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Skull morphology of Finnish muskrats: geographic variation, age differences and sexual dimorphism

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Morphological variation in Finnish muskrats *Ondatra zibethica* (L.) (n=735) was studied by taking 23 metric measurements of the cranium and the mandible, by counting the numbers of nerve foramina on ten areas of the skull, and by examining the patterns of the third upper molar teeth (M^3). Differences between age groups, between the sexes and between populations were analysed using mainly multivariate statistical methods. Differentiation of Palearctic and Nearctic muskrat populations was examined on the basis of Finnish and literature data.

The differential growth of various skull measurements is reflected in the comparison of age groups and in the age-related changes of correlations between different skull measurements. Among the skull variables diastema length grows relatively most; general size increase of the skull is well reflected in the growth of condylobasal length and zygomatic width. Correspondingly, both the upper and lower molar row lengths and interorbital width are fairly stable dimensions of the muskrat skull. Braincase dimensions grow less than the general size of the skull. As regards epigenetic characters, age does not affect nerve foramen numbers, but does affect molar patterns which change because of molar wear.

The skull measurements of males were mostly larger than those of females, though not as much as expected from sexual dimorphism in body weight. Dimorphism was greatest in diastema length, i.e., in the same variable that exhibits most intense growth among the skull measurements. The degree of sexual dimorphism of some dimensions associated with feeding is small, probably due to stabilizing selection.

Differences among Finnish muskrat populations are evident in skull measurements and epigenetic characters. Interorbital width is the variable discriminating most effectively between different Finnish and Holarctic populations. Rostrum shape in the muskrat does not seem to be as clearly determined by climatological factors as suggested earlier. Some measurements mostly related to feeding show little differentiation between the populations.

Even though populations from the same region tended to be grouped relatively close to each other in the principal component space, no evident geographical patterns, such as clines, emerged. The differences between populations in muskrat skull morphology increase when going from the subpopulation level to the population level within the same country, and further to regional level in different parts of the Palearctic region, where the muskrat is an introduced species. Genetic differences between the founder individuals and rapid differentiation after introduction are more probable causes for population differences than environmental factors. However, habitat quality has a prominent effect on skull size in the muskrat.

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Contents

1. Introduction

Morphological variation in animal populations partly reflects the historical background of the population, in which, e.g., different spreading routes or the degree of isolation are influential (Berry 1964, Berry et al. 1978, Davis 1983). Partly it also reflects the ecological circumstances of the individuals, because the size and shape of certain organs have an effect on fitness (Holbrook 1982). Morphology is therefore (more or less) closely connected with ecology. The study of morphological variation can thus give insight into the factors that are essential in the ecology of the species studied, and at its best also into general evolutionary mechanisms.

A major problem in the study of morphological variation is the difficulty of separating the effects of the environment and heredity as the causes of variation (Gould & Johnston 1972, Atchley et al. 1981). The exact evaluation of the proportions of these two components requires crossing experiments (Atchley et al. 1981). In studies based on samples from natural populations the genetic structure of the populations can evidently be better characterized by epigenetic features such as nerve foramina, bone joints or molar patterns, than by continuous variables (Berry 1963, Rees 1969, Berry et al. 1978, Hartman 1980, Andersen & Wiig 1982).

As the morphological variables depend on age and sex, the effect of these characters should be eliminated in studies of geographical variation. For example, the degree of sexual dimorphism shows geographical variation (Johnston & Selander 1973, Johnston & Fleischer 1981, Ralls & Harvey 1985). The aim of the present paper is to study geographical, as well as sex- and age-dependent, variation in Finnish muskrats (*Ondatra zibethica* (L.)) based on both metric measurements and epigenetic features of the skull.

The muskrat was introduced into Finland as a valuable fur-bearing animal in the 1920s and 1930s. It rapidly colonized the whole country, except for northernmost Lapland (Artimo 1960). About 1100 muskrats were introduced into Finland from Germany, Czechoslovakia and North America. Muskrats reared on Finnish fur farms and individuals caught in the wild were also released at new localities. About 2300 muskrats were released at about 300 localities all over the country (Artimo 1960). As the muskrat is an introduced species in Finland, the study of its morphological variation is particularly interesting. Morphological differentiation within their new ranges has been rapid in introduced species such as the house sparrow *Passer domesticus* in North America (Johnston & Selander 1964, 1971, 1973) and the muskrat in Central Europe (Pietsch 1970). On the other hand, the mixed origin of the Finnish muskrats leads to difficulties, for the variation observed may be traced to differentation in Finland or to the (unknown) difference among the founders.

This paper continues an earlier study on differences between localities and habitats in the size, growth and condition of Finnish muskrats (Pankakoski 1983). The dependence at the population level of epigenetic asymmetry on habitat suitability was documented from the same sample (Pankakoski 1985). The study of morphological characters is of importance also in assessing the suitability of different habitats for this species and is thus connected with habitat management and artifical regulation of populations in this game animal species.

