significance of differences between means, calculated for each pairwise combination of the means listed in Table 1 within each tooth measurement. The differences between *M. martes* and *M. foina* have appeared to be highly significant ($P < 0.001$) in most cases. Both for the two species and for all the measurements, the means have been discovered to be highly significantly ($P < 0.001$) higher for males than for females of the same species.

Table 1
Descriptive statistics for the tooth measurements made (mm), according to sex and body side.

Measur- ement	Sex	Body side	<i>Martes martes</i>					<i>Martes foina</i>				
			n=N	O.R.	\bar{x}	s	V	n=N	O.R.	\bar{x}	s	V
LP ^s	F	l	87	4.45—5.40	4.91	0.19	3.9	13	4.65—5.40	4.97	0.21	4.1
		r	92	4.45—5.75	4.96	0.23	4.7	13	4.55—5.30	4.93	0.21	4.2
	M	l	125	4.60—6.00	5.38	0.26	4.8	30	4.50—5.85	5.21	0.32	6.2
		r	119	4.85—6.00	5.41	0.23	4.3	30	4.70—5.80	5.26	0.27	5.2
WP ^s	F	l	87	2.30—3.10	2.71	0.15	5.7	13	2.35—2.70	2.57	0.10	4.0
		r	92	2.40—3.65	2.73	0.18	6.5	13	2.40—2.80	2.57	0.11	4.3
	M	l	125	2.40—3.95	3.02	0.21	6.9	30	2.35—3.00	2.72	0.15	5.5
		r	119	2.65—3.95	3.03	0.22	7.3	30	2.50—3.00	2.75	0.14	5.0
LM ¹	F	l	92	4.95—6.85	5.58	0.33	5.9	13	4.40—5.55	4.87	0.32	6.5
		r	89	4.65—6.30	5.56	0.32	5.8	13	4.30—5.50	4.84	0.34	7.0
	M	l	122	5.35—7.25	6.28	0.39	6.3	30	4.95—6.60	5.52	0.36	6.5
		r	122	5.45—7.25	6.25	0.39	6.3	30	5.00—6.50	5.45	0.35	6.4
WM ¹	F	l	92	7.15—8.85	7.82	0.30	3.9	13	7.35—8.25	7.93	0.23	2.9
		r	90	7.15—8.90	7.86	0.32	4.1	13	7.50—8.30	7.98	0.22	2.7
	M	l	121	7.55—9.55	8.51	0.35	4.1	29	7.85—9.20	8.36	0.30	3.6
		r	122	7.85—9.55	8.57	0.34	4.0	29	7.95—9.40	8.45	0.36	4.3
WM ₁	F	l	89	2.80—4.20	3.78	0.19	4.9	13	3.40—4.15	3.83	0.20	5.4
		r	87	3.10—4.25	3.77	0.17	4.5	13	3.35—4.20	3.81	0.20	5.3
	M	l	122	3.30—4.65	4.14	0.19	4.7	28	3.85—4.45	4.17	0.19	4.5
		r	121	3.35—4.60	4.13	0.19	4.7	29	3.80—4.45	4.18	0.20	4.7
DM ₂	F	l	84	2.55—3.65	3.21	0.24	7.5	12	2.70—3.65	3.12	0.31	10.0
		r	82	2.60—3.75	3.22	0.23	7.1	13	2.60—3.60	3.09	0.29	9.3
	M	l	108	3.20—4.45	3.71	0.26	7.0	29	3.05—4.00	3.45	0.27	7.8
		r	109	2.90—4.70	3.69	0.29	7.7	28	2.70—4.05	3.42	0.29	8.5

Table 2

Differences between the means for the tooth measurements made, based on data from Table 1.
 -=not significant ($P>0.05$), +=significant ($0.001<P<0.05$), ++=highly significant ($P<0.001$).

		<i>Martes martes</i>				<i>Martes foina</i>				<i>Martes martes</i>				<i>Martes foina</i>			
		F		M		F		M		F		M		F		M	
		l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
		LP ³								WP ³							
<i>Martes foina</i>	M r	++	++	+		++	++	+		-	-	++	++	++	++	+	
	l	++	++	++	++	++	++	++	++	-	-	++	++	++	++	++	++
<i>Martes martes</i>	F r	-	-	++	++	-				++	++	++	++	-			
	l	-	-	++	++					++	++	++	++				
<i>Martes martes</i>	M r	++	++	-						++	++	-					
	l	++	++							++	++						
<i>Martes martes</i>	F r	-								-							
	l																
		LM ¹								WM ¹							
<i>Martes foina</i>	M r	-	-	++	++	++	++	+		++	++	-	-	++	++	-	
	l	-	-	++	++	++	++	++	++	++	++	+	++	++	++	++	++
<i>Martes martes</i>	F r	++	++	++	++	-				-	-	++	++	-			
	l	++	++	++	++					-	-	++	++				
<i>Martes martes</i>	M r	++	++	-						++	++	-					
	l	++	++							++	++						
<i>Martes martes</i>	F r	-								-							
	l																
		WM ₁								DM ₂							
<i>Martes foina</i>	M r	++	++	-	-	++	++	+		++	++	++	++	++	++	++	-
	l	++	++	-	-	++	++			++	++	++	++	++	++	++	
<i>Martes martes</i>	F r	-	-	++	++	-				+	+	++	++	-			
	l	-	-	++	++					-	-	++	++				
<i>Martes martes</i>	M r	++	++	-						++	++	-					
	l	++	++							++	++						
<i>Martes martes</i>	F r	-								-							
	l																

3.1.2. Variation in Indexes

Table 3 and Figs. 2, 3, and 4 show variation in the indexes calculated basing on the tooth measurements. The coefficients of variation (V) range from 5.0 to 7.8 for *M. martes* and from 4.6 to 9.9 for *M. foina*. In both the species, they reach the lowest values for the index $(LM^1 \times 100)/WM^1$ and the highest ones for the index $(DM_2 \times 100)/WM_1$.

Table 4 shows a statistical significance of the differences between means and between frequency distributions, calculated for each pairwise combination of the means listed in Table 3 within each index and the absolute frequency distributions shown in Figs. 2, 3, and 4 within each

Table 3

Descriptive statistics for the indexes calculated from the measurements of the left and right teeth, according to sex (see Table 1; Figs. 2, 3, and 4).

Index	Sex	<i>Martes martes</i>						<i>Martes foina</i>					
		n	N	O.R.	\bar{x}	s	V	n	N	O.R.	\bar{x}	s	V
$\frac{WP^1}{LF^1} \times 100$	F	92	179	46.1—70.2	55.23	3.61	6.5	13	26	48.0—56.1	51.99	2.42	4.6
	M	125	244	45.6—73.8	56.19	4.29	7.6	30	60	43.9—64.0	52.33	3.58	6.8
$\frac{LM^1}{WM^1} \times 100$	F	93	181	61.1—86.2	71.07	3.85	5.4	13	26	53.1—67.9	60.96	3.33	5.5
	M	125	243	63.5—83.9	73.36	3.68	5.0	30	58	57.4—71.4	65.08	3.22	4.9
$\frac{DM_2}{WM_1} \times 100$	F	89	163	67.5—107.8	85.17	6.65	7.8	13	25	68.4—94.7	81.26	8.06	9.9
	M	118	216	73.4—114.1	89.46	6.73	7.5	29	56	65.1—96.5	82.49	6.29	7.6

of the figures. For all the indexes, the means are highly significantly ($P < 0.001$) higher in *M. martes* than in *M. foina*. Also the frequency distributions for the two species are highly significantly ($P < 0.001$) displaced by each other. Likewise, within both the species, the means

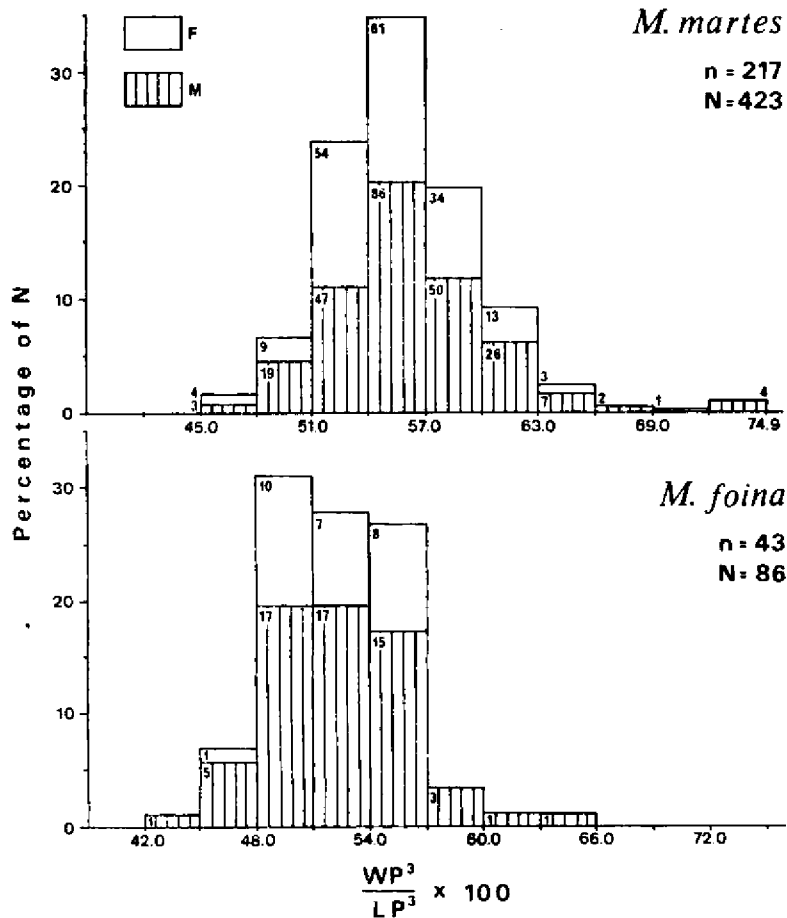


Fig. 2. Frequency distributions of the values of the index $(WP^3 \times 100) / LP^3$ calculated for the left and right teeth (see Table 3). Numbers given in/near rectangles of the histograms show the absolute frequencies of the index values for a given rectangle.

are higher for the males than for the females and the frequency distributions for both sexes are displaced by each other, highly significantly ($F < 0.001$) for the index $(LM^1 \times 100) / WM^1$, not significantly ($P > 0.05$) for the index $(WP^3 \times 100) / LP^3$, and for the index $(DM_1 \times 100) / WM_1$ highly

significantly ($P < 0.001$) in *M. martes* and significantly ($0.001 < P < 0.05$) for the frequency distributions or not significantly ($P > 0.05$) for the means in *M. foina*.

