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Skull Variability of *Martes martes* and *Martes foina* from Poland

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Reig S. & Ruprecht A.L., 1989: Skull variability of *M. martes* and *M. foina* from Poland. Acta theriol., 34, 41: 595—624 [With 13 Tables & 11 Figs]

A morphological study of sex, age, and population variation of *Martes martes* (Linnaeus, 1758) and *Martes foina* (Erxleben, 1777) was completed, using a collection of 236 and 47 skulls, respectively. Twenty-three measurements were taken on each specimen. Three age groups (juveniles, subadults and adults) were recognized, based on relative criteria such as suture obliteration, tooth wear, and development of *crista sagittalis*. Univariate and multivariate techniques were used to process the data. Sex dimorphism was clear, males being on average 12.1% and 9.5% larger than females in *M. martes* and *M. foina*, respectively. Masticatory apparatus was the region of the skull showing more significant sex dimorphism in both species. Statistical significance of sexual dimorphism in particular traits was distinct in both species. Weight and length of the mandible, and zygomatic width showed the highest differences among age classes in both species. In *M. martes*, two principal factors explained more than 70% of the total age variation; the first one was related to length of the skull, accounting for most of the variance (more than 50%), and the second to width of the skull. However, in *M. foina* the total amount of variation explained was also high but the relative importance of the length and width factors was similar. Rostral angle was the best character to classify the skulls into species. Using a dividing point of 54.9°, below which specimens should be classified as *M. martes* and *vice versa*, 98% of the skulls were correctly classified. 100% correct classification of Polish martens was achieved by a discriminant function which used only five skull measurements. Separation of species was also possible by plotting of two principal factors defining a length and width component of skull variation in each sex. Differences between four populations (Pomerania and Masurian Lake Region; Wielkopolska-Kujawy Lowlands; Białowieża Primeval Forest; Lower and Upper Silesia) were studied in *M. martes*. Significant differences were found in eleven measurements, skulls from Białowieża being smaller than from the other three populations. Most of the morphological changes in the skull of martens due to sex, age or species variation were explained by the association of measurements into a length and a width factor. However, in each species the relative importance of these factors to explain the variability observed was different. Phylogenetic and ecological reasons are the only possible explanation for different patterns of variation in the two marten species.

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1. INTRODUCTION

Earlier studies on the morphological characteristics of the pine marten *Martes martes* (Linnaeus, 1758) and the stone marten *M. foina* (Erxleben, 1777) have been dealing with the taxonomic characters

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which allow distinction between the two species (see Anderson, 1970 for review). Attempts to find diagnostic traits are still being made using skull measurements (Altuna, 1973), non metrical characters (Steiner & Steiner, 1986) or multivariate methods (Gerasimov, 1985). Other morphological studies on European martens deal with criteria for age determination (Röttcher, 1965; Habermehl & Röttcher, 1967), sex dimorphism (Bree *et al.*, 1970; Rossolimo & Pavlinov, 1974), or variations in dental morphology (Wolsan *et al.*, 1985, 1986). However, there is no complete information on the morphological pattern of variation of these species related to sex, age, or population differences.

Comparative study of morphological variation in *M. martes* and *M. foina* is particularly interesting because they have strong morphological similarities and at the same time exhibit noticeable differences concerning their ecology and especially the habitat preferences. *M. martes* is more selective for the choice of habitat, being associated with mature coniferous forest (Heptner *et al.*, 1967; Pulliainen, 1981a), while *M. foina* inhabits either mixed or coniferous forest, rocky hillsides, and often being close to human dwellings (Heptner *et al.*, 1967). The aim of this paper is to analyze the variation of the skull related to sex and age changes, the differences between populations and the differences between both species.

2. MATERIAL AND METHODS

This study is based on 236 skulls of *M. martes* and 47 of *M. foina*. Specimens were obtained from the Mammals Research Institute PAS (Białowieża), Institute of Systematic and Experimental Zoology PAS (Cracow), and the private collection of A. L. Ruprecht.

2.1. Age Classes

To avoid interferences due to age variation and to analyze the growth changes in the skull without splitting the material too much, three relative age classes were considered: Juveniles, Subadults and Adults. The criteria followed for this grouping were similar to those used by Buchalczyk & Ruprecht (1977) for *Mustela putorius* Linnaeus, 1758. These include the date of killing, obliteration of *sutura internasalis* and *nasomaxillaris*, general aspect of the skull (development of *crista sagittalis*, appearance of skull bone), degree of "denudation" of the canine teeth, and tooth wear.

Age class I (Juveniles) included martens killed from September to January, already with permanent teeth, clearly marked *sutura internasalis* and *nasomaxillaris*, and rugged aspect of the skull bones. Assuming that birth period takes place in May (Ryabov, 1962), the approximate age of this group was from five to eight months.

Age class II (Subadults) includes animals killed between February and April, with slightly visible sutures, and noticeable development of *crista sagittalis*. The approximate age was from nine to twelve months.

Age class III (Adults) corresponds to specimens killed after March of their first year, having smooth bone surface, sutures completely obliterated, well developed *crista sagittalis* and visible tooth wear. These martens were considered to be older than one year.

2.2. Cranial Measurements

Twenty three measurements commonly used in mustelids (Anderson, 1970; Buchalczyk & Ruprecht, 1977) were performed on each specimen, using vernier caliper with an accuracy of 0.1 mm. These were the following:

Length measurements (mm):

1. Condylobasal length	(CbL)
2. Profile length	(PrL)
3. Facial length	(FcL)
4. Braincase length	(BcL)
5. Condylo-molar length	(CmL)
6. Maxillary tooth-row length	(MxtL)
7. Palatal length	(PtL)

Width measurements (mm):

8. Zygomatic width	(ZyW)
9. Ectoorbital width	(EorW)
10. Interorbital constriction	(IorW)
11. Postorbital width	(PorW)
12. Mastoid width	(MstW)
13. Bimolar width	(BmW)
14. Rostrum width	(RtrW)

Mandible measurements (mm):

15. Lower canine length	(LcL)
16. First lower molar length	(LmL)
17. Mandibular tooth-row length	(MntL)
18. Mandible height	(MnbH)
19. Mandible length	(MnbL)
20. Mandible weight (g)	(MnbW)

Others:

21. Braincase height (mm)	(BcbH)
22. Braincase capacity (cc)	(BcC)
23. Rostral angle (°)	(RstA)

Definitions of particular measurements are clearly ascertained from enclosed figures (Fig. 1). RstA was measured following the procedure of Ruprecht (1972). BcC was measured by filling the braincase with fine shot (1.5 mm ф). To increase accuracy, the shot needed to fill the braincase cavity was weighed instead of measuring its volume (1cc=6.3 g).

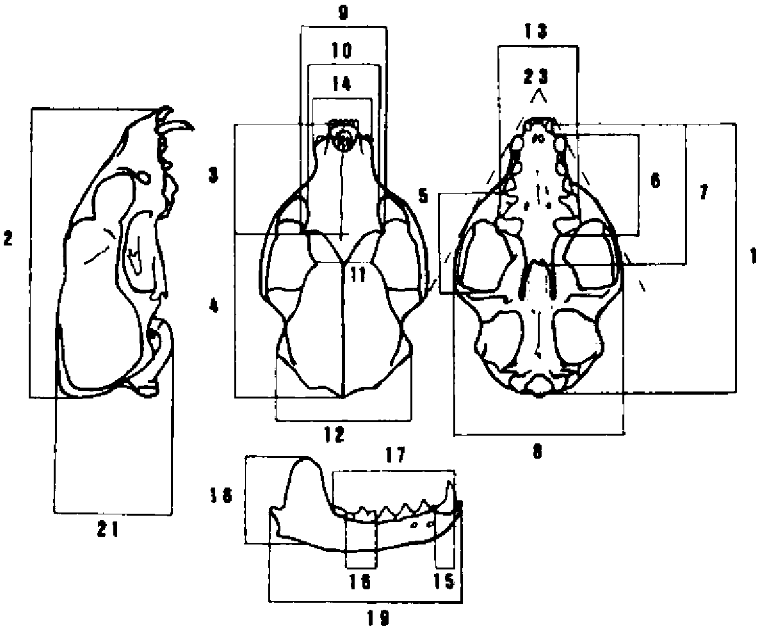

Fig. 1. Skull measuraments used in this study. Numbers indicate measurements listed in the text.

In addition to single measurements, ratios between two of them were calculated. Only those which showed greater significance than single characters in the differences among groups were mentioned in the results, as indicators of changes in skull proportions.

2.3. Population Groups

Differences among populations within the Polish territory were analyzed only in *M. martes* because of the larger number of skulls available. The material examined, adult males only, was grouped into four regions of particular faunistic and geographic significance: (1) Pomerania and Masurian Lake Region; (2) Wielkopolska-Kujawy Lowlands; (3) Białowieża Primeval Forest; (4) Lower and Upper Silesia.

2.4. Statistical Analysis

Sample statistics were calculated separately for each group considered (age class, sex, species). The simplest parameter used for comparison among groups was the percentage difference between means (%D), calculated relative to the group showing the smallest value [%D=(largest value−smallest value/smalest×100). Mean of %D ($\bar{x}_{\%D}$) among the 23 measurements was also calculated, being elucidated as the average size difference between the groups compared. All calculations were made using the computer package BMDP87 (Dixon, 1987).

Univariate methods were mainly restricted to analysis of variance (ANOVA), which tests the significance of the observed variation in individual characters among the respective groups (age class, sex, populations, species). Due to unequal sample size, Levene's test for equality of variances was performed simultaneously to asses the validity of this analysis (BMDP7D, Dixon, 1987). When the results of ANOVA are given, the F value expresses the degree of significance of the differences between groups beyond the $p<0.001$ level. Compared to %D, F epresents to what extent the percentage of differences found among the groups considered (age, sex, species) is due to hazard or not. Attention must be paid to the fact that F value is n-dependent, and hence, comparison of this value with other F obtained from a test performed in a group of different sample size is inappropriate because the degrees of freedom are not equivalent. Other univariate techniques used include pair-wise comparison between group means by Student's t test.

Multivariate analysis was carried out to examine variation from a multidimensional point of view (Sokal & Rinkel, 1963; Gould & Johnston, 1972). Stepwise discriminant analysis (BMDP7M, Dixon, 1987) was ued to construct from the original variables, a discriminant function (represented as canonical variables) which maximally separates the groups analyzed (sex, species). Association between measurements was investigated by Principal Factor Analysis (BMDP4M, Dixon, 1987) (Atchley, 1971b; Baker *et al.*, 1978, Wiig, 1985). This technique transforms the original set of variables into factors that join those measurements having a similar and independent variability pattern. Therefore, factors are characterized by different (opposite) loading's from each variable. Factors were subjected to an orthogonal rotation (Varimax) in order to facilitate interpretation (Atchley, 1971b; Baker *et al.*, 1978).