2. Material and methods

The main data set of 644 individuals was collected in 1978—80 at four localities (Fig. 1): Lohja, Lake Lohjanjärvi (60°15′ N, 24°00′ E), Kitee, Lake Kiteenjärvi (62°10′ N, 30°10′ E) and Ilomantsi, the rivers Koitajoki and Ilomantsinjoki (62°45′ N, 30°45′ E) and Kemijärvi (66°33′ N, 24°45′ E), Lake Kemijärvi and several smaller lakes (Table 1, Fig. 1). The study areas and methods of collecting the muskrats have been described in detail by Pankakoski (1983). Most of the animals were trapped between April 15 and May 15, or in Kemijärvi during the second half of May. In the laboratory the muskrats were weighed and sexed, then the head of the animal was removed and boiled for 1-1.5 h and cleaned. Both first molars of the upper jaw (M^1) were removed. In addition, a total of 112 muskrat skulls from the collections of the Zoological Museum, University of Helsinki, and 11 skulls (Pielisjärvi) from the collections of the Finnish Game and Fisheries Research Institute were included in the analysis

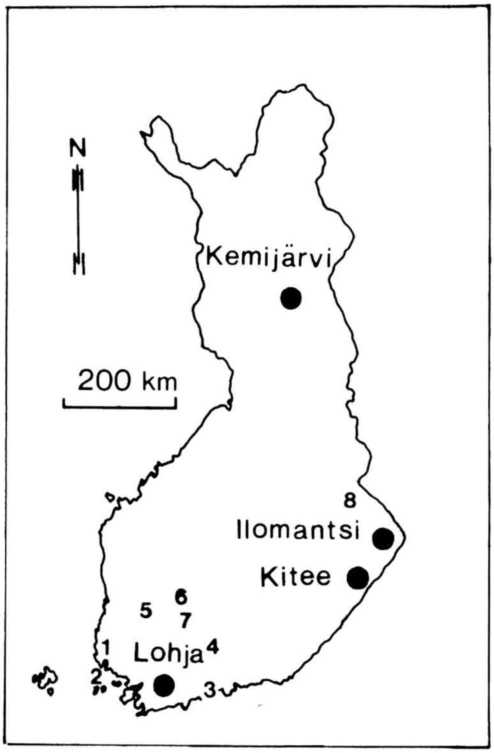


Fig. 1. Trapping localities of the muskrats. Museum samples are indicated in figures: 1 = Lokalahti, 2 = Kustavi, 3 = Helsinki, 4 = Riihimäki, 5 = Tyrvää, 6 = Kangasala, 7 = Sääksmäki, 8 = Pielisjärvi.

Table 1. Numbers of muskrat skulls used in the study. Animals not identified by sex are in parenthesis.

	Our sample		Museum samples			Total			
	♂♂	♀♀	♂♂		♀♀	♂♂		♀♀	Total
Lohja	206	174	10	(2)	17	216	(2)	191	409
Ilomantsi	94	75	—		—	94		75	169
Kitee	21	9	—		—	21		9	30
Kemijärvi	24	13	—		—	24		13	37
Lokalahti	—	—	2		1	2		1	3
Kustavi	—	—	4		1	4		1	5
Helsinki	—	—	19		23	19		23	42
Riihimäki	—	—	7		3	7		3	10
Tyrvää	—	—	9		—	9		—	9
Kangasala	—	—	3		4	3		4	7
Sääksmäki	—	—	1		2	1		2	3
Pielisjärvi	—	—	—	(11)	—	—	(11)	—	11
Total	345	271	55	(13)	51	400	(13)	322	735
	616			119					

Table 2. Abbreviations of the skull measurements and nerve foramina in Fig 1. For molar index, see Pankakoski (1980).

CL	Condylobasal length
RW	Rostrum width
ZW	Zygomatic width
IW	Interorbital width
BW	Braincase width
BL	Braincase length
SSL	Sagittal suture length
FIL	Foramen incisivum length
DL	Diastema length
UML	Upper molar row length
LML	Lower molar row length
MH1-MH6	Mandible height 1-6
ML1-ML5	Mandible length 1-5
MI	Molar index
fro	Foramen frontale
max a	Foramen maxillare a
max b	Foramen maxillare b
men a	Foramen mentale a
men b	Foramen mentale b

(Table 1). The museum animals had been trapped between 1946 and 1971 in southern and Central Finland (Fig. 1, Table 1).

Altogether 23 measurements were taken from each skull (molar index by EP (see Pankakoski 1980), all the other measurements by KN; Fig. 2, Table 2). The cranium was measured with a sliding caliper to within an accuracy of 0.1 mm. Mandible height and length measurements were taken in a small cardboard box lined with millimetre paper, by placing the ventral side of the right mandible on one side of the box and reading off the measurements perpendicularly to an accuracy of 0.5 mm. This is a modification developed for a larger species of Festing's (1972) technique, originally developed for mice (see also Berry et al. 1978). The numbers of foramina (small openings for nerves and small blood vessels) was counted under a dissecting binocular microscope. The nomenclature of foraminal openings primarily follows Berry (1963) and Berry & Searle (1963) (Fig. 2). The patterns of both third upper molar teeth (M^3) were examined under a dissecting binocular microscope. Molar index was measured from the first upper molar as a percentage of the tooth crown of the total height of M^1 (see Pankakoski 1980 for details). The mean of right and left molars was used. The age of each individual in months was estimated from the molar index (Pankakoski 1980).

Statistical analysis. Discriminant function analysis (DFA; HYLPS programs of the Computer Centre, University of Helsinki) was the main statistical method used. When classifying the observations using the discriminatory space of the analysis, generalized distances to all group centroids were calculated for each individual, and the classification was based on the *a posteriori* probabilities of group membership. Because sample size in the groups was usually quite different, this classification was performed by using a method in which each observation had an equal *a priori* probability to be assigned to each group, independently of group size.