3.2. Qualitative Variation

3.2.1. Morphotypical Variation

Fig. 6 shows variation in the morphotypes of group A (Fig. 5). All four morphotypes of the group have been found in P³ of *M. martes*, whereas in *M. foina* the morphotypes A 1 and A 2 have only occurred. In *M. martes*, the most frequent is the morphotype A 3, followed by A 2, A 1, and A 4, while in *M. foina* it is the morphotype A 1, followed by A 2.

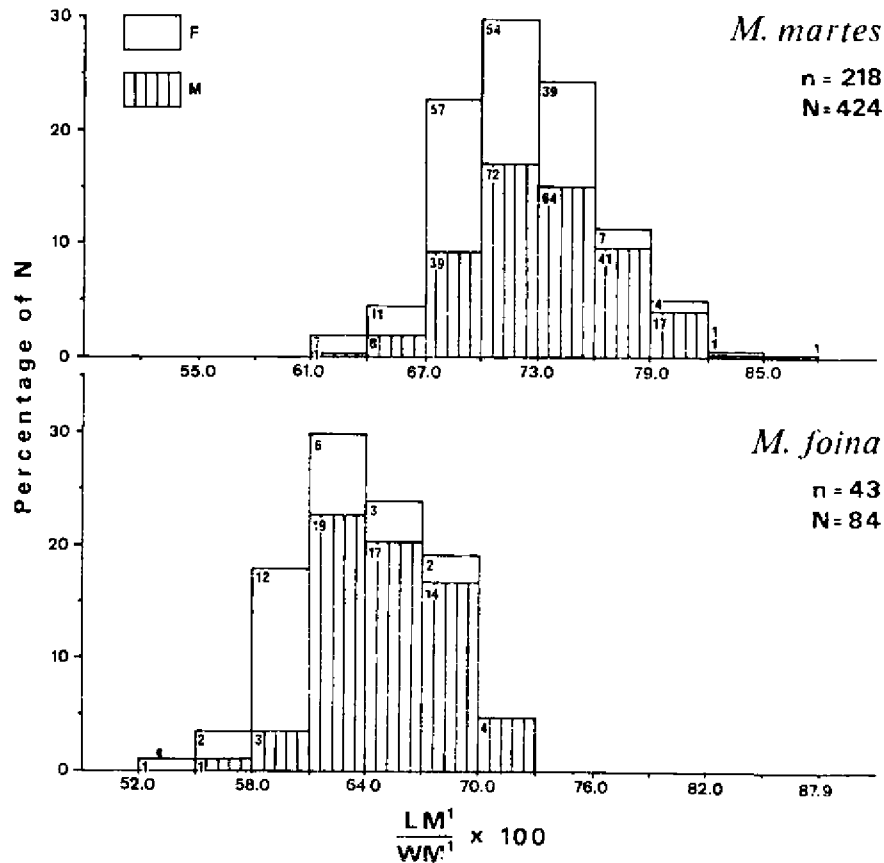


Fig. 3. Frequency distributions of the values of the index $(LM^1 \times 100) / WM^1$ calculated for the left and right teeth (see Table 3). Numbers given in/near rectangles of the histograms show the absolute frequencies of the index values for a given rectangle.

The frequency distributions of the morphotypes for both the species differ highly significantly ($P < 0.001$), whereas there is no significant difference ($P > 0.05$) between those for the males and females of the same species.

Fig. 8 shows variation in the morphotypes of group B (Fig. 7). For P_3 , the morphotypes B 1, B 2, and B 3 have been found in *M. martes*,

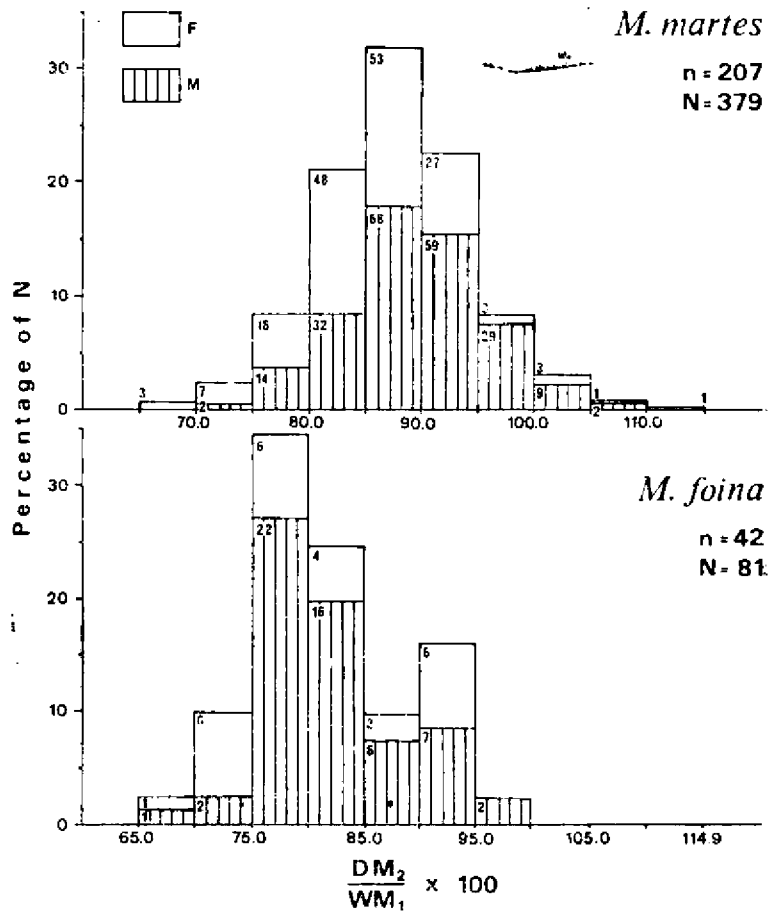


Fig. 4. Frequency distributions of the values of the index $(DM_2 \times 100) / WM_1$ calculated for the left and right teeth (see Table 3). Numbers given in/near rectangles of the histograms show the absolute frequencies of the index values for a given rectangle.

while in *M. foina* the morphotypes B 1 and B 2 have only occurred. The most frequent in both the species is the morphotype B 1, followed by B 2, and in *M. martes* also by B 3. There is no significant difference ($P > 0.05$) both between the frequency distributions of the morphotypes for the two species and between those for both sexes within the same.

species. For P_4 , the morphotypes B 2, B 3, B 4, and B 5 have been found in *M. martes*, while in *M. foina* all five morphotypes of the group have occurred. In *M. martes*, the most frequent are the morphotypes B 4 and B 3, followed by B 2 and B 5, whereas in *M. foina* it is the morphotype B 5, followed by B 4, B 1, B 3, and B 2. The frequency distributions of the morphotypes for both the species differ highly significantly ($P < 0.001$), while there is no significant difference ($P > 0.05$) between those for the males and females of the same species.

Fig. 10 shows variation in the morphotypes of group C (Fig. 9). The morphotypes C 1 and C 2 have been found in M^1 of *M. martes*, while in

Table 4

Differences between the means and between the absolute frequency distributions (in parentheses) for the indexes calculated, based on data from Table 3 and Figs. 2, 3, and 4 respectively. --=not significant ($P > 0.05$), +=significant ($0.001 < P < 0.05$), ++=highly significant ($P < 0.001$).

		<i>Martes martes</i>		<i>Martes foina</i>	
		F	M	F	M
(WP ² × 100)/LP ²					
<i>Martes foina</i>	M	++(++)	++(++)	--(--)	
	F	++(++)	++(++)		
<i>Martes martes</i>	M	--(--)			
	F				
(LM ¹ × 100)/WM ¹					
<i>Martes foina</i>	M	++(++)	++(++)	++(++)	
	F	++(++)	++(++)		
<i>Martes martes</i>	M	++(++)			
	F				
(DM ₂ × 100)/WM ₁					
<i>Martes foina</i>	M	+(++)	++(++)	--(+)	
	F	++(++)	++(++)		
<i>Martes martes</i>	M	++(++)			
	F				

M. foina all three morphotypes of the group have occurred. In *M. martes*, the most frequent is the morphotype C 1, followed by C 2, whereas in *M. foina* it is the morphotype C 3, followed by C 2 and C 1. The frequency distributions of the morphotypes for both the species differ highly significantly ($P < 0.001$), while there is no significant difference ($P > 0.05$) between those for the males and females of the same species.