Since multivariate methods require complete sets of data, missing values of each specimen were estimated by stepwise regression from the remaining set (minimum of 60%) of variables available for this specimen (BMDPAM, Dixon, 1987). This estimation was made separately for age class, sex, species and populations. The predicted values were then replaced in the data matrix. All variables were tested for skewness and kurtosis. When appropriate, data transformation by Log function were used to approach distribution to normality.

3. RESULTS

Sample statistics for all groups of Polish skulls are depicted in Tables 1 and 2. No remarkable differences were found between species, age, or sex groups, regarding CV. Characters more variable were those measuring non linear traits, as weight of the mandible or volume of the braincase. The remaining measurements exhibited similar CV, those related to width of the skull having little higher CV than length ones. Variability of postorbital width was very high in both species.

3.1. Sex Dimorphism

In both species, sex dimorphism was apparent, males being larger than females, although overlapping within the observed range of variation occurred in most measurements (Tables 1, 2). Univariate analysis was performed in both species using the group of adults only. Results obtained from ANOVA revealed significant differences ($p<0.001$) between sexes in both species and in all measurements except RstA (Table 3).

Measurements related to the mandible showed the most significant sex differences, having little or no overlapping (Tables 1, 2), MnbL and MnbH reaching the highest F value in *M. martes* and *M. foina*, respectively (Table 3). CbL, PrL, and CmL also had very high F value indicating that sexual dimorphism was more apparent in length than in width in both species. RtrW and ZyW also showed high significant sex differences (Table 3).

Sex dimorphism was more strong in *M. martes* than in *M. foina*. On an average, females were 12.1 and 9.5% smaller than males in *M. martes* and *M. foina* respectively (Table 3). In both species, strongest dimorphism was found in those traits related to size and weight of the mandible. On the contrary, BmW was the character more similar in males and females (Table 3).

Distinctive sex differences in the development of the *crista sagittalis* were observed, and consequently, related measurements like BcbH showed also high significant sex dimorphism, specially in *M. foina* (Table 3).

Character ratios examined were found to have low significance in sex dimorphism in comparison to single measurements, even though they include those traits with high F values. The indices MndW/PrL, MndW/MndL (Heptner & Morozova-Turova, 1951) and BcbH/MndW (Buchalczyk & Ruprecht, 1977) showed the greatest changes among sexes (Table 3). In particular, MndW and PrL, when plotted against each other clearly separate adult males and females in both species (Figs. 2, 3).

Table 1

Sample statistics of the 23 skull measurements performed (see the text for explanation C. V.: coefficient of variation, O.R.: observed range, $\bar{X}_{cv}$: mean of the coefficient of given. Actual sample size of particular measurements is on average 92% of the number

	Females (n=103)								
	Juveniles (n=44			Subadults (n=34)			Adults (n=25)		
	x̄	C. V.	O. R	x̄	C. V.	O. R	x̄	C. V.	O. R
CbL	76.8	2.2	72.0—80.2	78.0	1.7	75.3—80.6	78.8	1.8	75.5—81.6
PrL	87.6	2.3	73.6—81.8	79.8	1.8	75.5—82.3	81.0	2.0	76.8—83.5
FcL	35.0	3.2	32.2—37.3	36.0	3.0	33.5—37.8	36.2	2.7	34.3—37.8
BcL	49.7	2.5	47.6—52.9	49.7	2.5	46.2—52.0	50.9	2.6	47.2—53.4
CmL	30.6	2.6	28.0—32.0	31.3	2.3	29.4—33.1	31.6	2.5	30.0—33.0
MxtL	27.2	5.4	22.8—32.3	27.7	4.1	22.4—28.9	28.0	4.4	22.7—29.1
PtL	37.4	2.5	34.6—39.6	38.0	2.1	36.3—39.8	38.2	2.4	36.0—39.7
ZyW	43.4	2.7	40.1—45.3	44.6	2.7	41.9—46.4	45.3	2.4	43.0—48.0
EorW	22.0	3.1	19.1—23.5	23.1	5.1	20.7—25.7	22.9	3.4	21.9—24.7
IorW	18.7	4.7	17.0—20.3	19.4	4.1	18.0—21.4	19.4	3.8	18.4—21.2
PorW	18.4	6.3	15.9—20.8	18.5	6.3	15.8—20.3	17.3	6.3	15.3—20.0
MstW	36.1	2.8	33.8—38.2	36.8	2.9	33.0—38.2	37.3	3.0	34.4—39.3
BmW	21.3	3.4	19.3—22.8	21.7	4.0	20.2—23.2	22.1	4.7	20.0—24.0
RtrW	15.3	4.3	14.4—17.9	15.6	3.0	15.0—16.7	16.0	3.1	14.8—17.0
LcL	4.2	4.2	3.9—4.6	4.3	4.6	4.0—4.7	4.2	6.1	3.6—4.8
LmL	9.0	3.8	8.3—9.9	9.1	3.4	8.3—9.8	9.0	3.2	8.6—10.0
MntL	31.4	2.3	29.6—32.9	32.1	2.2	30.5—33.3	32.4	1.9	31.3—33.7
MnbH	21.4	4.0	19.3—23.0	22.0	3.7	20.6—24.4	22.1	3.9	20.7—24.0
MnbL	50.5	2.5	46.3—52.4	52.0	2.1	49.4—55.7	52.4	2.1	49.6—54.2
MnbW	4.3	9.7	3.5—5.2	4.6	9.1	3.7—5.3	4.9	9.7	4.1—5.7
BcbH	29.8	3.3	27.4—33.2	30.0	3.0	28.4—32.2	29.5	4.1	27.8—32.0
BcC	19.1	7.0	15.9—22.2	19.3	6.9	17.2—22.4	18.4	7.7	16.1—20.8
RstA	51.8	2.9	50.0—56.0	52.3	3.6	48.0—56.0	51.7	3.5	49.0—55.0
x̄C. V.		3.9			3.7			3.8	

Table 2

Sample statistics of the 23 skull measurements performed in *M. foina* from Poland.

	Females (n=22)								
	Juveniles (n=10)			Subadults (n=5)			Adults (n=7)		
	x̄	C. V.	O. R	x̄	C. V.	O. R	x̄	C. V.	O. R
CbL	76.1	2.0	73.7—78.8	77.8	2.4	75.2—79.7	78.6	1.3	76.6—79.9
PrL	79.3	1.8	77.7—82.1	80.2	2.9	77.4—83.2	81.9	1.4	80.1—83.5
FcL	53.5	3.0	33.7—37.5	36.5	3.1	35.2—37.8	36.3	1.9	35.2—37.1
BcL	49.9	1.4	48.9—51.1	50.5	5.0	47.8—53.8	51.8	3.2	49.8—54.7
CmL	30.7	3.7	29.3—32.9	31.3	3.9	30.5—33.2	31.5	0.7	31.1—31.8
MxtL	27.3	4.7	26.0—30.4	28.0	5.6	26.2—30.5	28.2	2.0	27.3—29.0
PtL	35.7	3.2	34.3—38.0	37.0	3.3	35.3—38.2	36.9	2.3	36.0—38.5
ZyW	45.2	4.6	41.8—47.6	46.6	1.4	45.6—47.1	48.1	1.1	47.2—48.8
EorW	24.0	6.3	22.3—27.2	25.1	1.8	24.4—25.6	24.9	9.4	22.8—28.7
IorW	20.2	3.3	19.2—21.3	20.7	1.4	20.4—21.1	20.7	2.9	20.0—21.8
PorW	18.5	2.8	17.6—19.2	20.1	1.4	19.9—20.3	17.6	4.2	16.4—18.4
MstW	36.1	5.0	31.6—38.4	36.0	6.7	32.6—38.0	37.0	5.3	33.3—39.3
BmW	22.3	4.3	20.9—24.0	22.8	2.7	22.2—23.5	23.9	5.6	21.0—25.3
RtrW	16.3	2.9	15.6—17.1	17.0	4.7	16.3—18.4	16.7	2.5	15.8—17.1
LcL	4.1	3.5	4.0—4.4	4.3	2.5	4.2—4.4	4.2	3.1	4.1—4.4
LmL	9.1	4.5	8.7—9.9	9.2	3.8	8.8—9.7	9.1	2.1	8.9—9.4
MntL	31.1	2.6	30.1—32.7	31.8	2.3	31.1—33.0	32.1	1.6	31.6—33.0
MnbH	22.9	3.9	21.6—24.2	23.5	2.3	23.0—24.3	23.4	2.4	22.6—24.2
MnbL	50.4	2.2	48.8—52.7	51.5	2.1	50.1—52.6	52.0	1.0	51.5—52.9
MnbW	4.7	7.7	4.1—5.3	5.2	1.5	5.1—5.3	5.4	3.6	5.1—5.6
BcbH	29.1	2.1	27.9—29.8	29.7	3.3	28.3—30.6	29.7	2.4	28.5—30.4
BcC	19.3	7.8	17.7—22.0	20.5	11.6	17.3—22.6	20.1	5.7	19.0—22.1
RstA	59.0	4.3	57.0—65.0	59.2	3.6	56.0—61.0	59.7	3.3	57.0—62.0
x̄C. V.		3.7			3.5			3.0	

of abbreviations) in *M. martes* from Poland, according, to sex and age groups. X̄: mean, variation. To simplify the table, only number of skulls (in brackets) of each group is of skulls.