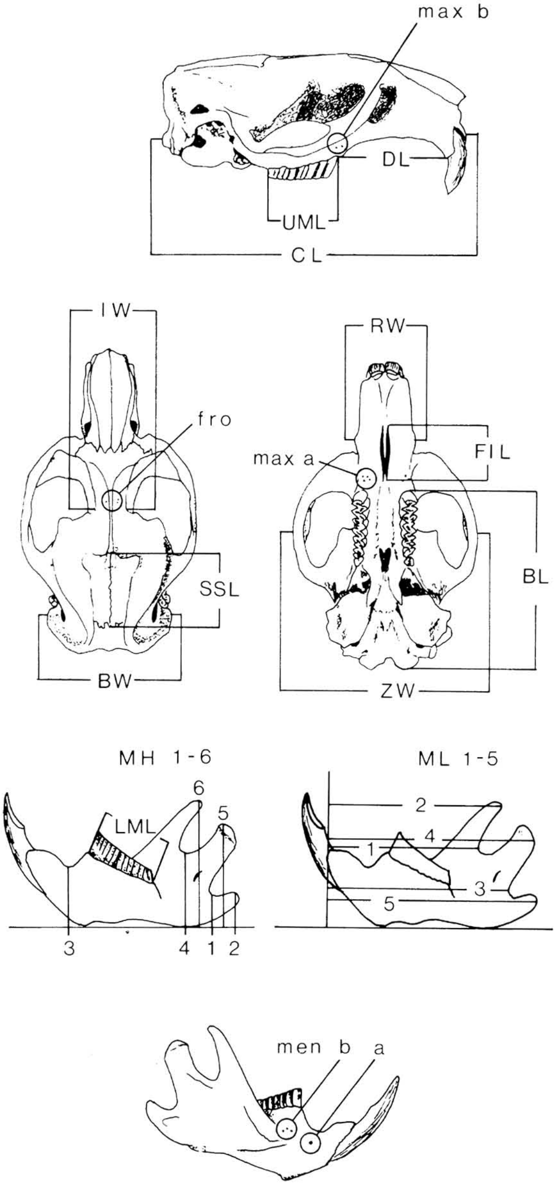


Fig. 2. Linear measurements taken in the study and the location of nerve foramina in the muskrat skull. For abbreviations, see Table 2. The molar index (*MI*), which describes the degree of tooth wear was measured according to Pankakoski (1980).

The maximum number of variables accepted in discriminant function analysis was about 1/3 of the number of observations in the smallest group. The variables were eliminated by using all the variables and choosing the "best" ones according to their discrimination efficiency. Principal component analysis based on covariance matrix (unstandardized variables) was used in comparisons with literature data.

For allometric comparisons relative values of each skull measurement were calculated by using condylobasal length (*CL*) as a size variable (see Mosimann & James 1979) according to the following formula (x_i = absolute values):

$$\text{relative value} = \ln x_i - \ln CL.$$

Our analyses indicate that the results would have been similar if zygomatic width (*ZW*) had been used as a size variable. Because *CL* has larger values than any other measurement taken, all relative values were negative. In order to improve readability, the relative values in tables are not logarithmic but simple ratios: $(x_i/CL)\times 100$. The customary multinormality assumption for the variables used in this study has been made. The arcsine transformation (Sokal & Rohlf 1981:427) was used in statistical comparisons of percentages, such as molar index.

3. Results

3.1. Skull measurements

3.1.1. Comparison between age groups

The comparison of skull measurements between the four age groups (see Fig. 3) was based on the Lohja sample in order to avoid the influence of differences in molar wear and accordingly in age grouping observed between localities (Pankakoski 1983). Owing to the small number of individuals in the oldest age group, only the ten best variables were chosen for analysis. The first step in the discriminant function analysis, the multivariate analysis of variance (MANOVA), showed that the age groups differ statistically highly significantly; the two first canonical functions were significant. The first canonical function explains 82%, and the second 16% of the total discrimination (Table 3, absolute values).

The first canonical function reflects the general size of the skull and correlates best with diastema length, zygomatic width and condylobasal length (Table 3). The second canonical function is best correlated with upper and lower molar row lengths, interorbital width and braincase length, reflecting the contrast of IW with other dimensions. In Fig. 3 the centroids and standard deviation ellipses of age groups II and III almost overlap, but age groups I and particularly IV are clearly deviating (see also Table 4).

Table 3. Correlation coefficients of the skull measurements with the first two canonical functions discriminating between the four age groups in the Lohja sample. The ten best variables were used in discriminant function analysis of absolute values; since *CL* is a size variable, it could not be used in the analysis of relative values.

Function:	Absolute values 1st	 2nd	Relative values 1st	 2nd
CL	0.78	0.12	–	–
ZW	0.80	-0.01	0.33	-0.41
IW	-0.01	-0.44	-0.41	-0.67
BW	0.48	-0.14	-0.33	-0.48
BL	0.58	0.39	-0.60	0.12
DL	0.85	0.07	0.55	-0.11
UML	0.26	0.55	-0.58	0.29
LML	-0.08	0.50	-0.85	0.14
MH4	0.58	0.14	0.15	0.01
ML4	0.74	0.05	-0.11	-0.37
Discrimination (%)	81.5	16.1	78.9	16.8