Table 5 shows variation in the morphotypes of group D (Fig. 11). All ten morphotypes of the group have been found in M^1 of *M. martes*, while in *M. foina* the morphotypes D 1, D 2, D 6, and D 8 have only

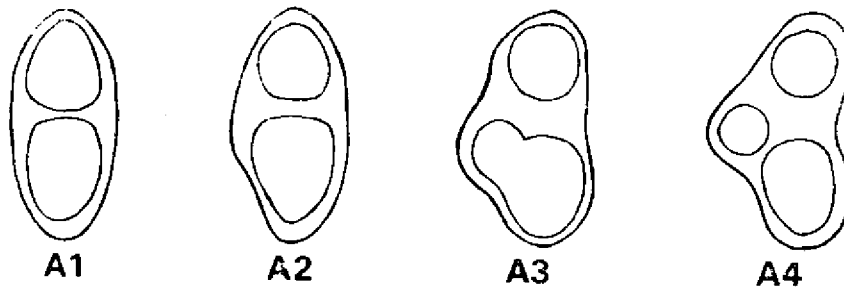


Fig. 5. Diagrams of the morphotypes of group A (for definitions see p. 81).

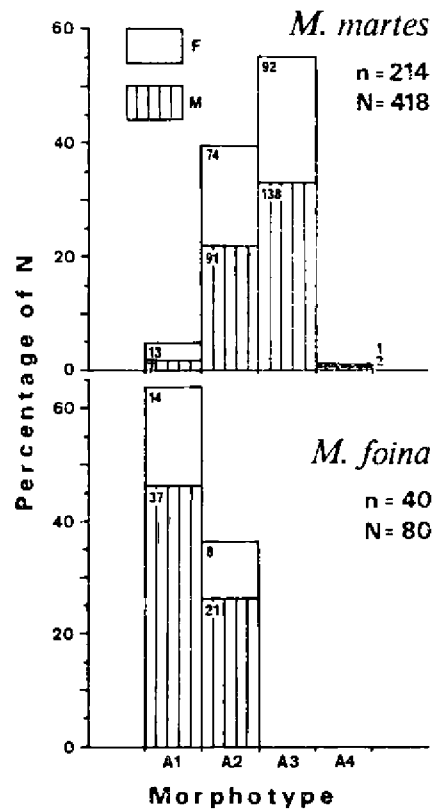


Fig. 6. Frequency distributions of the morphotypes of group A (Fig. 5) for the left and right P³s. Numbers given in/near rectangles of the histograms show the absolute frequencies of the morphotypes for a given rectangle.

occurred. In both the species, the most frequent is the morphotype D 1, with the frequency nearly 89%, second most frequent is the morphotype D 2 (about 5%), and all other morphotypes have occasionally been observed with the frequencies less than 4%.

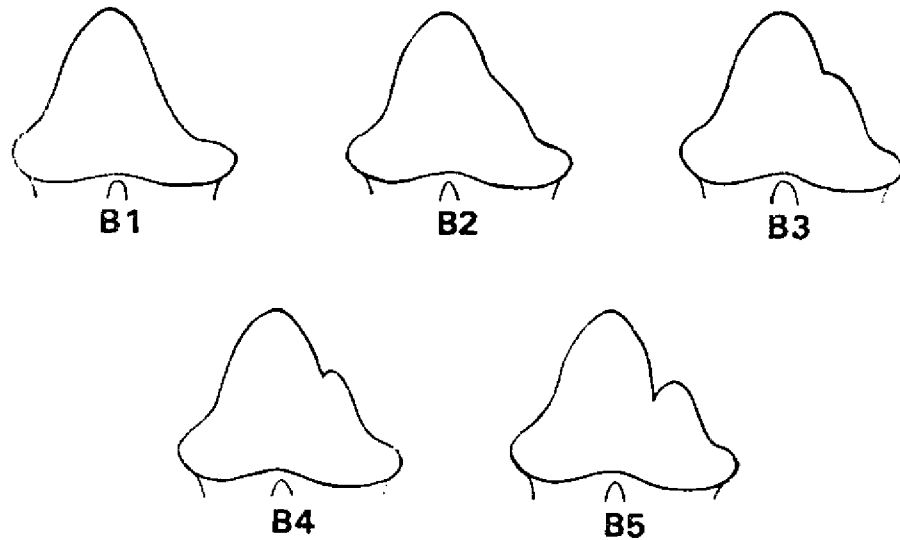


Fig. 7. Diagrams of the morphotypes of group B (for definitions see p. 82).

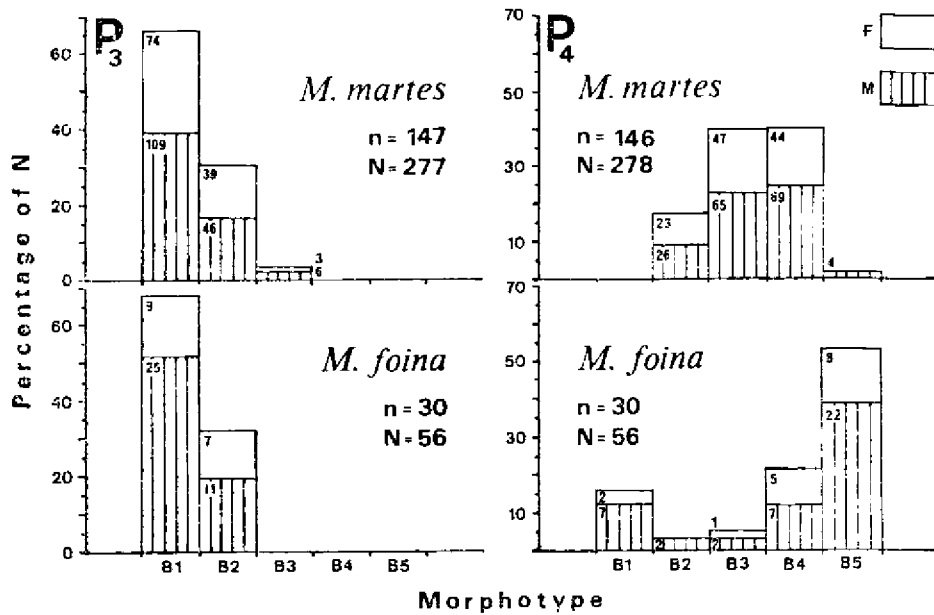


Fig. 8. Frequency distributions of the morphotypes of group B (Fig. 7) for the left and right P₃s and P₄s. Numbers given in/near rectangles of the histograms show the absolute frequencies of the morphotypes for a given rectangle.

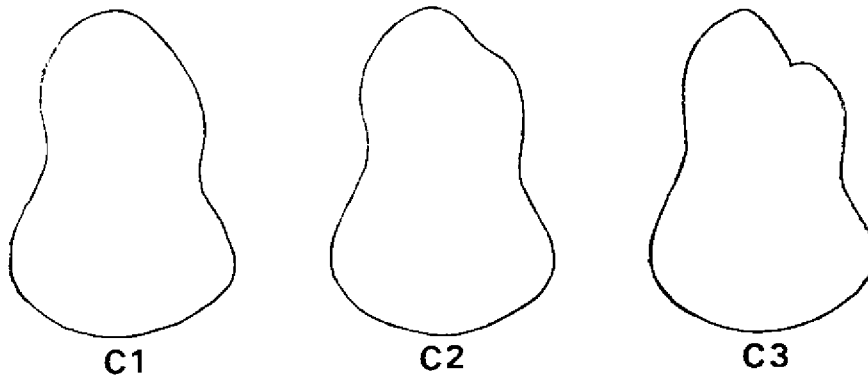


Fig. 9. Diagrams of the morphotypes of group C (for definitions see p. 82).

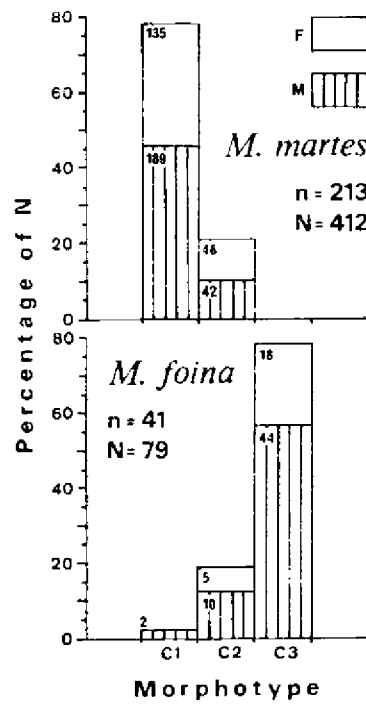


Fig. 10. Frequency distributions of the morphotypes of group C (Fig. 9) for the left and right M's. Numbers given in/near rectangles of the histograms show the absolute frequencies of the morphotypes for a given rectangle.