Males (n=133)								
Juveniles (n=33			Subadults (n=43)			Adults (n=57)		
x̄	C. V.	O. R	x̄	C. V.	O. R	x̄	C. V.	O. R
82.7	2.3	77.9—86.2	84.2	1.7	80.9—87.7	85.6	1.7	82.0—87.9
84.5	2.3	79.4—87.6	86.5	1.6	83.5—89.3	88.6	1.7	85.5—92.3
38.0	3.3	35.1—40.3	38.6	2.8	36.3—40.6	39.3	2.7	36.6—41.8
53.5	2.9	50.0—56.6	54.3	2.5	51.3—57.1	55.4	2.5	51.6—60.0
39.9	3.2	31.3—35.7	34.7	2.5	32.8—36.9	35.3	2.7	33.5—38.7
30.0	4.4	27.1—34.8	30.7	4.5	28.7—35.7	31.1	2.9	29.1—35.2
40.8	3.1	37.8—43.2	41.6	2.6	38.7—43.5	42.3	2.9	40.0—45.0
46.4	3.4	41.9—48.8	47.9	2.8	42.4—50.1	51.1	3.2	47.6—55.2
23.4	4.4	21.5—25.5	24.2	4.8	21.7—28.6	25.9	5.3	23.2—29.9
20.0	4.5	18.7—22.7	20.7	3.9	19.2—23.4	21.5	3.1	19.6—22.9
19.7	7.0	16.9—22.7	19.5	7.1	15.6—21.9	19.1	6.5	15.8—21.3
38.8	3.0	36.3—41.0	39.6	2.7	36.7—42.0	40.6	2.4	38.0—43.0
22.5	3.9	21.2—24.3	23.3	3.3	21.3—24.9	23.8	3.5	21.8—25.8
17.0	3.7	15.5—18.0	17.2	2.3	16.4—18.1	17.7	2.7	16.6—18.7
4.8	4.9	4.2—5.1	4.9	4.1	4.5—5.4	4.7	3.9	4.3—5.2
9.9	4.7	9.0—11.2	10.0	3.6	9.2—11.0	9.9	2.8	9.1—10.6
34.5	2.0	33.0—35.6	34.9	2.1	33.4—36.6	35.6	2.4	34.0—37.5
23.9	3.8	22.2—26.1	24.3	3.5	22.6—26.3	25.0	3.6	22.5—27.1
55.2	3.1	51.6—58.8	56.7	1.9	54.8—59.5	58.0	1.8	56.1—60.3
5.8	8.2	5.0—6.8	6.4	6.3	5.6—7.6	7.2	8.6	5.5—8.5
31.7	2.6	30.1—33.2	31.9	2.4	30.4—33.9	32.4	3.2	29.7—35.9
22.9	7.2	18.9—24.8	22.7	7.3	19.0—26.0	22.6	7.8	18.1—25.8
50.5	3.5	47.0—54.0	51.0	3.2	47.0—55.0	51.7	3.9	47.0—56.0
	4.0			3.5			3.6	

See Table 1 for explanation of symbols.

Males (n=25)								
Juveniles (n=4)			Subadults (n=9)			Adults (n=12)		
x̄	C. V.	O. R	x̄	C. V.	O. R	x̄	C. V.	O. R
80.4	1.5	78.7—81.4	81.1	1.7	78.2—82.3	82.4	1.6	80.7—84.9
83.4	1.3	82.3—84.7	85.3	1.7	82.6—86.7	86.7	1.6	83.6—88.3
37.2	1.4	36.8—38.0	38.1	1.7	36.7—38.9	38.5	1.8	37.6—40.0
52.8	1.9	51.8—54.1	54.0	1.7	52.4—55.2	55.6	2.2	54.4—57.9
32.8	3.3	31.8—34.3	33.4	2.9	31.7—34.6	34.5	2.4	33.0—35.6
29.1	2.6	28.4—30.1	29.2	2.8	28.2—30.7	29.7	2.3	28.7—30.9
38.8	2.8	37.6—40.0	38.4	1.6	37.4—39.2	39.6	2.3	38.2—40.9
47.8	3.1	46.1—49.4	49.3	2.7	47.3—51.5	52.3	2.9	51.0—55.6
25.8	2.1	25.3—26.4	26.3	2.9	25.2—27.2	28.2	4.0	26.1—30.0
21.5	4.9	20.7—23.0	21.6	2.9	21.1—23.2	22.9	3.6	22.0—24.2
17.5	4.6	16.6—18.0	20.0	4.5	18.5—21.1	19.8	6.1	18.3—21.5
37.7	2.3	36.8—38.7	38.4	2.4	36.3—39.5	39.6	2.6	37.8—41.4
24.3	2.4	23.7—25.0	24.8	3.7	23.5—26.3	24.8	3.6	23.8—26.4
17.3	2.8	16.7—17.9	17.6	3.6	16.8—18.5	18.3	1.6	17.9—18.8
4.7	3.7	4.4—4.8	4.7	3.8	4.4—4.9	4.8	3.2	4.5—4.9
9.8	5.5	9.0—10.3	9.7	4.6	8.7—10.2	10.0	4.3	9.3—10.9
33.7	1.8	33.1—34.6	33.4	1.6	32.7—34.3	34.1	2.8	32.6—35.9
25.0	5.9	23.7—27.2	25.1	2.6	24.4—26.4	26.6	2.2	25.7—27.7
54.0	1.5	53.3—55.0	54.8	1.7	52.9—55.9	55.9	1.7	54.7—57.7
5.9	7.6	5.2—6.3	6.5	3.8	6.1—6.9	7.5	6.5	6.7—8.3
30.3	2.8	29.3—31.2	31.2	2.4	30.4—32.5	31.8	1.4	31.2—32.5
21.1	2.2	20.6—21.7	23.2	7.2	22.2—25.0	22.2	7.5	20.0—24.7
57.2	3.8	55.0—60.0	58.7	2.3	57.0—60.0	60.6	4.3	58.0—65.0
	3.1			2.9			3.2	

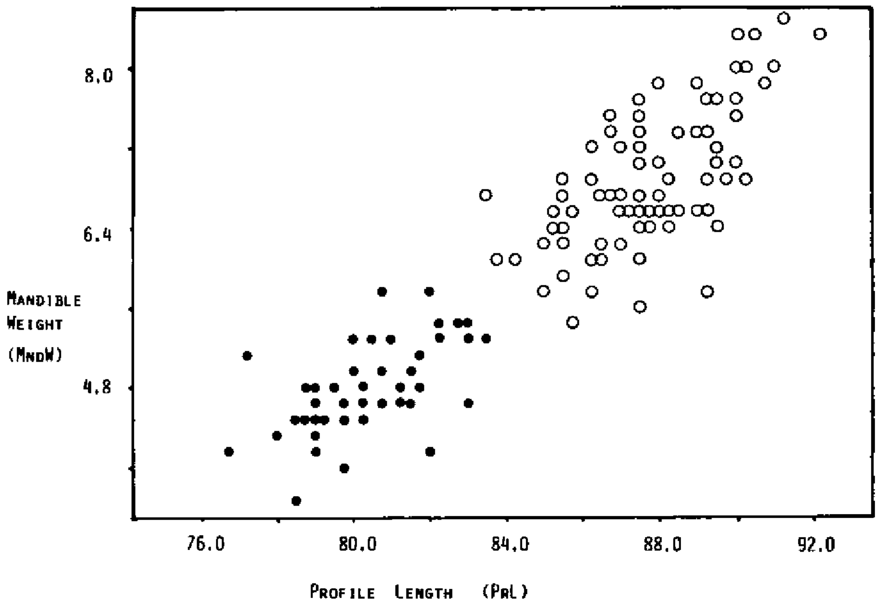

Fig. 2. Plot of Mandible Weight (g) against Profile Lenght (mm) to show the separation of males (open circle) and females (solid circle) in *M. martes*. Adult and subadult pooled.

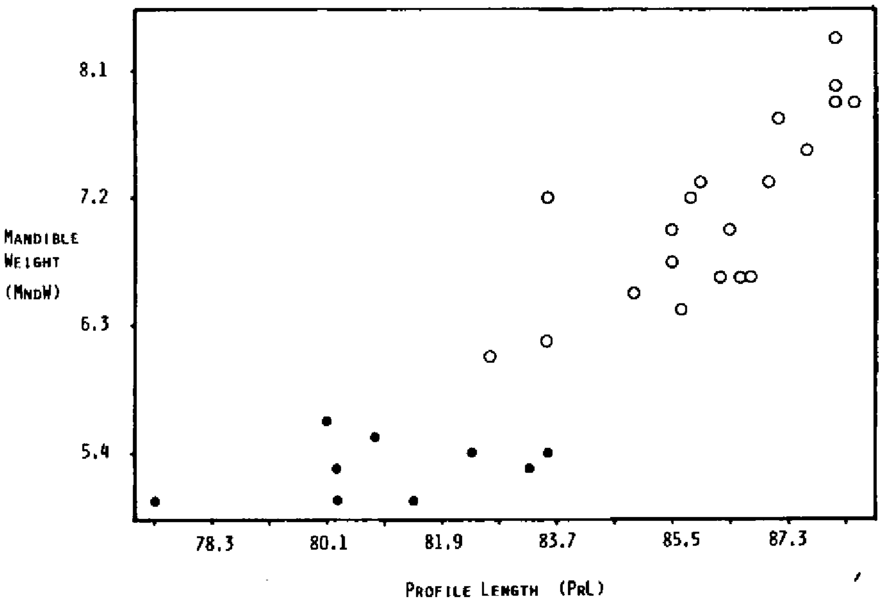

Fig. 3. Plot of the Mandible Weight (g) against Profile Lenght (mm) to show the separation of males (open circle) and females (solid circle) in *M. martes*. Adult and subadult pooled.

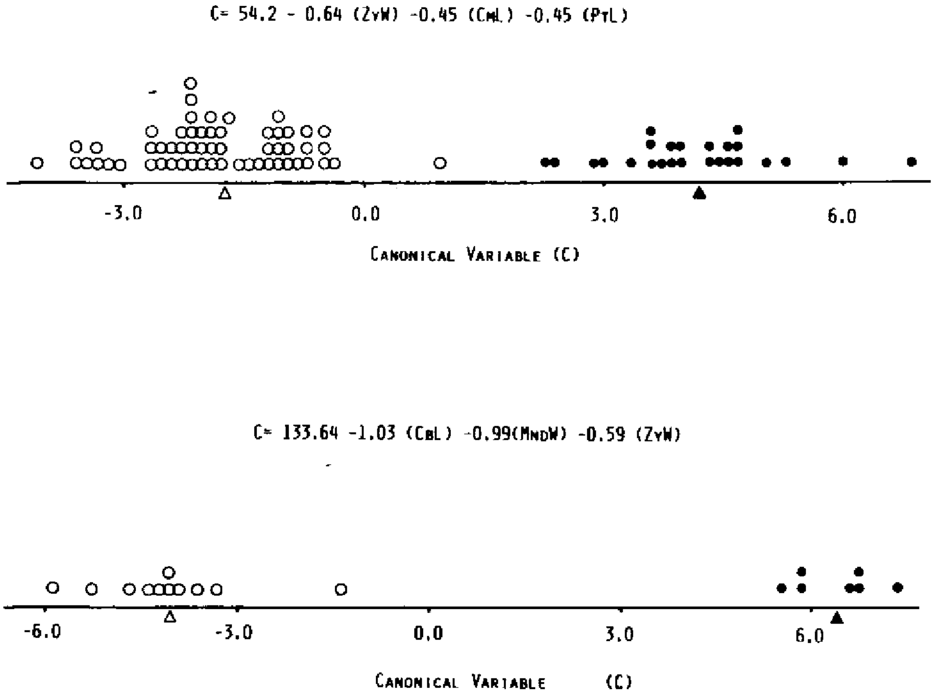

Fig. 4. Histogram of canonical variable score of adult male (open circle) and female (solid circle) of. *M. martes* (upper) and *M. foina* (lower). On the top of each histogram, coefficient of the measurements included in the canonical variable that separates males and females. Triangles indicate group centroids.