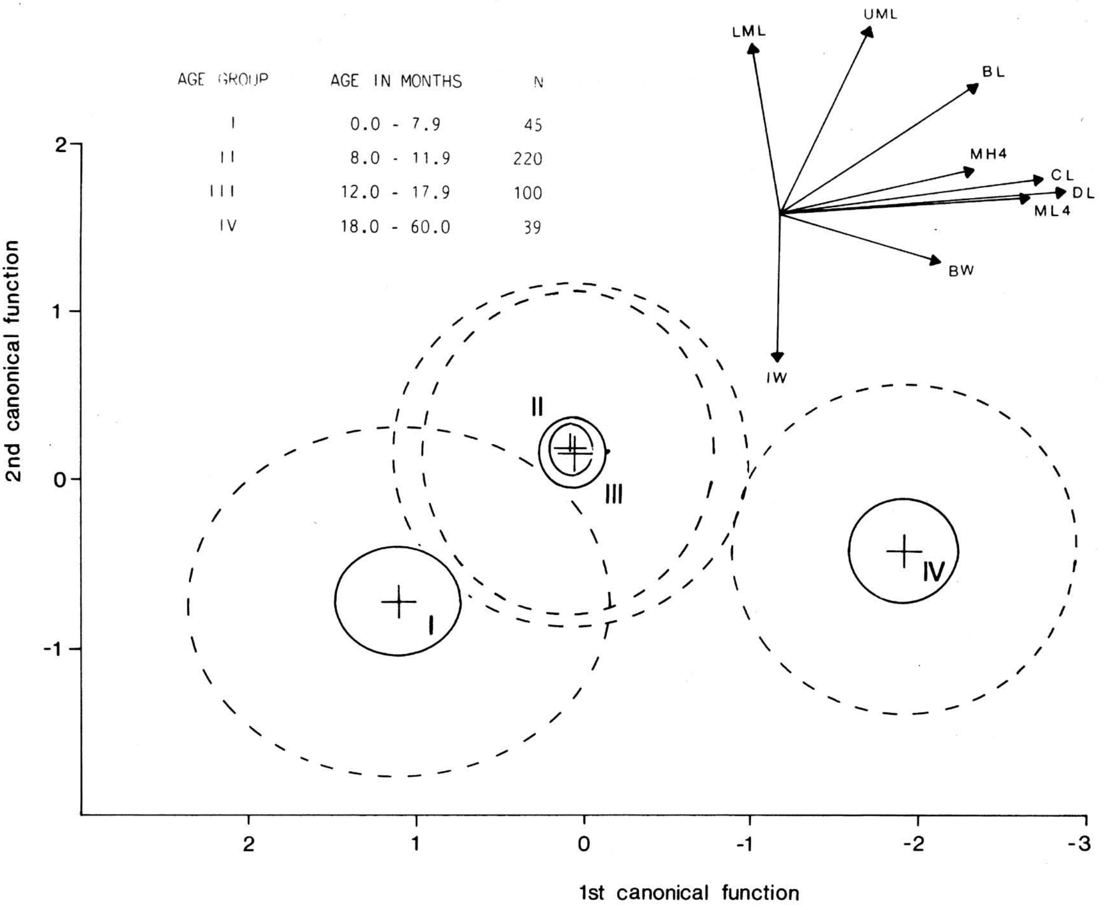
Table 4. Relationship between actual age groups and the age grouping from the discriminant function analysis (DFA) in Fig 3.

Actual groups	DFA grouping I	 II	 III	 IV	Total	Percent hits	
I	*26*	6	12	1	45	58	
II	38	*91*	67	24	220	41 }	69
III	22	23	*40*	15	100	40 }	
IV	1	3	3	*32*	39	82	

As it is quite expected that general size increases with age, it is more interesting to follow allometric changes, i.e., the relative measurements. The relative values discriminate between the age groups about as well as the absolute values. The two first canonical functions explain 79% and 17% of the total discrimination, respectively. The position of group centroids and standard deviations are almost identical with those in Fig. 3. Now the first canonical axis resembles the second function of the absolute values described above (Table 3), and it correlates best with both the molar row lengths, diastema length and braincase length. The second function correlates best with some width dimensions (*IW*, *BW*, *ZW*). As the skull measurements do not separate between age groups II and III, these groups were combined below.

3.1.2. Growth and correlations in skull measurements

In Fig. 4 the growth patterns of different skull measurements have been given in rela-



AGE GROUP	AGE IN MONTHS	N
I	0.0 - 7.9	45
II	8.0 - 11.9	220
III	12.0 - 17.9	100
IV	18.0 - 60.0	39

Fig. 3. Discrimination of the four age classes according to skull measurements. Lohja sample, 10 variables, absolute values. Broken lines indicate areas of mean ± one standard deviation, solid lines areas of 95 % probability level. Arrows indicate effect of each variable in the discriminatory space.

tion to the average in the combined age group II+III (=100 %). The growth has been divided into two phases. Phase *a* describes growth from age group I to II+III and phase *b* from age group II+III to IV. With the exception of variables *IW* and *LML* the means grow during both phases.

The variables have been classified into six groups according to their growth in regard to the general size of the skull (*CL*; Fig. 4). Some mandible height and length measurements (Group 1) exhibit isometric growth with *CL* in both *a* and *b* phases. The growth of *MH1* and *MH2* seems to be concentrated in advanced age, but due to the great variation separation from isometric growth is not possible. The variables in Group 2 (*SSL* and greatest lengths of the mandible) grow more slowly than *CL* during phase *a*; in Group 3 (*FIL* and *UML*) the growth is less during phase *b*, in Group 4 both in phases *a* and *b*. The last situation is clearest in *IW*, *LML* and the dimensions of the braincase (*BW*, *BL*) in Group 4. *RW*, *ZW*, *MH5* and *MH6* (Group 5) grow at first isometrically with general size, but the growth increases during phase *b*. *DL* (Group 6) shows an increase that overrides the intensity of general growth (Fig. 4). Total growth (from age group I to IV) is significantly smaller than growth in *CL* in *IW****, *BW****, *BL****, *UML****, *LML****, *MH3***, *ML1**, *ML3**, greater in *DL****, *MH6***, *ZW** and *MH5** (asterisks indicate the level of statistical significance).