Fig. 13 shows variation in the morphotypes of group E (Fig. 12). Two morphotypes distinguished have been found in both the species. In *M. martes*, however, the most frequent is the morphotype E 2, whereas

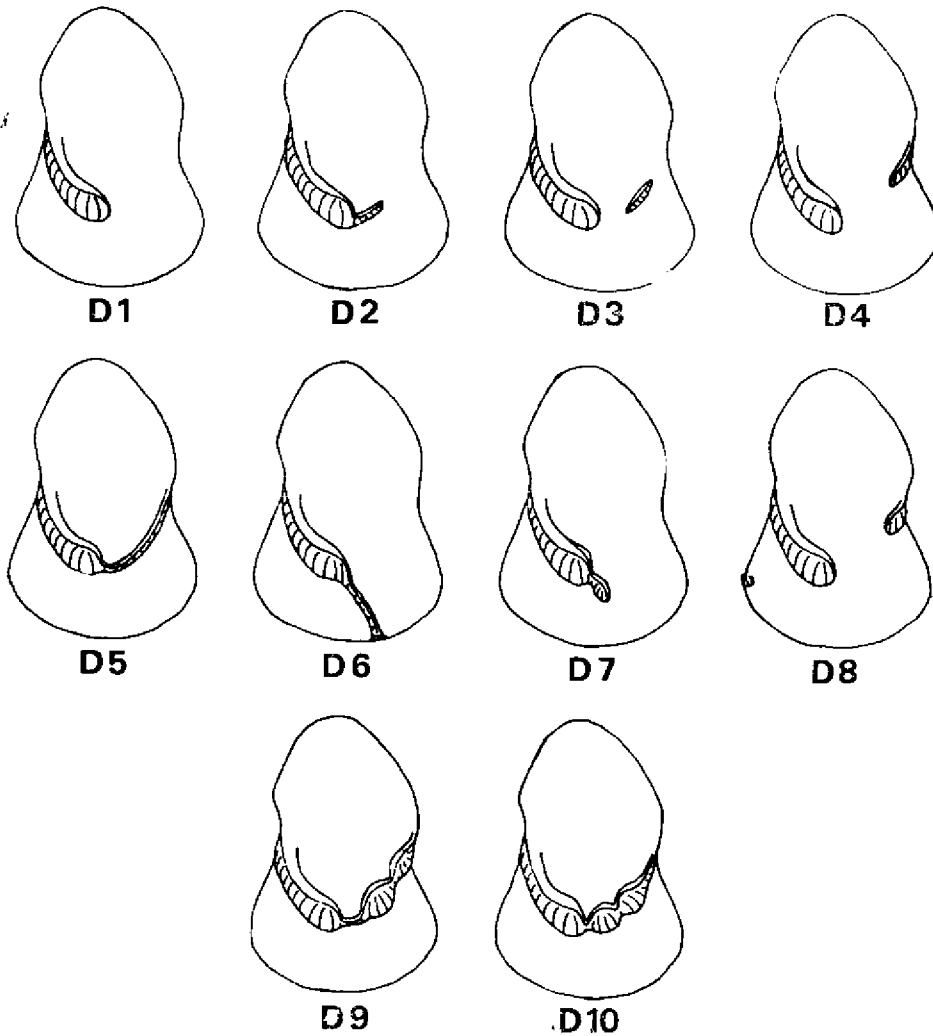


Fig. 11. Diagrams of the morphotypes of group D (for definitions see p. 82).

in *M. foina* it is E 1. The frequency distributions of the morphotypes for both the species differ highly significantly ($P < 0.001$), while there is no significant difference ($P > 0.05$) between those for the males and females of the same species.

3.2.2. Oligodonty

There are no extra teeth in the examined martens. There are no dental anomalies in the stone martens either, while those found in the pine martens have been described in an earlier paper (Wolsan, 1984 a).

Table 5

Absolute and percentage (in parentheses) frequency distributions of the morphotypes of group D (Fig. 11) for the left and right M's, according to sex.

Morphotype	<i>Martes martes</i> (n=198, N=390)			<i>Martes foina</i> (n=40, N=79)		
	F	M	Total	F	M	Total
D 1	141 (36.2)	205 (52.6)	346 (88.7)	26 (32.9)	44 (55.7)	70 (88.6)
D 2	6 (1.6)	13 (3.3)	19 (4.9)	0 (0)	4 (5.1)	4 (5.1)
D 3	1 (0.3)	0 (0)	1 (0.3)	0 (0)	0 (0)	0 (0)
D 4	0 (0)	3 (0.8)	3 (0.8)	0 (0)	0 (0)	0 (0)
D 5	5 (1.3)	1 (0.3)	6 (1.5)	0 (0)	0 (0)	0 (0)
D 6	0 (0)	1 (0.3)	1 (0.3)	0 (0)	3 (3.8)	3 (3.8)
D 7	2 (0.5)	1 (0.3)	3 (0.8)	0 (0)	0 (0)	0 (0)
D 8	6 (1.6)	2 (0.5)	8 (2.1)	0 (0)	2 (2.5)	2 (2.5)
D 9	0 (0)	1 (0.3)	1 (0.3)	0 (0)	0 (0)	0 (0)
D10	2 (0.5)	0 (0)	2 (0.5)	0 (0)	0 (0)	0 (0)

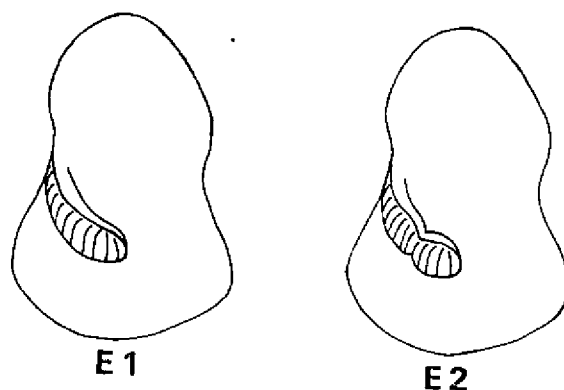


Fig. 12. Diagrams of the morphotypes of group E (for definitions see p. 82).

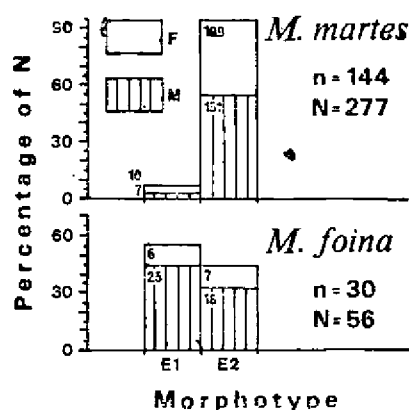


Fig. 13. Frequency distributions of the morphotypes of group E (Fig. 12) for the left and right M's. Numbers given in/near rectangles of the histograms show the absolute frequencies of the morphotypes for a given rectangle.

Table 6

Frequency distributions of the missing P¹, P₁, and M₂ (N) and the skulls showing absence of the teeth (n), according to sex and age class. Actual number of occurrence of each variant and number of scored teeth and skulls respectively as well as percentage in parentheses are given.

Tooth	Age class	F				M				Total (F and M)			
		N	(%)	n	(%)	N	(%)	n	(%)	N	(%)	n	(%)
<i>Martes martes</i>													
P ¹	1	0/0		0/0		0/2	(0)	0/1	(0)	0/2	(0)	0/1	(0)
	2	0/40	(0)	0/20	(0)	0/46	(0)	0/23	(0)	0/86	(0)	0/43	(0)
	3	0/95	(0)	0/48	(0)	0/109	(0)	0/55	(0)	0/204	(0)	0/103	(0)
	4	0/32	(0)	0/16	(0)	0/74	(0)	0/37	(0)	0/106	(0)	0/53	(0)
	5	0/18	(0)	0/9	(0)	0/13	(0)	0/7	(0)	0/31	(0)	0/16	(0)
Total	1—5	0/185	(0)	0/93	(0)	0/244	(0)	0/123	(0)	0/429	(0)	0/216	(0)
P ₁	1	0/0		0/0		0/2	(0)	0/1	(0)	0/2	(0)	0/1	(0)
	2	6/38	(15.8)	4/19	(21.1)	2/46	(4.3)	1/23	(4.3)	8/84	(9.5)	5/42	(11.9)
	3	8/93	(8.6)	5/47	(10.6)	1/108	(0.9)	1/54	(1.9)	9/201	(4.5)	6/101	(5.9)
	4	4/31	(12.9)	3/16	(18.7)	4/74	(5.4)	2/37	(5.4)	8/105	(7.6)	5/53	(9.4)
	5	0/18	(0)	0/9	(0)	2/13	(15.4)	1/7	(14.3)	2/31	(6.5)	1/16	(6.2)
Total	1—5	18/180	(10.0)	12/91	(13.2)	9/243	(3.7)	5/122	(4.1)	27/423	(6.4)	17/213	(8.0)
M ₂	1	0/0		0/0		0/2	(0)	0/1	(0)	0/2	(0)	0/1	(0)
	2	2/38	(5.3)	1/19	(5.3)	0/46	(0)	0/23	(0)	2/84	(2.4)	1/42	(2.4)
	3	0/94	(0)	0/47	(0)	0/109	(0)	0/55	(0)	0/203	(0)	0/102	(0)
	4	0/32	(0)	0/16	(0)	0/74	(0)	0/37	(0)	0/106	(0)	0/53	(0)
	5	0/18	(0)	0/9	(0)	0/14	(0)	0/7	(0)	0/32	(0)	0/16	(0)
Total	1—5	2/182	(1.1)	1/91	(1.1)	0/245	(0)	0/123	(0)	2/427	(0.5)	1/214	(0.5)
Total (P ¹ , P ₁ , and M ₂)	1—5	20/180	(11.1)	13/91	(14.3)	9/243	(3.7)	5/122	(4.1)	29/423	(6.9)	18/213	(8.5)

Table 6, concluded.