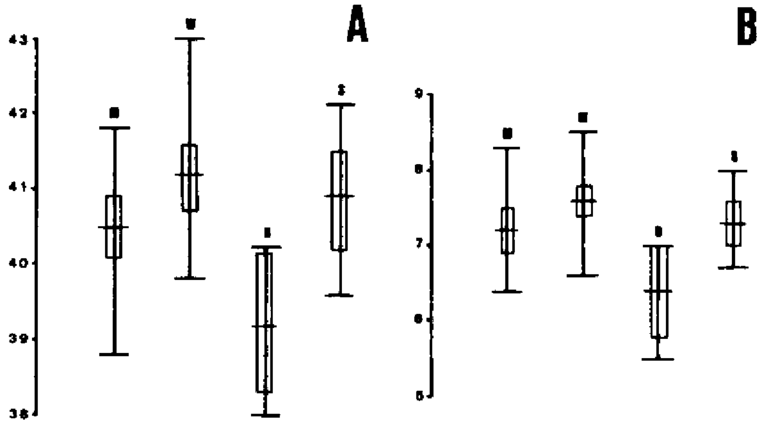

Fig. 5. Observed rangers, means, and 95% confidence intervals of and mastoid width (mm): A; mandible weight (g): B; of adult males of *M. martes* from 4 Polish populations. Pomerania and Masurian Lake Region; W: Wielkopolska-Kujawy Lowlands; B: Białowieża Primaeval Forest; S: Lower and Upper Silesia.

Stepwise discriminant analysis provided a set of three traits, out of the 23, being sufficient to separate males and females maximally, explaining 100% of the total variance. In *M. martes* these three measurements were ZyW, CmL and PtL, all of them with similar contributions to the canonical variable (Fig. 4). In *M. foina*, the same analysis resulted in a combination of CbL, ZyW and MndW, both CbL and MndW showing high contributions into the canonical variable (Fig. 4). Classification of specimens following the DF was 100% correct in both species.

3.2. Age Variation

Although the number of age groups was small for an analysis of ontogenic process, the three groups considered allowed a general view of the characters and regions of the skull which exhibited variation connected with age.

Table 3
Results of ANOVA between adult males and females of each species in the 23 skull measurements and three indices. *F* values were highly significant ($p<0.001$) in all traits, except RstA (not significant). d.f: degrees of freedom. %D: percentage of difference between means in both sexes [($\bar{x}$ male$-\bar{x}$female)/$\bar{x}$ female$\times$100]. $\overline{X}_{\%D}$: average of %D in the 23 measurements.

Meas./Indx.	*M. martes*		*M. foina*	
	%D	F[1]	%D	F[2]
CbL	8.7	364.6	4.8	39.2
PrL	9.4	380.7	5.9	54.5
FcL	8.6	142.4	6.1	49.3
BcL	8.9	177.6	7.3	25.3
CmL	11.9	282.6	9.5	88.0
MxtL	11.4	160.6	4.9	25.1
PtL	10.7	251.9	7.3	35.7
ZyW	12.9	327.0	8.7	50.2
EorW	13.2	135.2	13.3	24.0
IorW	10.9	132.1	10.6	44.1
PorW	10.5	35.7	12.5	23.4
MstW	8.9	173.5	7.0	13.6
BmW	7.6	54.4	3.8	2.8
RtrW	11.4	266.1	9.6	106.6
LcL	10.2	117.4	14.3	45.6
LmL	9.1	123.2	9.3	17.7
MntL	9.9	346.5	6.2	25.4
MnbH	13.2	178.0	13.7	123.6
MnbL	10.7	438.7	7.5	97.9
MnbW	46.7	267.2	38.9	105.3
BcbH	10.1	120.5	7.1	58.3
BcC	22.9	84.6	10.4	10.8
RstA	0.02	(ns)	1.5	(ns)
$\overline{X}_{\%D}$	12.1		9.5	
MndW/MndL	32.4	191.1	24.9	65.2
MndW/BcbH	33.2	208.0	26.7	119.7
MndW/Prl	34.1	194.5	25.8	82.2

[1] df=1,80; [2] df=1,17.

Four different ANOVA test were made among the three age classes, separating skulls by sex and species. Results indicated that MndW, MndL and ZyW are the measurements with maximum significance for age variation in both species (Tables 4, 5). Other mandible traits also showed highly significant differences, which accounts for the continuous mandibular growth found by Pavlinov (1977) in *M. martes*. In *M. foina*, *F* values were very low, especially in females. This reduced significance, rather than denote less age variation, might be explained as an artifact connected with the reduced and uneven sample size, since values of % D between juveniles and subadults were even higher than

Table 4

Differences between the three age classes considered in females and males of *M. martes*. %D: percentage of difference between means of juveniles and adults [($\bar{x}$ adult — $\bar{x}$ juvenile)/ $\bar{x}$ juvenile ×100]. $\bar{x}$ %D: average of %D for each sex in the 23 measurements. *F*: significance of the differences obtained by ANOVA between the three age groups. d.f.: degrees of freedom Asterisks indicate the degree of significance of pairwise comparison of means by *t*—test between juvenile and subadult (Juv/Sba); subadult and adult (Sba/Ad). *** $p<0.001$; ** $p<0.01$ * $p<0.05$; — not significant. All *F* values were highly significant ($p<0.001$), unless otherwise marked.

Meas./Indx	%D		F[1]	F[2]	Juv/Sba		Sba/Ad	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
CbL	2.7	3.5	14.0	32.0	**	***	*	***
PrL	3.0	4.8	14.7	60.0	**	***	**	***
FcL	3.3	3.4	12.1	12.4	***	*	—	**
BcL	2.3	3.6	7.4	17.7	—	*	***	***
CmL	3.1	4.2	13.2	21.5	***	***	—	**
MxtL	2.4	3.6	—	7.8	—	—	—	*
PtL	2.2	3.6	6.7**	14.7	*	**	—	*
Zyw	4.3	10.2	20.2	97.6	***	***	*	***
EorW	4.2	10.7	13.1	41.8	***	**	—	***
IorW	3.9	7.4	8.7	32.9	***	**	—	***
PorW	—6.3	—2.9	9.2	—	—	—	***	—
MstW	3.4	4.6	10.3	28.9	**	**	—	***
BmW	4.0	5.7	7.6	22.3	*	***	—	**
RtrW	3.6	4.5	7.7	27.5	*	—	—	***
LcL	1.1	—1.0	—	—	—	—	—	—
LmL	0.8	0.5	—	—	—	—	—	—
MntL	3.1	3.2	15.5	21.5	***	*	—	***
MnbH	3.5	4.9	7.2	18.3	**	*	—	***
MnbL	3.7	5.0	22.9	46.9	***	***	—	***
MnbW	13.6	23,9	14.5	74.5	***	***	—	***
BcbH	—1.2	2.2	—	6.4**	—	—	—	**
BcC	—4.0	—1.3	—	—	—	—	*	—
RstA	—0.3	2.4	—	4.1*	—	—	—	—
$\bar{X}_{\%D}$	2.3	4.5						
PorW/ZyW	—10.3	—9.8	20.8	24.5	—	*	***	***
MndW/PorW	20.9	28.6	21.3	68.7	**	***	***	***
MndW/BcbH	10.2	22.9	21.7	82.8	***	***	*	***

[1] df=2, 100; [2]=2, 130.

in *M. martes* (Tables 4, 5). Width measurements exhibited higher *F* values than length ones, while the only ones related to height of the skull had no significant differences except in males (Tables 4, 5). Characters related to tooth size varied independently of age (Tables 4, 5). Pairwise comparison between contiguous age groups revealed significant differences between subadults and adults, especially in male specimens (Tables 4, 5), indicating that growth of the skull continues after the first year of age. Sexual differences were observed in the age variation of the characters. Males showed greater differences between juvenile and adults (%D) and more significant differences (*F* values) among age classes. Differences between age class II and III were also more significant among males. Specific differences were observed in the growth of traits related to the braincase region of the skull. BcC decreases with age in *M. martes* and the opposite was found for *M. foina*, although *F* values were not significant in the two species. BcL showed high significant age variation in males of *M. foina*,

Table 5
Differences between the three age classes considered in females and males of *M. foina*. See Table 4. for explanation of symbols.

Meas./Indx	%D		F[1]	F[2]	Juv/Sba		Sba/Ad	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
CbL	3.3	2.5	6.0**	4.2*	—	—	—	*
PrL	3.2	4.0	5.5**	8.5**	—	*	—	—
FcL	2.1	3.3	—	5.1*	—	*	—	—
BcL	3.8	5.5	—	10.6	—	—	—	**
CmL	2.4	5.1	—	5.5**	—	—	—	*
MxtL	3.5	2.4	—	—	—	—	—	—
PtL	3.5	1.9	3.7*	4.6*	*	—	—	**
Zyw	6.3	9.5	7.0**	17.7	—	—	—	***
EorW	3.7	9.4	—	13.1	—	—	—	***
IorW	2.6	6.9	—	7.5**	—	—	—	**
PorW	—4.6	13.2	12.4	6.6**	**	**	***	**
MstW	2.5	4.9	—	6.0**	—	—	—	*
BmW	7.2	2.1	4.6*	—	—	—	—	—
RtrW	2.3	5.8	—	9.7**	*	—	—	**
LcL	2.0	1.7	—	—	—	—	—	—
LmL	—0.3	1.7	—	—	—	—	—	—
MntL	3.0	1.1	—	—	—	—	—	—
MnbH	2.1	6.3	—	11.3	—	—	—	***
MnbL	3.0	3.5	4.7*	7.3**	—	—	—	*
MnbW	15.4	27.6	12.2	29.2	**	*	—	***
BcbH	2.2	4.8	—	7.0**	—	*	—	—
BcC	4.0	5.4	—	—	—	—	—	—
RstA	1.2	5.9	—	4.0*	—	—	—	—
$\bar{X}_{\%D}$	3.2	5.8						
PorW/ZyW	—10.7	10.1	18.6	5.2	—	**	**	*
MndW/PorW	24.1	9.0	16.5	8.6	—	—	**	***
MndW/BcbH	8.2	23.6	10.4	38.0	**	**	—	***

[1]df=2, 19; [2]=2, 22.

but very low in *M. martes* (Tables 4, 5). Finally, age variation in the height of the braincase was also very different in both species, %D being much more larger in *M. foina* (Tables 4, 5). Some skull proportions changed more significantly with age than single traits. Among them, ZyW/PorW, BcbH/MndW (Buchalczyk & Ruprecht, 1977) and PrL/MndW, the last two being the most significant (Tables 4, 5). These results suggest allometric growth of MndW and ZyW, relative to the rest of measurements.