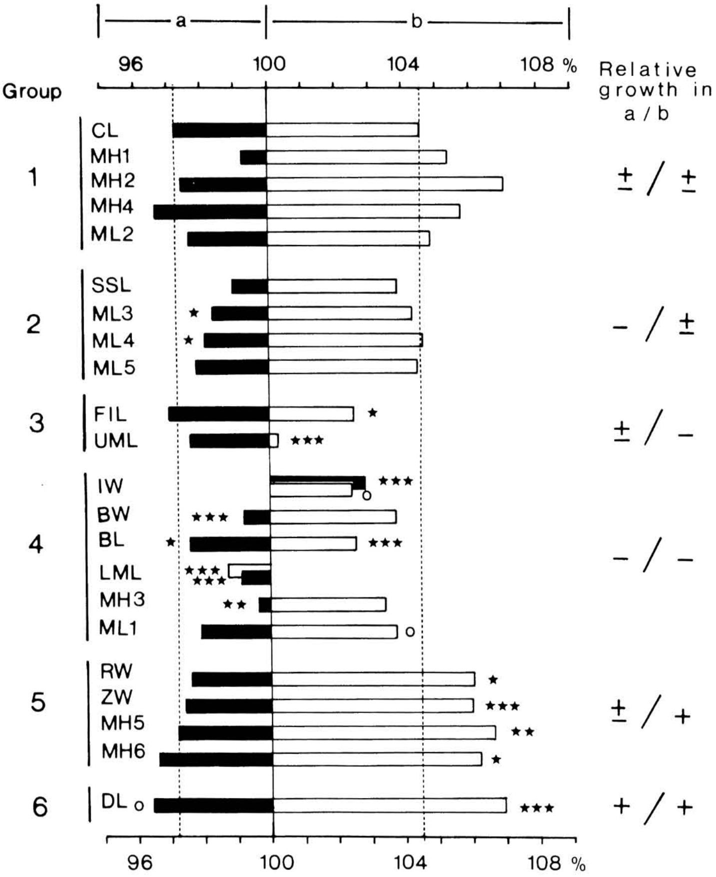
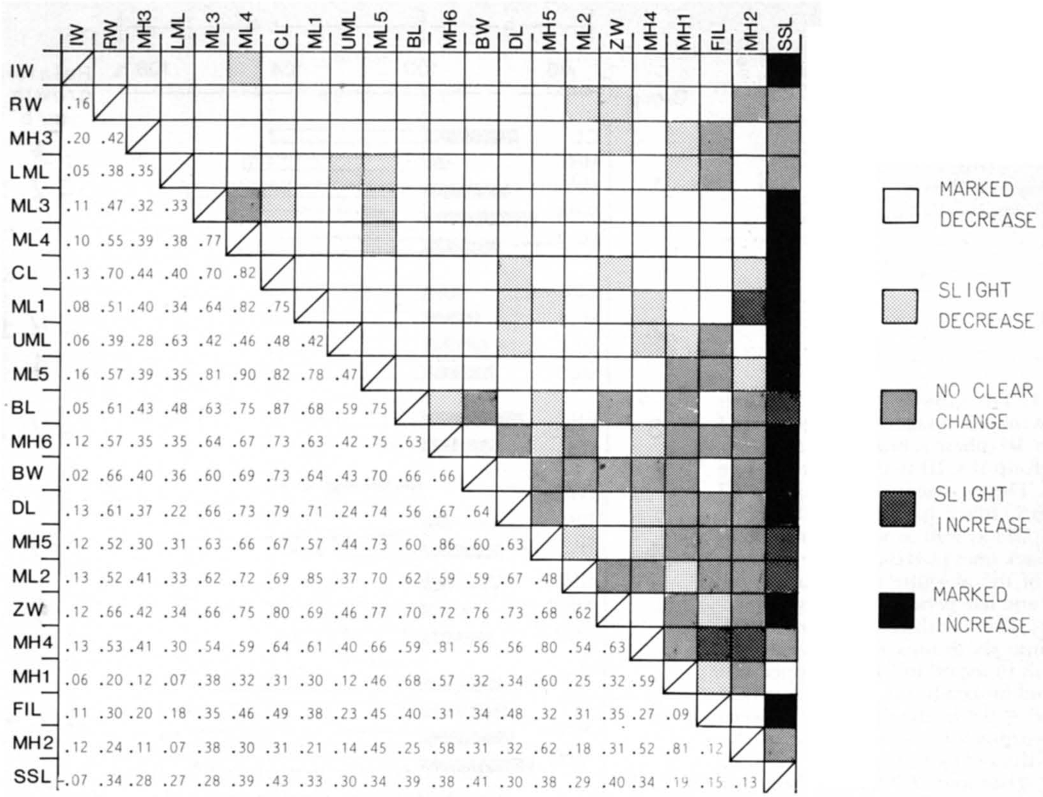


Fig. 4. The growth of skull measurements (in percentages) from age group I to II + III (phase a, black bars) and from age group II + III to IV (phase b, white bars). The average in age group II + III is 100%. Black bars among the white ones (*IW*) as well as white bars among the black ones (*LML*) indicate *diminution* of the absolute mean during the early and late periods of ageing, respectively. The variables have been classified into six groups according to their growth in regard to *CL* (the uppermost bar and broken lines). In this classification $P = 0.2$ in the difference between the two growths (*t*-tests between the relative values of two age groups) was used as a criterion: $P>0.2$ = isometric growth (±), $P<0.2$ = smaller (—) or greater (+) growth than in *CL*. Lohja sample. For the method, see also Kurtén & Werdelin (1984).