<i>Martes foina</i>													
P ¹	1	0/0		0/0		0/0		0/0		0/0		0/0	
	2	0/4	(0)	0/2	(0)	0/8	(0)	0/4	(0)	0/12	(0)	0/6	(0)
	3	0/16	(0)	0/8	(0)	0/34	(0)	0/17	(0)	0/50	(0)	0/25	(0)
	4	1/4	(25.0)	1/2	(50.0)	0/8	(0)	0/4	(0)	1/12	(8.3)	1/6	(16.7)
	5	0/0		0/0		0/6	(0)	0/3	(0)	0/6	(0)	0/3	(0)
Total	1—5	1/24	(4.2)	1/12	(8.3)	0/56	(0)	0/23	(0)	1/80	(1.2)	1/10	(2.5)
P ₁	1	0/0		0/0		0/0		0/0		0/0		0/0	
	2	0/4	(0)	0/2	(0)	1/8	(12.5)	1/4	(25.0)	1/12	(8.3)	1/6	(16.7)
	3	3/16	(18.7)	2/8	(25.0)	2/32	(6.2)	2/16	(12.5)	5/48	(10.4)	4/24	(16.7)
	4	0/4	(0)	0/2	(0)	1/8	(12.5)	1/4	(25.0)	1/12	(8.3)	1/6	(16.7)
	5	0/0		0/0		3/6	(50.0)	2/3	(66.7)	3/6	(50.0)	2/3	(66.7)
Total	1—5	3/24	(12.5)	2/12	(16.7)	7/54	(13.0)	6/27	(22.2)	10/78	(12.8)	8/39	(20.5)
M ₂	1	0/0		0/0		0/0		0/0		0/0		0/0	
	2	0/4	(0)	0/2	(0)	0/8	(0)	0/4	(0)	0/12	(0)	0/6	(0)
	3	0/16	(0)	0/8	(0)	0/32	(0)	0/16	(0)	0/48	(0)	0/24	(0)
	4	0/4	(0)	0/2	(0)	0/8	(0)	0/4	(0)	0/12	(0)	0/6	(0)
	5	0/0		0/0		0/6	(0)	0/3	(0)	0/6	(0)	0/3	(0)
Total	1—5	0/24	(0)	0/12	(0)	0/54	(0)	0/27	(0)	0/78	(0)	0/39	(0)
Total (P ¹ , P ₁ , and M ₂)	1—5	4/24	(16.7)	3/12	(25.0)	7/54	(13.0)	6/27	(22.2)	11/78	(11.1)	9/39	(23.1)

Some of the tooth deficiencies described by the author clearly result from developmental disturbances in the embryogeny caused by the influence of environmental factors. There are, however, also those caused most probably by a mutation. Such congenital deficiencies affected the right I₁ in the juvenile (age class 2) and subadult (age class 3) females of *M. martes* (Wolsan, 1984a).

Other cases of congenital oligodonties found in the examined material, which may be included in Wolsan's (1984b) first group of congenital departures from the typical number, shape, or size of mammalian teeth, affect the smallest and peripheral teeth of the cheek dentition. Their frequency distributions are shown in Table 6. Both in *M. martes* and in *M. foina*, the most frequently missing tooth is P₁. In addition, the bilateral absence of M₂ has occurred in a female of *M. martes* and P¹ has been found to be unilaterally missing in a female of *M. foina*. The oligodonty is more frequent in *M. foina*, where it affects 23.1% of the scored skulls and 14.1% of the scored teeth, than in *M. martes*, where the corresponding values are 8.5% and 6.9%. Furthermore, it is a more frequent phenomenon in females than in males, both in *M. martes*, where it affects respectively 14.3% and 4.1% of the scored skulls and 11.1% and 3.7% of the scored teeth, and in *M. foina*, where the corresponding values are 25.0% and 22.2% for the skulls and 16.7% and 13.0% for the teeth. The tooth deficiencies noted, assumed to be congenital, involve for the most part the age classes 2–4. Thus, it seems that only for some of the missing P₁s noted in the stone martens of age class 5 there is a high probability of incorrect recognition of a tooth lack as congenital.

3.3. Asymmetry

3.3.1. Asymmetry in Quantitative Traits

Table 7 shows the amount of bilateral asymmetry for the tooth measurements. The correlation coefficients (r), used as a measure of the left-right asymmetry, range from 0.647 to 0.921 for *M. martes* and from 0.422 to 0.953 for *M. foina*. They reach the lowest values for WP³ and LP³, ranging from 0.647 to 0.782, in *M. martes*, and for LP³ and WM¹, with the ranges being respectively 0.422–0.591 and 0.730–0.827, in *M. foina*. The correlation coefficients for the remaining measurements are of distinctly higher values in both the species, ranging from 0.801 to 0.953. For P³ the width is slightly more asymmetrical than the length, with the ranges of the correlation coefficients being respectively 0.647–0.757 and 0.672–0.782 in *M. martes*, whereas in *M. foina* the length has distinctly greater asymmetry than the width, with the ranges being

respectively 0.422—0.591 and 0.801—0.953. For M^1 the length is slightly more asymmetrical than the width, showing the correlation coefficients ranging from 0.853 to 0.889 and from 0.856 to 0.915 respectively, in *M. martes*, while in *M. foina* the width distinctly exceeds the length in asymmetry, with the correlation coefficients ranging from 0.730 to 0.827 and from 0.904 to 0.953 respectively. The ranges of the correlation coefficient for WM_1 are 0.818—0.921 in *M. martes* and 0.870—0.920 in *M. foina*, while for DM_2 they are 0.858—0.900 and 0.899—0.918 respectively.

Table 1 shows statistics quantifying variation of the tooth measurements for both body sides. Both in *M. martes* and in *M. foina*, the differences between the coefficients of variation (V) for the left and right body sides are generally distinctly higher for the measurements of M_2 and P^3 than those for M_1 and M^1 . Furthermore, the means of the tooth measurements for both body sides are generally different. The differences, however, are of no significance ($P > 0.05$) (Table 2).

Table 7

Correlation coefficients (r) between the left and right tooth measurements, according to sex (see Table 1).

Measurement	Sex	<i>Martes martes</i>		<i>Martes foina</i>	
		$n = \frac{1}{2} N$	r	$n = \frac{1}{2} N$	r
LP ³	F	87	+0.672	13	+0.422
	M	119	+0.782	30	+0.591
WP ³	F	87	+0.647	13	+0.953
	M	119	+0.757	30	+0.801
LM ¹	F	88	+0.853	13	+0.953
	M	119	+0.889	30	+0.904
WM ¹	F	89	+0.856	13	+0.730
	M	118	+0.915	28	+0.827
WM ₁	F	87	+0.921	13	+0.920
	M	118	+0.818	28	+0.870
DM ₂	F	76	+0.900	12	+0.899
	M	99	+0.858	28	+0.918

3.3.2. Asymmetry in Qualitative Traits

3.3.2.1. Asymmetry in Morphotypes

Table 8 shows the amount of bilateral asymmetry for the occurrence of the morphotypes distinguished. Of the morphotypes of group A, the most asymmetrical in occurrence is A 1, followed by A 4¹, A 2, and A 3, with the frequencies of asymmetrical occurrences being respectively about 73%, 50%, 36%, and 21% in *M. martes*, whereas in *M. foina* it is the morphotype A 2, followed by A 1, with the frequencies of about

Estimation based on a very small number of occurrences.

Table 8

Frequency distributions of the bilateral and unilateral occurrences of the morphotypes distinguished, according to sex (see Table 5; Figs. 6, 8, 10, and 13). Percentage frequencies of the unilateral occurrences are given in parentheses. Where only a very small number of occurrences could be scored no percentage has been calculated; $n=1/2 N$.

Tooth, morphotype, and sex		<i>Martes martes</i> Occurrence		<i>Martes foina</i> Occurrence		
		bilateral	unilateral (%)	bilateral	unilateral (%)	
		n=204		n=40		
P ₃	A 1	F	3	6 (66.7)	5	4 (44.4)
		M	1	5 (83.3)	15	7 (31.8)
	A 2	F	28	17 (37.8)	2	4 (66.7)
		M	35	18 (34.0)	7	7 (50.0)
	A 3	F	39	12 (23.5)	0	0
		M	60	15 (20.0)	0	0
	A 4	F	0	1	0	0
		M	1	0	0	0
		n=130		n=26		
P ₃	B 1	F	29	11 (27.5)	4	1 (20.0)
		M	43	17 (28.3)	11	5 (31.2)
	B 2	F	11	14 (56.0)	3	1 (25.0)
		M	13	18 (58.1)	2	5 (71.4)
	B 3	F	0	3 (100.0)	0	0
		M	1	3 (75.0)	0	0
	B 4	F	0	0	0	0
		M	0	0	0	0
	B 5	F	0	0	0	0
		M	0	0	0	0
		n=132		n=26		
P ₄	B 1	F	0	0	1	0
		M	0	0	2	3 (60.0)
	B 2	F	7	8 (53.3)	0	0
		M	7	10 (58.8)	0	2
	B 3	F	15	17 (53.1)	0	1
		M	20	21 (51.2)	1	0
	B 4	F	15	13 (46.4)	1	3 (75.0)
		M	26	12 (31.6)	2	3 (60.0)
	B 5	F	0	0	3	2 (40.0)
		M	1	1	3	2 (20.0)
		n=199		n=38		
M ¹	C 1	F	61	8 (11.6)	0	0
		M	83	14 (14.4)	1	0
	C 2	F	19	8 (30.0)	1	3 (75.0)
		M	14	14 (50.0)	3	4 (57.1)
	C 3	F	0	0	7	3 (30.0)
		M	0	0	19	4 (17.4)
		n=192		n=39		
M ¹	D 1	F	66	8 (10.8)	13	0 (0)
		M	96	9 (8.6)	20	3 (13.0)
	D 2	F	1	4 (80.0)	0	0
		M	2	9 (81.8)	2	0

Table 8, concluded.