To investigate the association between measurements which synthesized distinct patterns of age variation, principal factor analysis (PFA) was performed in both species separately for males and females, using a data matrix in which skulls of the three age classes were pooled. In *M. martes* results were similar for males and females, the first three principal factors (PF) accounting for more than 87% of the total variance (Tables 6, 7). PF I and PF II clearly separates the measurements in length and width, respectively, while PF III joins those related to the braincase (Tables 6, 7). This third factor is characterized by negative loadings from various measurements indicating shape variation. BmW and tooth measurements showed low loadings in the three PF. In *M. foina* four PF were obtained, results being different for males and females. In males the first three PF related width, length, and braincase measurements, respectively, while PF IV had only positive loadings from PorW (Table 8). In comparison with *M. martes,* the results found in *M. foina* differ in the relative significance of each PF. In the latter species, length and width factors showed similar contributions to the total variance explained (Table 8), while in *M. martes,* the length factor explained two times more variance than the width one (Table 6). PFA of females in *M. foina* resulted in non-meaningful factors, the first four PF only explaining 84.1% of the total variance (Table 9). This result must be related to the low *F* values obtained for age variation and the small sample size metioned above.

3.3. Inter-populaton Variation in *M. martes*

Eleven measurements exhibited signficant differences between populations of adult males of *M. martes*. The results of ANOVA of the four samples considered showed that width and height of the skull show the highest significant differences (Table 10), MndW and MstW exhibiting the highest *F* values (Fig. 5).

Pairwise comparison of the four populations indicates that the results found by ANOVA are mainly due to differences between the Białowieża population and the other three. Wielkopolska and Silesia samples exhibited the most significant differences form the Białowieża one, skulls from the latter population being the smallest of the whole

Polish territory. Table 11 shows the values of CbL in the four populations of *M. martes*.

3.4. Species Differentiation

Although general appearance of the skull is distinctive in both species (Anderson, 1970), accurate identification based on skull measurements alone needs special indices (Altuna, 1973) or multivariate methods (Gerasimov, 1985), since measurements overlap widely (Tables 1, 2). Generally speaking, in the material examined, the skull of *M. martes* is more elongated, narrower and more flattened than that of *M. foina*.

Table 6

Rotated factor loadings of the first three principal factors (PF) derived from 23 skull measurements of males of *M. martes* from the three age classes pooled. These factors account for 86.9% of the total variance. VE: percentage of variance explained by each factor. Measurements have been rearranged so that the columns appear in decreasing order of variance explained by factors. Rows have also been rearranged so that for each successive factor, loadings greater than 0.500 appear first (Dixon, 1987). To facilitate the identification of the measurements associated in each factor boldface was used to show those measurements having highest loadings in a particular factor.

Meas.	PF I	PF II	PF III
CbL	**0.906**	0.255	0.045
PrL	**0.885**	0.238	0.002
MndL	**0.858**	0.161	—0.020
PtL	**0.853**	—0.018	0.175
MntL	**0.813**	0.211	—0.039
CmL	**0.803**	0.156	0.053
Fcl	**0.746**	0.223	—0.064
MndW	**0.736**	0.452	—0.018
RstW	**0.666**	0.277	0.063
MndH	**0.642**	0.387	0.252
BcL	**0.579**	0.181	—0.028
MxtL	**0.553**	0.071	0.037
EorW	0.343	**0.732**	0.007
ZyW	0.560	**0.660**	0.039
MstW	0.534	**0.626**	0.040
RstA	—0.239	**0.625**	0.126
IorW	0.434	**0.623**	—0.003
BcbH	0.270	—0.018	**0.901**
BcC	0.120	—0.005	**0.816**
PorW	—0.162	0.192	**0.788**
LmL	0.364	0.016	0.089
BmW	0.359	0.403	0.058
LcL	0.306	0.136	0.144
VE	51.3%	18.9%	16.7%

An ANOVA was performed separately for each sex, pooling together adult and subadult specimens. This pooling of age groups helped to solve the problem of small sample size in *M. foina* compared to *M. martes*.

With the exception of BcC, all measurements showed significant differences, in one or both sexes (Table 12). RstA was the character with highest *F*, being the only one with no overlap between species when groups of the same sex and age are compared (Tables 1, 2, Fig. 6). Two character ratios showed large differences among species. These ratios were relating length and width of the skull: RstA/PtL and RstA/CbL (Table 12). Plotting of PtL against RstA allowed clear separation of species in both sexes (Figs. 7, 8). This difference between species in PtL must be related to the shape of the posterior edge of palatine which is usually more developed in *M. martes* (Vericad, 1970).

Specific differences were found to be different in males and females,

Table 7
Rotated factor loadings of the first three principal factors (PF) derived from 23 skull measurements of females of *M. martes* from the three age classes pooled. These factors account for 87.6% of the total variance. VE: percentage of variance explained by each factor. Measurements have been rearranged as in Table 6.

Meas.	PF I	PF II	PF III
CbL	**0.903**	0.255	0.160
MndL	**0.872**	0.363	0.001
PrL	**0.859**	0.382	0.110
PtL	**0.827**	0.076	0.179
MntL	**0.817**	0.206	0.070
CmL	**0.703**	0.209	0.098
FcL	**0.697**	0.203	0.216
BcL	**0.632**	0.246	0.196
MstW	**0.586**	0.566	0.281
MndH	**0.545**	0.430	0.306
MxtL	**0.500**	0.140	0.114
EorW	0.256	**0.813**	0.090
ZyW	0.390	**0.794**	—0.044
IorW	0.344	**0.757**	0.077
MndW	0.569	**0.679**	0.039
RstA	—0.178	**0.593**	0.094
RstW	0.518	**0.530**	0.217
BcC	0.259	—0.086	**0.987**
PorW	—0.008	—0.006	**0.646**
BcbH	0.359	0.355	**0.626**
BmW	0.438	0.396	0.117
LcL	0.435	0.139	0.323
LmL	0.476	—0.026	0.156
VE	46.6%	26.5%	14.5%

some characters exhibiting significant differences only in females, and vice versa. Eight traits, out of the 23, had significant differences in both males and females, eleven had significant *F* only in males, and three only in females. Males had higher *F* values in the group of length measurements, PtL and CbL being the most different between both species (Table 12). However, the opposite was found in females, in which ZyW and RtrW had the highest *F* values (Table 12). Sexual differences were found also in the relative size differences (%D) between the species. Females of *M. foina* are, on the average, 3.2% larger than *M. martes* (Table 12). However, in males the average of %D was close to zero, although differences were more apparent than in females, exhibiting an opposite trend between length and width measurements. *M. martes* is longer, while *M. foina* is larger in width (Table 12). The largest %D were found in RstA, EorW, BmW, and MndW.

Accepting that the rostral angle is the best discriminating metrical character, a dividing point was determined for separation of the spe-

Table 8
Rotated factor loadings of the first four principal factors (PF) derived from 23 skull measurements of males of *M. foina* from the three age classes pooled. These factors account for 85.6% of the total variance. VE: percentage of variance explained by each factor. Measurements have been rearranged as in Table 6.

Meas.	PF I	PF II	PF III	PF IV
IorW	**0.818**	0.079	0.066	0.091
ZyW	**0.804**	0.207	0.342	0.091
EorW	**0.801**	0.129	0.057	0.263
RtrW	**0.761**	0.253	—0.022	0.074
MstW	**0.719**	0.139	0.034	0.040
MnbW	**0.716**	0.451	0.282	0.277
RstA	**0.668**	—0.241	0.443	—0.100
MnbH	**0.604**	0.278	0.225	0.039
Bcl	**0.601**	0.337	0.484	0.112
MntL	0.006	**0.899**	—0.179	0.219
MxtL	0.074	**0.819**	0.404	0.036
MnbL	0.455	**0.796**	0.061	0.301
PtL	0.395	**0.774**	—0.095	—0.211
LmL	—0.071	**0.719**	0.282	—0.016
CbL	0.439	**0.714**	0.023	0.107
CmL	0.412	**0.683**	0.265	0.213
PrL	0.488	**0.644**	0.316	0.295
BmW	0.083	0.072	**0.762**	—0.016
BcC	0.049	—0.138	**0.700**	0.342
BcbH	0.447	0.365	**0.578**	0.339
PorW	0.157	0.134	0.164	**0.841**
LcL	0.074	0.103	0.421	—0.010
FcL	0.268	0.457	0.156	0.445
VE	31.7%	29.9%	16.7%	9.3%

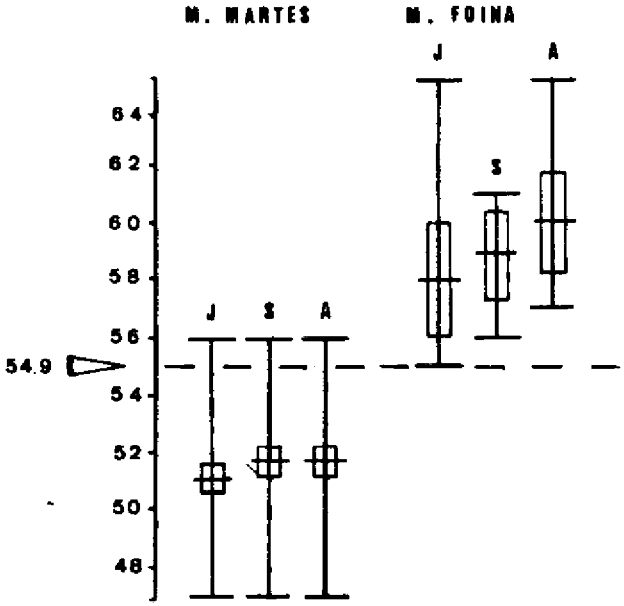

Fig. 6. Observed ranges, means, and 99% confidence intervals of rostral angle (°) in *M. martes* and *M. foina*, of the three age classes (males and females pooled). J: juveniles, S: subadult, A: adult. Dividing point of 54.9° is marked, see the text for further details.