Ruprecht (1974) has shown that the positive correlations between the skull measurements of the muskrat diminish with age. This phenomenon can also be observed in Finnish muskrats (Fig. 5): in 171 (74.0%) out of 231 total correlations between skull variables the coefficients decreased with age. In 42 cases (18.2%) the correlations were rather stable, and in only 18 cases (7.8%) the correlations increased with age. The change of correlations with age is shown in the upper part of Fig. 5. The decreasing trend in correlations is most evident in interorbital width, but obvious also in rostrum width, mandible height 3 and lower molar row length. The decrease is greater in variables representing mandible length than mandible height (except *MH3*). The increase of correlations with age, a situation not found at all by Ruprecht (1974), is clear in sagittal suture length.

The change of correlations between the skull measurements according to age is no doubt connected with the growth processes of the skull, because the variables in which growth was observed to be exceptional are discerned also in this connection. Three examples of a scatter diagram between two skull measurements in the youngest and oldest age groups are given in Fig. 6. The decrease of correlations in old age (A) seems to result when the growth of one variable has stopped at a certain level while still continuing in the other. If the growth of both measurements is continuous (B), the correlations remain equally high in both young and old age groups. In C one measurement (*SSL*) increases more than the other in advanced age. In the latter case also the variability of the measurements decreases in old age.

Correlation coefficients between skull measurements in the Lohja sample (age groups



	IW	RW	MH3	LML	ML3	ML4	CL	ML1	UML	ML5	BL	MH6	BW	DL	MH5	ML2	ZW	MH4	MH1	FIL	MH2	SSL
IW																						
RW	.16																					
MH3	.20	.42																				
LML	.05	.38	.35																			
ML3	.11	.47	.32	.33																		
ML4	.10	.55	.39	.38	.77																	
CL	.13	.70	.44	.40	.70	.82																
ML1	.08	.51	.40	.34	.64	.82	.75															
UML	.06	.39	.28	.63	.42	.46	.48	.42														
ML5	.16	.57	.39	.35	.81	.90	.82	.78	.47													
BL	.05	.61	.43	.48	.63	.75	.87	.68	.59	.75												
MH6	.12	.57	.35	.35	.64	.67	.73	.63	.42	.75	.63											
BW	.02	.66	.40	.36	.60	.69	.73	.64	.43	.70	.66	.66										
DL	.13	.61	.37	.22	.66	.73	.79	.71	.24	.74	.56	.67	.64									
MH5	.12	.52	.30	.31	.63	.66	.67	.57	.44	.73	.60	.86	.60	.63								
ML2	.13	.52	.41	.33	.62	.72	.69	.85	.37	.70	.62	.59	.59	.67	.48							
ZW	.12	.66	.42	.34	.66	.75	.80	.69	.46	.77	.70	.72	.76	.73	.68	.62						
MH4	.13	.53	.41	.30	.54	.59	.64	.61	.40	.66	.59	.81	.56	.56	.80	.54	.63					
MH1	.06	.20	.12	.07	.38	.32	.31	.30	.12	.46	.68	.57	.32	.34	.60	.25	.32	.59				
FIL	.11	.30	.20	.18	.35	.46	.49	.38	.23	.45	.40	.31	.34	.48	.32	.31	.35	.27	.09			
MH2	.12	.24	.11	.07	.38	.30	.31	.21	.14	.45	.25	.58	.31	.32	.62	.18	.31	.52	.81	.12		
SSL	.07	.34	.28	.27	.28	.39	.43	.33	.30	.34	.39	.38	.41	.30	.38	.29	.40	.34	.19	.15	.13	

Fig. 5. Change of correlations between variables during ageing (upper triangle). The variables are arranged according to their correlation patterns, from marked decreases to marked increases. In the lower triangle correlation coefficients (r) over age groups II+III pooled (n=320) are given. The criteria of classification in the change of correlation coefficients during phases *a* and *b* are: *clear change* = change >0.1 in the one phase and >0.02 in the same direction (increase or decrease) in the other; *slight change* = change >0.02 in both phases or >0.1 in one phase and <0.02 in the other. Cases with a conflicting direction of change during phases *a* and *b* were also classified in this category, if the total difference in r between the two extreme age groups (I and IV) is >0.2; *no clear change* = all other cases.

II+III pooled, n=320) are given in the lower part of Fig. 5. The correlations are usually highly significantly positive. The variables with marked decrease/increase in the correlations (especially *IW* and *SSL*) show low correlations in this total sample.

The following general trends are evident in the growth of muskrat skull measurements both in comparisons between the growth of each separate variable and change of correlations, and in discriminant function analyses. The growth of general size of the skull according to age is evident above all in the growth of condylobasal length and zygomatic width. The growth of diastema length is even more intense. Correspondingly, growth is slight in both upper and lower molar row lengths (the mean of *LML* at later growth stages even absolutely decreases), and in interorbital width, which exhibits the largest means in the youngest age groups. Some measurements describing braincase dimensions (braincase length and width, sagittal suture length) grow less than the general size of the skull.