M ¹	D 3	F	0	1	0	0
		M	0	0	0	0
	D 4	F	0	0	0	0
		M	0	3	0	0
	D 5	F	0	5 (100.0)	0	0
		M	0	1	0	0
	D 6	F	0	0	0	0
		M	0	0	1	1
	D 7	F	0	2	0	0
		M	0	1	0	0
	D 8	F	3	0	0	0
		M	0	2	0	2
	D 9	F	0	0	0	0
		M	0	1	0	0
	D10	F	1	0	0	0
		M	0	0	0	0
			n=133	n=26		
M ¹	E 1	F	3	4 (57.1)	2	2 (50.0)
		M	1	5 (83.3)	9	7 (43.7)
	E 2	F	51	4 (7.3)	1	2 (66.7)
		M	69	5 (6.8)	5	7 (58.3)

55⁰/₀ and 35⁰/₀ respectively. Of the morphotypes of group B, in the case of P₃, the most asymmetrical in occurrence is B 3, followed by B 2 and B 1, with the frequencies of asymmetrical occurrences being respectively about 86⁰/₀, 57⁰/₀, and 28⁰/₀ in *M. martes*, and in *M. foina* it is the morphotype B 2, followed by B 1, with the frequencies of about 55⁰/₀ and 29⁰/₀ respectively, whereas in the case of P₄, it is B 2, followed by B 3, B 5¹, and B 4, with the frequencies of about 56⁰/₀, 52⁰/₀, 50⁰/₀¹, and 38⁰/₀ respectively, in *M. martes*, and in *M. foina* it is the morphotype B 2¹, followed by B 4, B 3¹ and B 1, and B 5, with the frequencies of about 100⁰/₀¹, 67⁰/₀, 50⁰/₀¹, 50⁰/₀, and 27⁰/₀ respectively. Of the morphotypes of group C, the most asymmetrical in occurrence is C 2, followed by C 1, with the frequencies of asymmetrical occurrences being respectively about 40⁰/₀ and 13⁰/₀ in *M. martes*, while in *M. foina* it is the morphotype C 2, followed by C 3 and C 1¹, with the frequencies of about 64⁰/₀, 21⁰/₀, and 0⁰/₀¹ respectively. Of the morphotypes of group D, in both the species, the least asymmetrical in occurrence is D 1, with the frequencies of asymmetrical occurrences being about 9⁰/₀ for *M. martes* and about 8⁰/₀ for *M. foina*, whereas the remaining morphotypes have generally occurred asymmetrically. Of the morphotypes of group E, the more asymmetrical in occurrence is E 1, followed by E 2, with the frequencies of asymmetrical occurrences being respectively about 69⁰/₀ and 7⁰/₀ in *M. martes*, whereas in *M. foina* it is E 2, followed by E 1, with the frequencies of about 60⁰/₀ and 45⁰/₀ respectively.

¹ Estimation based on a very small number of occurrences.

3.3.2.2. *Asymmetry in Oligodonties*

Table 9 shows the amount of bilateral asymmetry for the occurrence of the missing cheek teeth in the examined martens. The absence of the most frequently missing tooth, that is of P_1 , has generally occurred asymmetrically in *M. foina*, showing the frequency of about 75% for the unilateral deficiencies, while in *M. martes* it is slightly less frequent, with the frequency of asymmetrical occurrence being about 41%. There was only one case of the absence of P^1 , found asymmetrically in a stone marten, and only in one pine marten has there occurred the symmetrical absence of M_2 . In addition, two pine martens showed the asymmetrically missing I_1 (Wolsan, 1984a).

Table 9

Frequency distributions of the bilateral and unilateral occurrences of the missing P^1 , P_1 , and M_2 , according to sex (see Table 6). Percentage frequencies of the unilateral occurrences are given in parentheses. Where only a very small number of occurrences could be scored no percentage has been calculated; $n=1/2N$.

Tooth	Sex	<i>Martes martes</i> Occurrence		<i>Martes foina</i> Occurrence	
		bilateral	unilateral (%)	bilateral	unilateral (%)
P^1	F	0	0	0	1
	M	0	0	0	0
P_1	F	6	6 (50.0)	1	1 (50.0)
	M	4	1 (20.0)	1	5 (83.3)
M_2	F	1	0	0	0
	M	0	0	0	0

4. DISCUSSION

4.1. Distinction between *M. martes* and *M. foina*

M. martes and *M. foina* are relatively close to each other in dental morphology. As yet a few dental characteristics have been proposed in literature to separate the two species. The present paper suggests several others. All the characteristics, however, show the overlapping ranges of variation in more numerous samples (Kurtén, 1965; Anderson, 1970; the present paper), making the distinctions not so clear as they seem to be. Therefore, as many traits as possible should simultaneously be taken into consideration to increase the probability of correct determination. The dental characteristics suggested to be useful in distinguishing between the two species are:

(1) Those described qualitatively by the morphotypes of group A and quantitatively by the index $(WP^2 \times 100)/LP^2$ (commonly quoted in literature).

(2) The proportions for P^4 : the tooth is longer and its protocone less developed in *M. foina* than in *M. martes*, with the length of the protocone being some half of the width of the blade in *M. foina* and about equal to the width in *M. martes* (commonly quoted).

(3) Those described by the index $(LM^1 \times 100)/WM^1$ (cited by many authors) and the morphotypes of groups C (commonly quoted) and E (the present paper).

(4) The size of P_1 : the tooth is smaller in *M. foina* than in *M. martes* (Kurtén, 1965; Anderson, 1970), which is supported by the more frequent absence of the tooth in *M. foina* than in *M. martes* (Abeljencev, 1968; Cpatrný, 1972, 1973; the present paper)².

(5) Those described by the morphotypes of group B (the present paper).

(6) The relation of the trigonid to the talonid for M_1 : the trigonid is relatively longer in *M. foina* than in *M. martes* (Kurtén, 1965; Anderson, 1970).

(7) Those described by the index $(DM_2 \times 100)/WM_1$ (the present paper).

4.2. Sexual Dimorphism

Members of the family *Mustelidae* are characterized by an especially distinct sexual dimorphism in body size, with males being larger than females. Miller (1912), Rode & Didier (1944), Abeljencev (1968), Anderson (1970), van Bree *et al.* (1970), and Gerasimov (1983a, 1983b) have documented the sexual dimorphism in the dentition of *M. martes* and *M. foina*, showing the teeth of males to be generally larger, especially the canines and the carnassials. The results of the present paper, showing the means of all the tooth measurements, both in *M. martes* and in *M. foina*, to be highly significantly ($P < 0.001$) higher in males than in females, are in agreement with the literature data. However, the observed ranges of the measurements show overlap between sexes. Moreover, the present paper reveals the sexual dimorphism in the proportions of M^1 (especially distinct) and P^3 (poorly marked) as well as in the relative size of M_2 in both the species. The values of the indexes are generally lower for females, but with the observed ranges extensively overlapping between sexes. No sexual dimorphism has been discovered in the frequency distributions of the morphotypes. The females have appeared to be

² It has been evidenced that the progressive reduction in size of a tooth in the course of evolution, accompanied by a simultaneous simplification in its shape, have clearly preceded its phylogenetic loss (Kurtén, 1953; Ziegler, 1971; Hendey, 1980), and that the smaller and more simple in shape a tooth is the more probability there is of its loss (Grüneberg, 1951, 1965, 1976; Kurtén, 1953; Searle, 1954a, 1954b, 1957, 1959, 1960; Grüneberg *et al.*, 1972; Glass & Todd, 1977).

more frequently affected by the congenital tooth loss, which has especially been distinct in *M. martes*. Furthermore, the oligodonties have clearly occurred more frequently in *M. foina* than in *M. martes*, and they have almost exclusively been involved in the smallest of the cheek teeth (P_1), which is smaller in *M. foina* than in *M. martes* (Kurtén, 1965; Anderson, 1970). Thus, it seems very probable that the sexual dimorphism in the frequencies of the congenitally missing P_1 s observed in the present paper results from the sexual dimorphism in size of the tooth (see footnote on p. 103). Abeljencev (1968) did not discover such a dimorphism in the pine and stone martens from the Ukraine, however he considered all the cases of missing teeth, not excluding those being clearly lost during an animal's life.

4.3. Patterns of Variation and Asymmetry in the Cheek Dentition

Nearly all mammals show evidence of a gradient of tooth shape and size in the cheek dentition, with the teeth occupying the central position in the tooth row characterized both by the most complex form and by the greatest dimensions, and the peripheral ones being generally both simplest and smallest among the cheek teeth. Such a morphological gradient is accompanied by gradients in tooth variability (Gingerich, 1974; Gingerich & Schoeninger, 1979; Gingerich & Winkler, 1979; Zhang, 1982; Pengilly, 1984) and bilateral asymmetry (Garn *et al.*, 1967, 1981; Bailit *et al.*, 1970; Garn & Bailey, 1977; Smith *et al.*, 1982), with generally lower variability and asymmetry for the central teeth than for the peripheral ones.

The results of the present study are generally in agreement with the general mammalian patterns of variation and asymmetry characterized above. The most peripheral, simplest in shape and smallest of the measured teeth, M_2 , shows the greatest variability. The congenital oligodonties affect the most simplified in form and smallest peripheral cheek teeth. The bilateral asymmetry is generally greater for P^3 than for the more complex morphologically and greater M_1 and M^1 . However, M_2 , being the most variable, shows relatively great amount of bilateral symmetry. Moreover, there is the apparent relationship between the frequencies of the morphotypes and the asymmetry in their occurrence: the more frequent a morphotype is the lesser asymmetry there is in its occurrence.