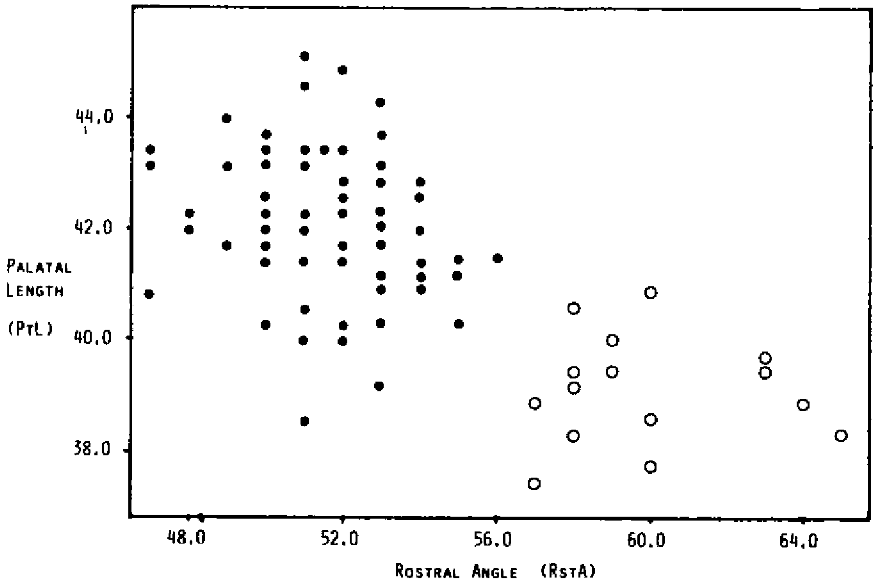

Fig. 7. Plot of palatal length (mm) against rostral angle (°) in females of *M. martes* (solid circle) and *M. foina* (open circle) to show the seperation of species. Adults and subadults pooled.

Table 9

Rotated factor loadings of the first four principal factors (PF) derived from 23 skull measurements of females of *M. foina* from the three age classes pooled. These factors account for 84.1% of the total variance. VE: percentage of variance explained by each factor. Measurements have been rearranged as in Table 6.

Meas.	PF I	PF II	PF III	PF IV
BcC	**0.929**	—0.033	—0.015	0.093
MnbH	**0.757**	0.207	0.136	0.064
PrL	**0.657**	0.582	—0.019	0.412
CbL	**0.586**	0.552	0.030	0.362
BcbH	**0.568**	0.180	0.473	0.418
BcL	**0.536**	0.254	—0.019	0.464
MnbL	0.505	**0.765**	0.070	0.374
MntL	0.322	**0.745**	0.010	0.517
CmL	0.577	**0.623**	—0.126	0.124
PtL	0.348	**0.567**	0.108	0.477
MstW	0.058	**0.522**	0.240	—0.165
IorW	0.047	0.186	**0.842**	0.185
BmW	—0.143	0.157	**0.796**	0.287
MnbW	0.365	0.201	**0.729**	0.256
EorW	0.067	—0.124	**0.705**	—0.061
ZyW	0.395	0.579	**0.633**	0.057
MxtL	0.079	0.259	—0.181	**0.782**
RtrW	—0.034	0.061	0.413	**0.779**
FcL	0.306	0.471	0.310	0.283
LcL	0.253	0.165	0.058	0.499
PorW	0.118	—0.428	0.084	—0.096
RstA	—0.068	—0.259	0.496	—0.204
LmL	0.335	0.019	0.174	0.438
VE	23.8%	20.7%	20.3%	19.3%

Table 10

Measurements showing significant differences between adult males of *M. martes* from 4 Polish populations. M: Pomerania and Masurian Lake Region; W: Wielkopolska—Kujawy Lowlands; B: Białowieża Primaeval Forest; S: Lower and Upper Silesia. Number of skulls in brackets. *F* values were obtained by ANOVA. Asterisks indicate the degree of significance of pairwise comparison of means by *t*-test between Masurian and Wielkopolska populations (M/W); Masurian and Białowieża (M/B); Wielkopolska and Białowieża (W/B); and Silesia (B/S).

*** $p<0.001$; ** $p<0.01$;* $p<0.05$; — not significant.

Meas.	*F*	M(16)	W(17)	B(6)	S(11)	M/W	M/B	W/B	B/S
PrL	3.3*	88.5	89.5	87.7	88.3	*	—	**	—
ZyW	3.3*	51.5	51.8	49.6	50.8	—	—	**	—
EorW	6.4**	26.1	26.3	24.0	26.0	—	***	***	**
IorW	6.0**	21.6	21.6	20.6	21.9	—	***	**	***
MstW	8.4**	40.5	41.2	39.2	40.9	*	***	***	**
RtrW	3.4*	18.0	17.7	17.3	18.0	—	**	—	**
BcbH	5.9*	32.3	33.1	31.4	32.9	*	—	***	**
MndH	4.3*	24.8	25.4	24.3	25.6	*	—	**	**
MndW	8.9**	7.2	7.6	6.4	7.3	*	***	***	***
RstA	5.1*	51.7	52.3	49.4	52.6	—	**	***	***
BcC	3.9*	22.0	22.9	20.4	22.8	*	—	*	*

cies. We assumed that RstA is normally distributed and, therefore, the dividing point corresponds to the value of the middle within 2.6 standard deviations (99% confidence interval) from the mean of RstA in

Table 11

Sample statistics of condylobasal length in adult specimens of *M. martes* in four Polish populations. n: number of skulls; $\overline{X}$: average; C. V.: coefficient of variation; O. R.: observed range.

Population	Females				Males			
	n	$\overline{X}$	C.V.	O.R.	n	$\overline{X}$	C.V.	O.R.
Pomerania and Masurian Lake Region	3	78.6	1.1	77.6–79.4	17	85.4	1.7	82.1–87.7
Wielkopolska–Kujawy Lowlands	7	79.7	2.8	77.5–84.1	18	86.1	1.5	83.3–87.8
Białowieża Primaeval Forest	2	78.4	1.6	77.5–79.3	6	84.2	2.7	80.9–87.5
Lower and Upper Silesia	3	79.1	2.3	77.9–81.2	11	85.0	1.5	83.7–87.9

Table 12

Differences between *M. martes* in both sexes. %D: procentage of diference between means in both species [($\bar{x}$ *M. foina* — $\bar{x}$ *M. martes)/M. martes* × 100]. $\bar{X}_{\%D}$: average of %D in the 23 measurements. *F* values were obtained by ANOVA between the two species, adults and subadults pooled. *F* values were highly signifcant ($p< 0.001$, unless otherwise marked.** $p< 0.01$; *$p< 0.05$ — not significant.

Meas./Indx.	%D		F^1	F^2
	♀♀	♂♂	♀♀	♂♂
CbL	0.01	—3.7	—	60.9
PrL	1.2	—1.9	—	13.9
FcL	8.8	—1.9	—	7.7**
BcL	2.3	—0.1	5.2	—
CmL	0.1	—3.0	—	17.3
MxtL	1.2	—4.4	—	24.8
PtL	—2.9	—7.0	15.0	102.3
ZyW	5.9	2.6	45.8	5.6*
EorW	8.4	8.5	24.1	31.1
IorW	6.6	5.3	27.5	25.4
PorW	1.8	3.2	—	—
MstW	—0.9	—2.8	—	15.2
BmW	7.2	5.2	22.2	30.8
RtrW	6.6	3.0	40.1	15.6
LcL	—0.8	—2.0	—	3.9*
LmL	0.9	—1.8	—	4.2*
MntL	—0.9	—4.2	—	48.3
MnbH	6.3	4.8	28.0	26.4
MnbL	—0.8	—3.5	—	43.7
MnbW	10.3	3.0	11.0**	—
BcbH	—0.03	—2.2	—	8.9**
BcC	7.1	0.04	—	—
RstA	14.2	16.3	143.5	283.8
$\bar{X}_{\%D}$	3.2	0.62		
RstA/CbL	14.9	20.8	120.4	312.5
RstA/PtL	17.4	25.2	109.2	342.3

[1] df=1,69; [2] df=1,119;

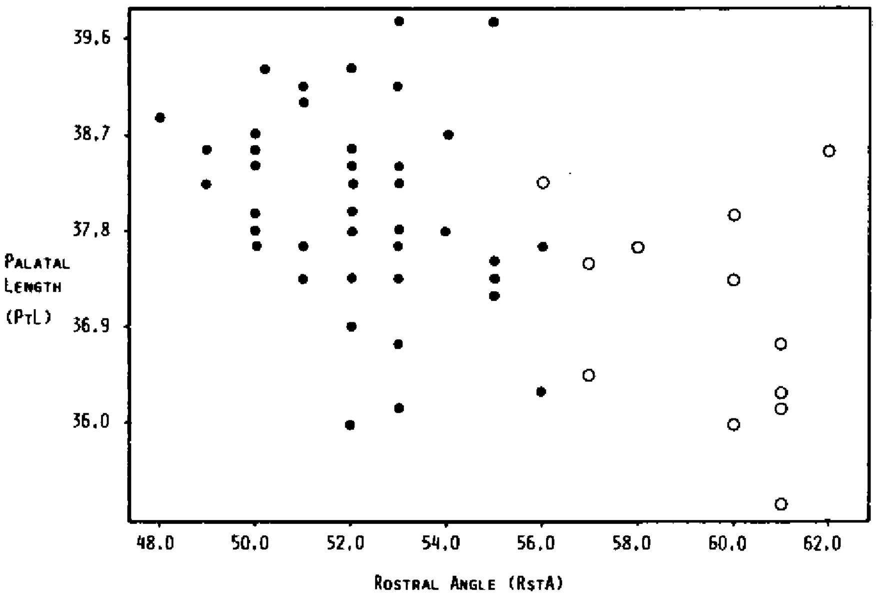

Fig. 8. Plot of palatal length (mm) against rostral angle (°) in males of *M. martes* (solid circle) and *M. foina* (open circle) to show the seperation of species. Adults and subadults pooled.