3.1.3. Comparison between sexes

The size difference between sexes in favour of males, observed in the body and carcass weight of Finnish muskrats (Pankakoski 1983) is obvious also in cranial measurements: in most characteristics males have larger mean values (Table 5). The difference is not significant in those measurements in which the mean is small and/or variation is great (in

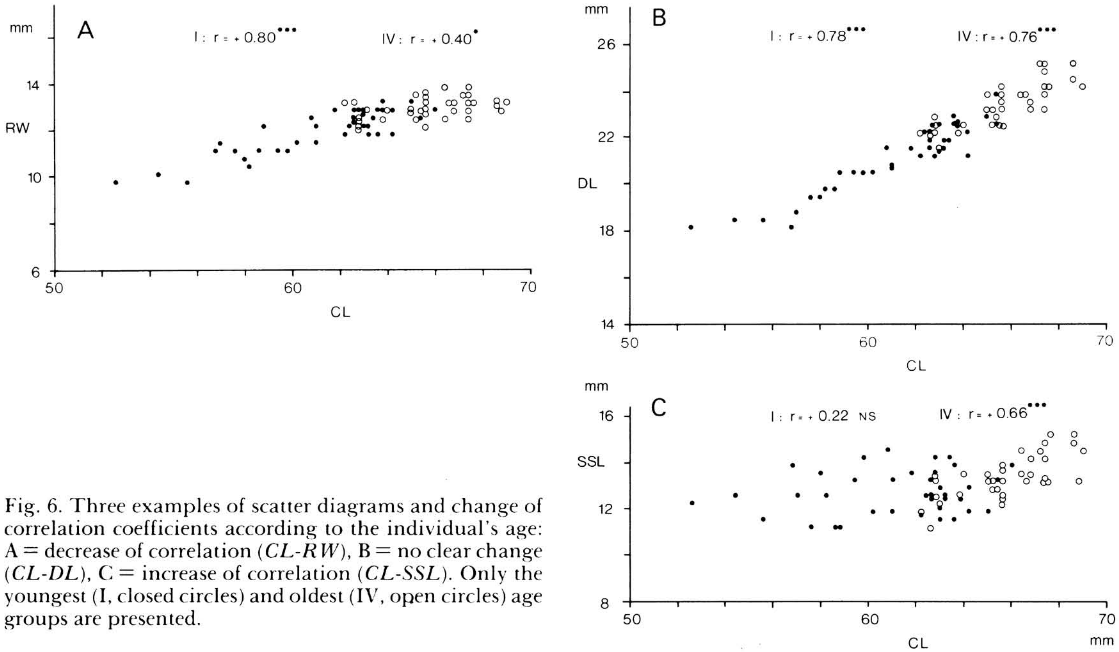


Fig. 6. Three examples of scatter diagrams and change of correlation coefficients according to the individual's age: A = decrease of correlation (*CL-RW*), B = no clear change (*CL-DL*), C = increase of correlation (*CL-SSL*). Only the youngest (I, closed circles) and oldest (IV, open circles) age groups are presented.

Table 5. Sexual dimorphism in muskrat skull measurements (mean ± *SD*). Variables are arranged in decreasing order of male dominance in absolute size. Abs = absolute, rel = relative values. Total Finnish sample, April-May, animals under 1 year old only (ns = not significant, o = $P<0.10$, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$).

Variable	Males Mean	Males *n*	Females Mean	Females *n*	Dimorph. %	Difference abs	Difference rel	Bigger sex (rel)
DL	22.3 ± 0.97	321	21.8 ± 0.99	249	2.40	***	o	(♂)
ML2	36.9 ± 1.44	322	36.1 ± 1.30	247	2.24	***	ns	
RW	12.2 ± 0.58	323	11.9 ± 0.56	250	2.10	***	ns	
BW	27.0 ± 1.19	313	26.5 ± 1.20	248	1.89	***	ns	
SSL	12.9 ± 0.91	323	12.6 ± 0.92	249	1.89	**	ns	
ZW	38.8 ± 1.54	311	38.1 ± 1.56	241	1.87	***	ns	
CL	63.4 ± 2.04	305	62.3 ± 1.99	239	1.82	***	—	
ML1	31.7 ± 1.08	323	31.2 ± 1.00	249	1.81	***	ns	
BL	37.9 ± 1.17	304	37.2 ± 1.17	237	1.77	***	ns	
MH4	12.7 ± 0.88	324	12.5 ± 0.81	250	1.42	*	ns	
ML5	42.2 ± 1.56	320	41.7 ± 1.50	250	1.23	***	**	♀
FIL	12.9 ± 0.78	324	12.7 ± 0.76	249	1.20	*	ns	
MH3	10.9 ± 0.54	324	10.8 ± 0.48	250	1.19	**	o	(♀)
UML	16.3 ± 0.66	321	16.1 ± 0.63	246	1.09	**	*	♀
ML3	36.4 ± 1.20	323	36.1 ± 1.12	250	1.07	***	***	♀
ML4	42.3 ± 1.38	322	41.9 ± 1.29	250	1.01	***	***	♀
MH6	21.8 ± 1.17	323	21.6 ± 1.13	248	0.93	*	**	♀
LML	15.6 ± 0.51	324	15.4 ± 0.46	250	0.88	**	**	♀
IW	6.7 ± 0.49	324	6.6 ± 0.47	249	0.76	ns	ns	
MH5	17.4 ± 0.97	323	17.3 ± 1.00	250	0.56	ns	**	♀
MH1	4.1 ± 0.67	321	4.1 ± 0.67	250	0.02	ns	ns	
MH2	4.5 ± 0.67	321	4.5 ± 0.70	250	-0.02	ns	ns	