4.4. Evolutionary Interpretation of Dental Variation

4.4.1. Variation in P^3

The morphotypes of group A (Fig. 6) and the index $(WP^3 \times 100)/LP^3$ (Fig. 2; Table 3) describe the variation of P^3 in the pine and stone martens from Poland. Judging from the common use of the same morphological

characteristics of P^3 by many authors for discrimination between the two species, most likely also in other populations the dominant morphotypes are A 3 and A 2 for *M. martes* and A 1 for *M. foina*. The other species of the genus *Martes*, both the recent and fossil ones, show various patterns in the morphology of P^3 (see, e.g., Anderson, 1970). All the patterns, however, are contained in the variation range described by the morphotypes of group A. The polymorphism of P^3 found in *M. martes* (Pavlinin, 1962; the present paper), *M. foina* (the present paper), *Martes americana* (Turton, 1806), and *Martes zibellina* (Linnaeus, 1758) (Pavlinin, 1962) is in all likelihood characteristic of the other species of the genus as well. Furthermore, the morphological patterns of P^3 found in the members of the early mustelid genera, such as *Paragale* (Petter, 1967a) and *Plesogale* (Simpson, 1946; de Beaumont, 1968; Müller, 1970), and in the members of the mustelid stem group genera, such as *Plesictis* (Zittel, 1893; Gaillard, 1899; Simpson, 1946; Dehm, 1950; Viret, 1955; Müller, 1970; de Beaumont & Weidmann, 1981), *Broiliana*, *Stromeriella*, *Amphictis* (Dehm, 1950), and *Mustelictis* (Lange, 1970), may also be included in the variation range described by the morphotypes of group A. Moreover, the tooth was clearly polymorphic in some species of the fossil genera mentioned above (e.g. *Stromeriella franconica* Dehm, 1950; see Dehm, 1950), which was probably true also for the other species. The miacids, accepted to be ancestral for the modern *Carnivora* (e.g. Romer, 1966), showed a great variety in the morphological pattern of P^3 , ranging from the three-rooted tooth resembling an isosceles triangle with rounded vertices and concave sides in the crown outline (e.g. *Ictidopappus muselinus* Simpson, 1935; see Simpson, 1937) to the tooth with morphology of the morphotype A 1 (e.g. *Vulpavus ovatus* Matthew, 1909; see Matthew, 1909; Thenius, 1969), with triangle crown outlines being prevailing (Zittel, 1893; Wortman, 1901; Matthew, 1909; Matthew & Granger, 1915; Simpson, 1937; Butler, 1946; Romer, 1966; Thenius, 1969; Müller, 1970; Savage, 1977).

Therefore, there is a general trend in the evolution of the lineage of *M. martes* and *M. foina* involving progressive simplification in the morphological pattern of P^3 . In terms of the trend the morphotype A 4 is most primitive and the morphotype A 1 most progressive. Thus, *M. foina* is more progressive than *M. martes* in respect of the P^3 morphology.

4.4.2. Variation in M^1

4.4.2.1. Variation in the Outer Lobe

The morphotypes of group C describe the variation of the outer lobe of M^1 in the examined martens (Fig. 10). Judging from the common use

of the same morphological characteristics of the M^1 outer lobe to discriminate between the two species, it is most likely also in other populations that the dominant morphotypes are C 1 for *M. martes* and C 3 for *M. foina*. The other living species of the genus *Martes* show various patterns in the morphology of the outer lobe of M^1 (see, e.g., Anderson, 1970). All the patterns, however, are contained in the variation range described by the morphotypes of group C. The polymorphism of the M^1 outer lobe found in *M. martes* (Pavlinin, 1962; the present paper), *M. foina* (Opatrný, 1972; the present paper), *M. americana*, and *M. zibellina* (Pavlinin, 1962) is in all likelihood characteristic of the other species of the genus as well. M^1 in the middle Pleistocene *Martes vetus* Kretzoi, 1942 [= *M. intermedia* Heller, 1933], considered to be the probable ancestor of both studied species (Heller, 1933; Kurtén, 1968; Anderson, 1970), shows a variable indentation of the outer lobe (Heller, 1933; Dehm, 1962; Anderson, 1970; Rabeder, 1976). The tooth in a specimen of the Pliocene *Martes wenzensis* Stach, 1959 (MF/342/60 Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Cracow), which might have been in the direct line of ancestry towards *M. vetus* (Anderson, 1970), represents the morphology of the morphotype C 3 (see also Stach, 1959; Anderson, 1970; Rabeder, 1976; Czyżewska, 1981). There was a concavity in the outline of the outer lobe of M^1 in most other Tertiary martens of the genera *Martes* and *Pliomartes*, very often showing the morphology of the morphotype C 3 (Gaillard, 1899; Viret, 1933; Dehm, 1950; Petter, 1967b; Rabeder, 1976; Ginsburg, 1977; Schmidt-Kittler, 1981). Similar concavities were shown also by the early mustelids of the genera *Paragale* (Petter, 1967a) and *Plesiogale* (Simpson, 1946; de Beaumont, 1968; Müller, 1970) as well as by the members of the mustelid stem group genera, such as *Plesictis* (Zittel, 1893; Gaillard, 1899; Simpson, 1946; Dehm, 1950; Viret, 1955; Müller, 1970; Rabeder, 1976; de Beaumont & Weidmann, 1981; Schmidt-Kittler, 1981), *Broiliana* (Dehm, 1950), *Stromeriella* (Dehm, 1950; Schmidt-Kittler, 1981), *Amphictis* (Dehm, 1950) and *Mustelictis* (Lange, 1970; Schmidt-Kittler, 1981), in which the posterior cusp of the M^1 outer lobe or the metacone was clearly much more developed than it is characteristic of the genus *Martes*. The above was also true for the miacids (e.g. Matthew, 1909).

Therefore, there is a general trend in the evolution of the lineage of *M. martes* and *M. foina* involving progressive reduction of the metacone and postero-buccal root, generally accompanied by decline of the concavity in the outer lobe of M^1 . In terms of the trend the morphotype C 3 is most primitive and the morphotype C 1 most progressive. Thus, *M. martes* is more progressive than *M. foina* in respect of the morphology of the M^1 outer lobe.

4.4.2.2. *Variation in the Relative Length of the Inner Lobe*

The index $(LM^1 \times 100) / WM^1$ describes the variation of the relative length of the inner lobe of M^1 in the Polish martens (Fig. 3; Table 5). Judging from the common use of the relative length of the M^1 inner lobe to discriminate between the two species, most likely also in other populations of the species the values of the index are generally higher for *M. martes* than for *M. foina*. The available specimens of the middle Pleistocene *M. vetus* show the variation in the index values ranging from about 64 to about 70 (calculated from the data of Heller, 1933: Abb. 3, Dehm, 1962: p. 33, Anderson, 1970: Table 3, and Rabeder, 1976: Abb. 26, Fig. 6), while in the Cracow specimen of the Pliocene *M. wenzensis* (MF/342/60) the value is about 63. For the early Pliocene martens, such as *Martes stirtoni* Wilson, 1968, *Martes campestris* Gregory, 1942, and *Martes anderssoni* Schlosser, 1924, the values of the index are about 57, 56, and 42–59 respectively (calculated from the data of Anderson, 1970: Table 2 for the first two species and for the latter from those of Schlosser, 1924: p. 14, Petter, 1967b: Pl. I, Fig. 3b, and Anderson, 1970: Tables 1 and 2), while in the late Miocene *Martes khelifensis* Ginsburg, 1977 it is about 47 (calculated from the data of Ginsburg, 1977: p. 226) and in the available specimens of the early Miocene *Martes laevidens* Dehm, 1950 the values range from about 39 to about 54 (calculated from the data of Dehm, 1950: p. 66, Anderson, 1970: Table 2, and Schmidt-Kittler, 1981: Fig. 21). For the early mustelids *Paragale hürzeleri* Petter, 1967 and *Plesiogale angustifrons* Pomel, 1846 they are about 38 and 39–43 respectively (calculated from the data of Petter, 1967a: Pl. I, Fig. 1d for the former species and for the latter from those of Simpson, 1946 Fig. 4b, de Beaumont, 1968: Fig. 5, and Müller, 1970: Abb. 168B). In the members of the genus *Martes*, the inner lobe of M^1 exceeds the outer one in length. In the genus *Paragale* the two lobes are nearly equally long (Petter, 1967a), whereas in *Plesiogale* the inner lobe is shorter (e.g. Simpson, 1946). Both the members of the mustelid stem group (e.g. Dehm, 1950) and the miacids (e.g. Matthew, 1909) showed the distinctly greater length for the outer lobe.

Therefore, there is a general trend in the evolution of the lineage of *M. martes* and *M. foina* involving progressive relative antero-posterior extension in the inner lobe of M^1 . In terms of the trend *M. martes* is more progressive than *M. foina* in respect of the relative length of the M^1 inner lobe.