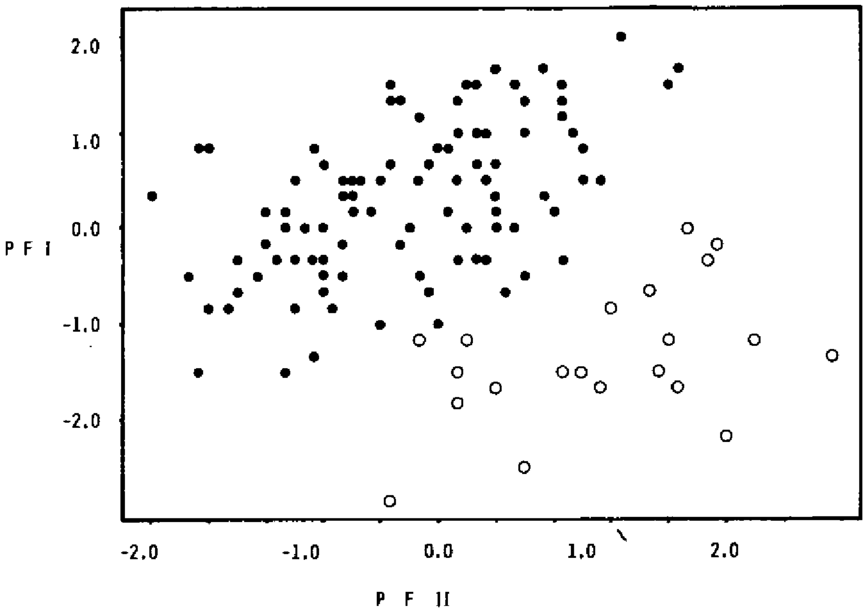

Fig. 9. Plot of Principal Factor I (PF I), (related to skull length) against Principial Factor II (PF), (related to skull width) in females of *M. martes* (solid circle) and *M. foina* (open circle) to show the seperation of species. Adults and subadults pooled.

each species (all groups of age and sex pooled). This results in a value of 54.9°, above which, specimes should be classified as *M. foina* and vice versa. Using this criterion, 98% of the skulls were correctly classified, 97% of *M. martes* and 100% of *M. foina* (Fig. 6).

Principal factor analysis yielded three PF which explained 87.9 and 85.5% of the total variance in males and females, respectively (Table 13). Results were similar in both sexes, PF I was related to skull and mandible length, while PF II joined width measurements, RstA, MndH and MndW. PF III showed high loadings from traits related to the *neurocranium*, such as BcC, BcbH, and PorW, which are characterized by little specific differences, and consequently with also little amount of variance explained. BcL, LmL, MstW and LcL are not clearly contributing to any of the three factors (Table 13). Attention must be paid to the fact that in the three PF, negative and positive loadings occur simultaneously. This suggests that, rather than size features, a general shape factor synthesized the differences between species. To estimate the effectiveness of PF to separate both species, PF I was plotted against PF II (Figs 9, 10).

Table 13

Rotated factor loadings of the first three principial factors (PF) showing differences between *M. martes* and *M. foina* in both sexes, adults and subadult specimens pooled. These factors account for 85.5% and 87.9% of the total variance in females and males, respectively. Measurements have been rearranged as in Table 6

Meas.	Females			Males		
	PF I	PF II	PF III	PF I	PF II	PF III
CbL	0.842	0.194	0.059	0.951	—0.024	0.071
MntL	0.797	—0.014	—0.077	0.892	—0.004	—0.064
PrL	0.795	0.340	0.069	0.877	0.293	0.152
MndL	0.777	—0.032	—0.006	0.943	0.136	—0.025
CmL	0.771	0.130	0.105	0.711	0.022	0.048
PtL	0.762	0.372	0.102	0.855	—0.225	0.057
FcL	0.587	0.249	0.037	0.683	0.081	0.180
BmW	0.562	0.123	0.090	0.634	—0.065	0.028
BcL	0.558	0.345	—0.031	0.449	0.421	0.264
ZyW	0.267	0.877	0.068	0.185	0.798	—0.040
RstA	—0.289	0.848	0.143	—0.599	0.671	0.161
EorW	—0.032	0.770	0.117	—0.055	0.856	0.064
IorW	0.091	0.751	0.135	—0.031	0.845	0.025
RtrW	0.385	0.683	0.080	0.182	0.734	0.086
CmW	0.210	0.681	0.042	—0.147	0.498	0.227
MndW	0.541	0.654	0.010	0.438	0.733	0.049
MndH	0.345	0.646	0.320	0.130	0.645	0.334
BcbH	0.303	0.029	0.828	0.547	0.209	0.535
BcC	0.037	0.191	0.776	0.193	—0.003	0.944
PorW	—0.173	0.132	0.726	—0.032	0.098	0.602
LmL	0.406	0.110	0.181	0.449	0.049	0.104
MstW	0.389	0.169	—0.093	0.659	0.300	0.156
LcL	0.313	—0.045	0.303	0.447	0.175	0.154
VE	37.0%	31.0%	17.5%	45.5%	29.4%	12.9%

Stepwise discriminant analysis was performed, using a data matrix which included all groups of skulls. After five steps, the DF extracted explained 100% of the total variance, classifying correctly all cases (Fig. 11). Out of the five characters selected for the DF, three were related to width of the skull (MstW, RstA and Rtrw) and the other two

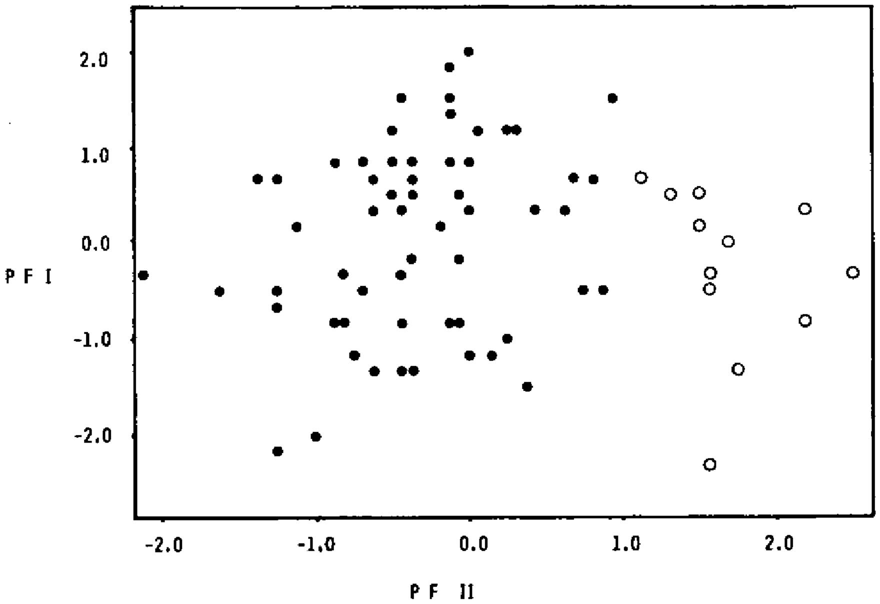

Fig. 10. Plot of Principal Factor I (PF I), (related to skull length) against Principial Factor II (PF), (related to skull width) in males of *M. martes* (solid circle) and *M. foina* (open circle) to show the seperation of species. Adults and subadults pooled.

C= 16.35 + 0.96 (MstW) +0.86 (MndH) +0.84 (RstA) -0.70(RstW) -0.60(BcbH)

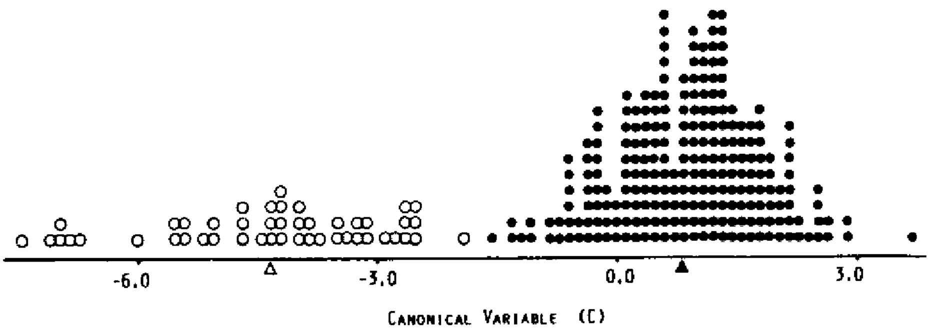

Fig. 11. Histogram of canonical variable scores of the whole collection o skulls to show the seperation of species by stepwise discriminant analysis. On the top the histogram, coefficient of measurements included in the cancional variable. Triangles indicate group centroids. Solid circle: *M. martes*; open circle: *M. foina*.

to height of the skull (MndH and BcbH). The highest contribution to the discriminant function was not from RstA but from MstW, suggesting that these two measurements are correlated, and therefore, some of the species discriminating usefulness of RstA is explained by its correlation with MstW.

4. DISCUSSION

4.1. Methods

Integrated use of univariate and multivariate methods proved to be essential for the study of variability (Gould & Johnston, 1972; Pankakoski & Nurmi, 1986). Univariate analysis is needed because it provides specific information about the variation of particular traits or regions of the skull which may have special interest for taxonomical or biological reasons. Moreover, comparison of the results with other species or other studies is only possible through single characters. On the other hand, multivariate methods enabled a better understanding of biological processes, which are more likely to be multidimensional complexes (Gould & Johnston, 1972; Wiig, 1985).

To describe the relationships between characters, factor analysis (Atchley, 1971 a; Wiig, 1985) was preferred instead of correlation of measurements by minimum squares (Caboń-Raczyńska, 1964; Buchalczyk & Ruprecht, 1977; Pankakoski & Nurmi, 1986). The main advantages of this method in comparison to simple correlation were: (1) different sample size of the groups compared (age, sex, populations, species) does not alter the results and meaning of the factors constructed, (2) the amount of variance explained by each association of measurements (factor) can be calculated, (3) the associations between measurements does not have a fixed structure but varies according to the different sources of variation analyzed (Tables 6, 7, 13), (4) instead of the pairwise associations between measurements provided by the coefficient of correlation, PFA present multiple set of measurements in meaningful subsets.