4.4.2.3. Variation in the Morphology of the Occlusal Surface of the Inner Lobe

The morphotypes of groups D and E describe the variation in the morphology of the occlusal surface of the inner lobe of M^1 in the martens from Poland (Table 9; Fig. 13). In two recent pine martens from the Soviet Union Pavlinov (1974) found still one morphotype of group D, showing the crescent-shaped crista running across the waist of the tooth from the anterior to posterior cingula. The morphotype D 1 is typical of the living species of the genus *Martes* (e.g. Anderson, 1970), which seems to be true for *M. vetus* as well (Rabeder, 1976). Both the morphotype E 1 and E 2 occur in the living martens, with E 1 being more frequent in *M. foina* and E 2 prevailing in *M. martes* (Rabeder, 1976; the present paper). The morphology of the inner lobe of M^1 in the Cracow specimen of *M. wenzensis* (MF/342/60) resembles the morphotypes D 8 and E 2. Other Tertiary martens of the genera *Martes* and *Pliomartes* showed various patterns in the morphology of the crista, as well as a clear intraspecific polymorphism, ranging from the crescent-shaped crista resembling that described by Pavlinov (1974), which prevailed, to that described by the morphotype D 1, which was relatively rare (Gaillard, 1899; Viret, 1933; Dehm, 1950; Ginsburg, 1961, 1977; Petter, 1967b, 1971; Rabeder, 1976; Schmidt-Kittler, 1981). In the holotype specimen of *Paragale hürzeleri* the crista connects the antero-medial part of the cingulum with its postero-lingual part (Petter, 1967a), whereas a specimen of *Plesiogale angustifrons* reproduced both by Simpson (1946) and by Müller (1970) shows the crista being long but not attaining the posterior cingulum. Both the members of the mustelid stem group (e.g. Dehm, 1950) and the miacids (e.g. Matthew, 1909) generally showed the crescent-shaped crista. In addition, there was a clear depression in the crista in members of the genus *Plesictis* (e.g. de Beaumont & Weidmann, 1981), presumably homologous to the indentation involved in the morphotype E 2.

Therefore, there is a general trend in the evolution of the lineage of *M. martes* and *M. foina* involving progressive simplification and reduction of the crista or the protocone in the inner lobe of M^1 . In terms of the trend the Pavlinov's (1974) morphotype and the morphotypes D 9 and D 10 are most primitive, while the morphotype D 1 is most progressive. Likewise, the morphotype E 2 seems to be more primitive than E 1. Thus, *M. foina* is more progressive than *M. martes* in respect of the morphology of the occlusal surface of the M^1 inner lobe.

4.4.3. Variation in P_3 and P_4

The morphotypes of group B describe the variation in the morphology of the posterior ridge of the protoconid of P_3 and P_4 in the Polish martens

(Fig. 8). Judging by descriptions and figures included in many papers of authors from various countries, it is most likely also in other populations that the dominant morphotypes are B 1 and B 2 for P_3 and B 3 and B 4 for P_4 in *M. martes*, while in *M. foina* they are B 1 and B 5 respectively. P_4 in a specimen of *M. vetus* reproduced both by Dehm (1962) and by Anderson (1970) shows a small posterior accessory cusp, while in the Cracow specimen of *M. wenzensis* (MF/342/60) P_3 and P_4 resemble in morphology the morphotypes B 2 and B 4 respectively, in spite of a slight wear of the teeth. Other members of the genus *Martes*, both the recent and fossil ones, show various patterns in the morphology of P_3 and P_4 , with the former tooth being usually cusplless (the morphotypes B 1—B 3) and the latter cusped (the morphotypes B 4 and B 5). All the patterns, however, are contained in the variation range described by the morphotypes of group B. The polymorphism of P_3 and P_4 found in *M. martes* (Miller, 1912; Pavlinin, 1962; the present paper), *M. foina* (the present paper), *M. americana*, and *M. zibellina* (Pavlinin, 1962) is in all likelihood characteristic of other recent and fossil species of the genus as well. P_4 in a specimen of *Paragale hürzeleri* reproduced by Petter (1967a) resembles the morphotype B 3 in morphology, while in members of the genus *Plesiogale* both P_3 and P_4 were cusped (Dehm, 1950) or resembled the morphotype B 3 (Simpson, 1946; Müller, 1970). All the morphotypes of group B may be seen in the two teeth both in the members of the mustelid stem group (e.g. Dehm, 1950) and in the miacids (e.g. Matthew, 1909), which showed a great variety in respect of the morphology of the posterior ridge of the protoconid.

Therefore, there is a general trend in the evolution of the lineage of *M. martes* and *M. foina* involving progressive simplification in the morphological pattern of the posterior ridge of the protoconid in P_3 and P_4 . In terms of the trend the morphotype B 5 is most primitive and the morphotype B 1 most progressive. P_3 has more distinctly been affected by the trend, resulting in the more simplified morphology than it is for P_4 , which is in accordance with a gradient of tooth shape and size in the cheek dentition.

4.4.4. Variation in P^1 , P_1 , and M_2

Table 6 and Fig. 4 show the variation in number of the cheek teeth and in relative size of M_2 respectively in the Polish martens. Judging by the literature data (Röttcher, 1965; Abeljencev, 1968; Opatrný, 1972, 1973), also other populations of the two species are most likely affected by the congenital tooth loss involving P^1 , P_1 , and M_2 and occurring more frequently in *M. foina* than in *M. martes*, with P_1 being most frequently missing. The above is also true for *M. americana* (Hall, 1940; Marshall,

1952) and most likely for most other members of the genus, in which P^1 , P_1 , and M_2 are typically small one-rooted teeth (e.g. Anderson, 1970). The index $(DM_2 \times 100)/WM_1$ calculated from the means given by Anderson (1970: Table 3) for *M. vetus* is about 93 and that calculated from Dehm's (1962: Taf. 4, Fig. 4b) data is about 102. For the Miocene martens, such as *Martes kinseyi* Gidley, 1927 and *Martes sansaniensis* (Lartet, 1851), the index values are respectively 109 and 105—130 (calculated from the data of Gidley, 1927: Fig. 1 and Ginsburg, 1961: Pl. IX, Fig. 6b, Pl. X, Fig. 4c, respectively). The two-rooted M_2 was characteristic of the most members of the mustelid stem group and P^1 and P_1 were generally less reduced than it is typical of the genus *Martes*, often showing two roots (e.g. Dehm, 1950). The above was also true for a great many miacids (e.g. Matthew, 1909).

Therefore, there is a general trend in the evolution of the lineage of *M. martes* and *M. foina* involving progressive reduction in size, accompanied by simultaneous simplification in shape, with subsequent loss of the peripheral teeth of the cheek dentition. P_1 has most distinctly been affected by the trend. Thus, in terms of the trend *M. foina* is more progressive than *M. martes*.

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ZMIENNOŚĆ I ASYMETRIA W UZĘBIENIU KUNY LEŚNEJ I DOMOWEJ
(*MARTES MARTES* I *M. FOINA*) Z POLSKI

Streszczenie

Badania przeprowadzono na 220 (126 samców i 94 samice) czaszkach kuny leśnej, *Martes martes* (Linnaeus, 1758), oraz 43 (30 samców i 13 samic) czaszkach kuny domowej, *Martes foina* (Erxleben, 1777), pochodzących z obszaru Polski. Dokonano pomiarów długości i szerokości P^3 i M^1 , a także szerokości talonidu M_1 i największej średnicy M_2 (Tabela 1). Na ich podstawie obliczono indeksy charakteryzujące względną szerokość P^3 ($WP^3 \times 100/LP^3$), względną długość płata wewnętrznego M^1 ($LM^1 \times 100/WM^1$) oraz względną wielkość M_2 ($DM_2 \times 100/WM_1$) (Tabela 3; Ryc. 2—4). Wyodrębniono pięć grup morfotypów (A—E) opisujących zmienność morfologiczną P^3 (Ryc. 5 i 6), P_3 i P_4 (Ryc. 7 i 8), oraz M^1 (Tabela 5; Ryc. 9—13), a także obliczono częstości wrodzonych ubytków w uzębieniu policzkowym (Tabela 6). Ponadto scharakteryzowano dwuboczną asymetrię dokonanych pomiarów (Tabela 1 i 7) oraz występowania morfotypów (Tab. 8) i wrodzonych oligodoncji (Tab. 9).

Zakresy zmienności cech uzębienia dla odróżnienia kuny leśnej od domowej, zarówno tych dotychczas proponowanych w literaturze jak i zaprezentowanych po raz pierwszy w tej pracy, zachodzą na siebie. Aby zwiększyć prawdopodobieństwo prawidłowego oznaczenia, powinno się więc rozważać wszystkie możliwe w danym przypadku cechy równocześnie. Do przydatnych pod tym względem należą: (1) zarys cingulum P^3 , związany z liczbą korzeni (morfotypy grupy A i indeks $WP^3 \times 100/LP^3$), (2) wielkość i kształt P^4 , (3) względna długość płata wewnętrznego M^1 (indeks $LM^1 \times 100/WM^1$) oraz zarys cingulum płata zewnętrznego (morfotypy grupy C) i morfologia protokonu (morfotypy grupy E), a także (4) wielkość P_1 , (5) morfologia tylnej krawędzi protokonidu P_3 i P_4 (morfotypy grupy B), (6) stosunek trigonidu M_1 do talonidu, oraz (7) względna wielkość M_2 (indeks $DM_2 \times 100/WM_1$).

Dymorfizm płciowy zaznacza się nie tylko w wielkości zębów, z samcami na ogół większymi od samic, ale także w ich kształcie i tendencji do wrodzonych oligodoncji, bardziej częstszych u samic aniżeli u samców.

Zarówno zmienność jak i asymetria są na ogół większe dla zębów skrajnych uzębienia policzkowego, co związane jest z istnieniem gradientu kształtu i wielkości w szeregu zębowym. Ponadto, stwierdzono związek pomiędzy częstością występowania danego morfotypu w populacji a asymetrycznością jego pojawiania się: im **morfotyp bardziej rzadki tym częściej występuje asymetrycznie** (jednostronnie).

Operując się na danych paleontologicznych, wykazano, że obserwowana u badanych kun zmienność odzwierciedla ich przeszłość filogenetyczną, tzn. warianty skrajne zakresów zmienności mogą być interpretowane jako najbardziej prymitywne lub progresywne.