4.2. Sex Dimorphism

Skull proportions showed little sex dimorphism in both species. Differences between males and females were mainly related to general size of the skull, as occurs in most carnivores (Ewer, 1973). The average difference between sexes in the 23 characters indicate that sex dimorphism was more apparent in *M. martes* than in *M. foina* (Table 3). However, in both species size differences between sexes were low in comparison with other mustelids. Using condylobasal length as a measure of skull size (Hagmeier, 1958; Ralls & Harvey, 1985), adult females are 18.2% smaller in *Mustela putorius* (Buchalczyk & Ruprecht, 1977), 16.3% in *Martes pennanti* (Erxleben, 1777) (Anderson, 1970), 15.5% in *Mustela erminea* Linnaeus, 1758 (Hall, 1951), while in *M. martes* and *M. foina* females are, respectively, only 8.7% and 4.8%, smaller than males (Table 3). Even a closely related species like *Martes zibellina* (Linnaeus, 1758), has larger sex dimorphism (10.0%, after Anderson 1970).

Two principal hypothesis are maintained to explain sexual dimorphism in mustelids. One postulates that size differences between sexes reduce intraspecific competition for food (Brown & Lasiewski, 1972; Powell, 1979; Moors, 1980; Powell & Leonard, 1983), while the other hypothesis claims that fighting between males for coupling in polygamous species had selected for increased male size (Erlinge, 1979; Moors, 1980). Summarizing the first hypothesis as a direct correlation between food competition and sex dimorphism, the results of this study would fully support this argument, knowing the generalistic feeding strategy of both species (Erlinge, 1986), specially *M. foina*. Moreover, detailed studies on the food of *M. martes* did not show differences between the food habits of males and females (Pulliainen, 1981b; Marchesi, 1989).

Masticatory apparatus, in particular weight and height of the mandible, exhibited the most significant sex dimorphism in both species of martens (Table 3), as found by Rossolimo & Pavlinov (1974) in *M. martes*. This is a common feature small mustelids (Yurgenson, 1947; Petrov, 1956), and has been explained also as a consequence of their sexual differences in food habits. Nevertheless, Wiig (1989) explaining similar features of the sexual dimorphism in *Gulo gulo* (Linnaeus, 1758), suggested that female's differences in the masticatory apparatus might be just a morphological expression of maintaining the same chewing efficiency in a smaller skull, since food habits are the same in individuals of both sexes. Such an explanation seems to be also valid for the two species of martens studied.

4.3. Age Variation

Proportions between measurements exhibited important age changes, suggesting allometric growth of the skull. Clear age changes were observed in indices which combine PorW and BcbH, showing negative rate, with other characters. Weight of the mandible and zygomatic width of the skull were the traits exhibiting most significant age variation (Tables 4, 5) as in most of mammals (Yablokov, 1974).

The division of the material into three age calsses was appropriate, regarding the differences found between groups. Further division of the material into more age groups was not only limited by the number of skulls avilable, but also by the difficulties of determining new groups using only external features. Methods commonly used in carnivores such as suture obliteration are not suitable for martens since most sutures are completely closed at very early age (Ryabov, 1962). On the other hand, Brown (1983) analyzing the age variation in *M. americana* (Turton, 1806) and having absolute age determined by cementum incremental lines, suggested also the division of the material into three age groups for studies of cranial variation in martens.

The growing process of the marten skull is highly precocious. Ryabov (1962) found that CbL of males of *M. martes* from Caucasus region attain 88.6% of adult size (86.6% in the case of ZyW) at only two months of age. Two important consequences for our study are derived from this finding. The first one is that skulls older than five months (the material used in this study) reflect only a small fragment of the whole postnatal growth of martens. Secondly, age groups used correspond to a period of stabilized growth process, when the animals are said to be already fully grown.

For these reasons, differences between juvenile and subadults exhibited similar degree of significance than differences between subadults and adults, especially on males (Tables 4, 5). This growing of the skull after the first year of life agrees also with Rossolimo & Pavlinov (1974), who observed a slow growth process prolonged throughout the life of the individual in *M. martes*, and also the existence of significant sex differences in the growth rates, females growing more rapidly than males. Nevertheless, our results for particular traits differ from that study because authors mentioned above used %D between means from both sexes as the main indicator of the significance of age variation, instead of considering *F* values obtained by ANOVA. Also in other carnivores like the European lynx (Wiig & Andersen, 1986) the skull of adult individuals continues to grow, specially in males.

In both species more than 60% of the total age variation was explained only by two principal factors, one joining most length traits, the other joining width traits. Noticeable differences between species were found in the relative importance of each of these two factors for the skull growth. In *M. martes* length factor was more important, explaining 51.3% of the total variance, while the width factor only accounted for 18.9% (Table 6). On the contrary, in *M. foina* length and width factors showed similar amount of varinace explained (29.9% and 31.7%, respectively, Table 8), the width factor being a little more important.

Postorbital width was characterized by a progressive narrowing with age in both species. Previous studies in *M. martes* (Mal'dzhyunaite, 1957), and *M. foina* (Röttcher, 1965) agree with this results, although the significance of the age variability of this trait in *M. martes* and *M. foina* was first quantified in this study (Tables 4, 5). Negative growth of postorbital width is also a common feature in other mustelids, like *Martes americana* (Brown, 1983), *M. putorius* (Buchalczyk & Ruprecht, 1977), and also in other mamals *e.g. Ondatra zibethicus* (Linnaeus, 1766) (Pankakoski & Nurmi, 1986). Age variation of this measurement must be related to overall changes in the brain case capacity (Wiig, 1982), since the results of factor analysis indicated that this measurement is associated with BcC and BcbH.

4.4. Variability between Populations in *M. martes*

The observed differences between the Białowieża population and the rest of Polish territory, accords with the north-south axis of skull increase found by Reig (1989). However, the similarity of Wielkopolska and Masurian samples (Table 10) suggest that results are mainly due to distinctive features of the Białowieża population. Similar results were also observed in *Mustela putorius* (Buchalczyk & Ruprecht, 1977), and in two species of *Erinaceus* (Ruprecht, 1972). Among the eleven traits showing significant differences between populations, MndW, ZyW, and EorW are charactreized also by an important age variation, while others like RstA or BcC showed low age variation. This may suggest that the differences observed between populations are not only related to environmental factors affecting skull growth, but with phenetical peculiarities of the Białowieża population.

4.5. Species Differentiation

Rostral angle (RstA), despite being a trait very seldom used in craniometrical studies of mammals, proved to have an important taxonomic value in European martens since it allowed the distinction between *M. martes* and *M. foina*. Fully accurate identification of both species is, however, better achieved using non-metrical traits (Anderson, 1970; Wolsan *et al.*, 1985; Steiner & Steiner, 1986). Among most frequently used metrical characters for this purpose are the distance between *foramina mentalia* (Gaffrey, 1953) which is not fully precise because of the great variability of these openings and the index between some interorbital measurements (Altuna, 1973) which has the main disadvantage of being based on a graphic representation. However, using RstA, no overlapping between species was obtained when groups of the same sex and age were matched (Tables 1, 2). The accuracy of this trait was high; 98% of the complete collection of skulls (n=283) were correctly calassified into species using a dividing point of 54.9°(Fig. 6). Moreover, RstA has the advantage of exhibiting very little variation with age or sex, not significant in most of the cases.

Considering the association of measurements by principal factor analysis, RstA seems to be related to width of the skull (Tables 6, 7, 8, 9), although it is not coincident with width measurements as concerns pattern of age and sex variation (Tables 3, 4, 5). An attempt was made to separate both species using indexes based on combinations of another measurements than RstA, but related to this region of the skull, as ZyW, RtrW, FcL and PtL (Fig. 3). However, results were not satisfactory, suggesting that RstA reflects a more camplex ratio between width and length of the skull.

The final conclusion in that the patterns of variability are distinct in two species showing remarkable morphological similarities. Differences were concerning not only particular traits reflecting the most significant changes related to sex or age, but also the main pattern of skull variability. Most of the morphological changes in the skull of martens due to sex or age variation were explained by the association of measurements into a length and a width factor. However, in each species the relative importance of these factors to explain the variability observed was different, and in some cases opposite. The most substantial testimony of this argument was the clear separation of species by plotting these two factors (length and width of the skull) against each other (Figs. 9, 10).

An alternative explanation for distinct variability patterns in these marten species, besides their different ecological characteristics, is connected with the phylogeny of the genus *Martes,* since both species are considered to belong to separate phylogenetic groups. *M. martes* is much closer to *M. zibellina, M. melampus* (Wagner, 1841), and *M. americana* than to *M. foina* (Anderson, 1970; Wolsan, 1986).

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ZMIENNOŚĆ MORFOLOGICZNA CZASZKI KUNY LEŚNEJ I KAMIONKI Z POLSKI

Streszczenie

Zbadano zmienność 23 pomiarów czaszkowych oraz kilku wskaźników ilorazowych na materiale 236 czaszek *M. martes* (133 samców i 103 samic) i 47 czaszek *M. foina* (25 samców i 22 samic) z terenu Polski w aspekcie płci i wieku. Liczniejszy materiał *M. martes* badano w 4 grupach regionalnych (Pojezierze Pomorskie i Mazurskie, Nizina Wielkopolsko-Kujawska, Puszcza Białowieska oraz Górny i Dolny Śląsk). Wyróżniono 3 grupy wiekowe w oparciu o datę odłowu i stan zachowania szwów czaszkowych a także stopień starcia zębów i wykształcenia grzebienia strzałkowego. Oba gatunki kun odznaczają się wyraźnym dymorfizmem płciowym w wymiarach czaszki — samce są większe od samic przeciętnie o 12,1% u kuny leśniej i 9,5% u kamionki (Tabela 3). Zaznacza się on przede wszystkim w okolicach czaszki związanych funkcjonalnie z przyjmowaniem pokarmu. Najsilniej zaznaczone różnice wiekowe obserwowano w przypadku masy i długości żuchwy (MnbW i MnbL) oraz szerokości jarzmowej (ZyW), wyraźniej widoczne u kuny leśnej (Tabela 4 i 5). Zmiany wiekowe czaszki badane metodą analizy czynnikowej u M. martes widoczne są z reguły w pomiarach długościowych, w mniejszym stopniu w szerokościowych (łącznie oba czynniki stanowią 70%). U *M. foina* natomiast metoda analizy czynnikowej ujawniła tendencję odwrotną, z tą różnicą że oba czynniki pozostają w proporcji 1:1 (Tabela 6—8). Obydwa gatunki kun najlepiej różnicuje kąt rostralny (RstA), który u *M. martes* jest ostry u *M. foina* bardziej rozwarty. Porównanie w obrębie trzeciej grupy wiekowej samców ujawniło 11 różnic populacyjnych w pomiarach czaszki między kunami leśnymi z Puszczy Białowieskiej i pozostałymi trzema populacjami (Pojezierze Pomorskie i Mazurskie, Nizina Wielkopolsko-Kujawska oraz Dolny i Górny Śląsk) (Tabela 10).