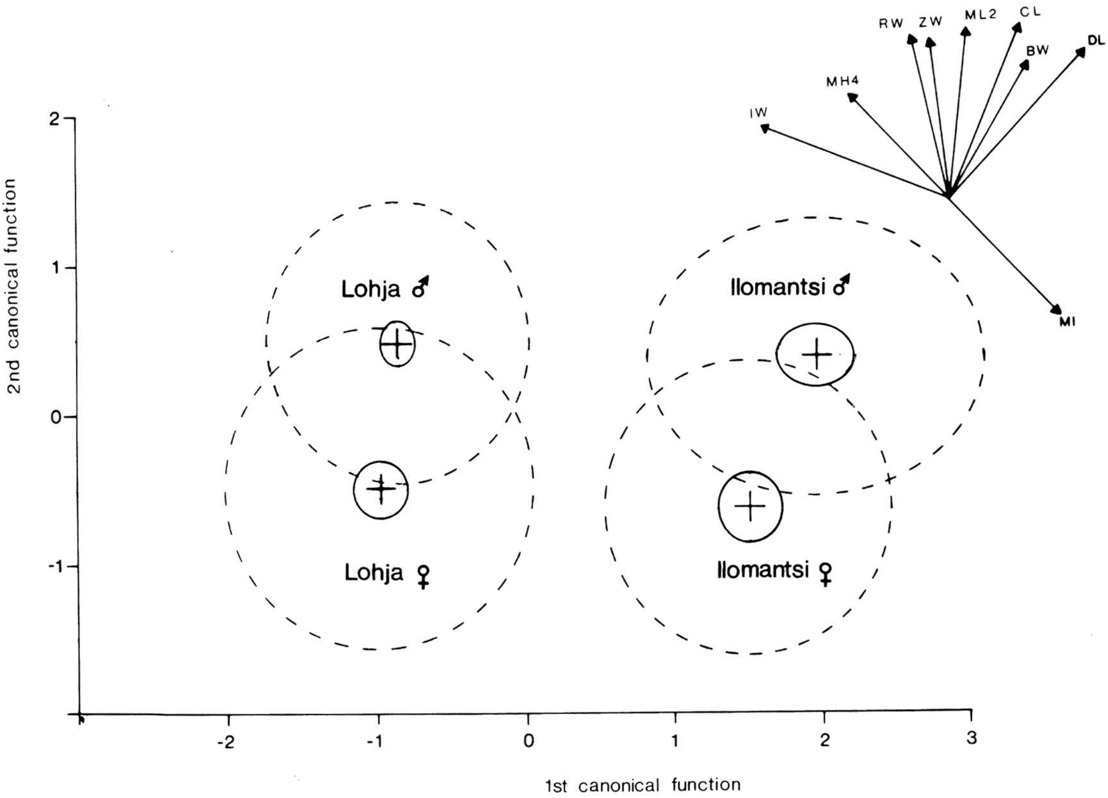


Fig. 7. Discrimination of Lohja and Ilomantsi samples (sexes separated) according to skull measurements (absolute values, 10 variables). For explanations, see Fig. 3 and text.

some mandible heights and *IW*.

The average degree of male size dominance in skull measurements is 1.51 % (each variable weighed in proportion to the mean; 1.32 % if weighed equally). Sexual dimorphism is greatest in diastema length (2.4 %), mandible length 2 (2.2 %), and rostrum width (2.1 %; Table 5). In diastema length even the relative values tend to be larger in males, though not significantly so ($P = 0.08$). In the other relative values the difference is usually not significant, but in several mandible dimensions, especially in lengths, the females have significantly greater relative values (mandible height 5,6, mandible length 3,4,5, and both molar row lengths, particularly in the lower jaw).

3.1.4. Comparison between localities

Discriminant function analysis. Because the actual age structure was similar in the four muskrat populations studied (Pankakoski 1983) the comparisons between localities in skull measurements were performed without separating the age groups. In contrast to comparisons between age groups, only April and May samples were used here. The samples from Lohja and Ilomantsi were large enough to allow separation of the sexes in the discriminant function analysis over all the skull measurements, including molar index.

The discriminant function analysis gave statistically highly significant results both on absolute and relative values. Two out of three canonical functions were significant; the first separates the two localities, the second separates the sexes. The pattern of group centroids in discriminating space of these functions is symmetric (Fig. 7). The first canonical function correlates best with interorbital width, which has greater values in Lohja (Table 6). Diastema length, molar index (both small in Lohja) and mandible height 4 (large in Lohja)

Table 6. Correlation coefficients of all the skull measurements with the first two canonical functions, discriminating between the populations of Lohja and Ilomantsi (first function) and the sexes (second function). Both results of analyses on 23 absolute and 22 relative variables are presented.

	Absolute values		Relative values	
Function:	1st	2nd	1st	2nd
MI	0.36	-0.39	0.37	-0.46
CL	0.24	0.58	–	–
RW	-0.13	0.54	-0.40	0.20
ZW	-0.07	0.52	-0.41	0.05
IW	-0.63	0.25	-0.67	-0.05
BW	0.26	0.45	0.11	0.02
BL	0.10	0.62	-0.28	-0.01
SSL	-0.01	0.21	-0.13	-0.08
FIL	0.30	0.17	0.18	-0.22
DL	0.45	0.49	0.49	0.22
UML	-0.21	0.38	-0.41	-0.17
LML	0.10	0.36	-0.13	-0.27
MH1	0.03	0.06	-0.01	-0.08
MH2	-0.09	0.07	-0.15	-0.08
MH3	-0.04	0.33	-0.21	-0.11
MH4	-0.34	0.36	-0.55	0.06
MH5	-0.22	0.24	-0.46	-0.20
MH6	-0.25	0.30	-0.55	-0.15
ML1	0.15	0.55	-0.13	-0.04
ML2	0.06	0.57	-0.19	0.13
ML3	0.22	0.38	-0.04	-0.42
ML4	-0.01	0.34	-0.40	-0.49
ML5	-0.07	0.41	-0.48	-0.26
Discrimination (%)	85.5	13.2	90.2	8.6

Table 7. Correlation coefficients of relative skull measurements with the three first canonical functions discriminating between the four Finnish populations (Lohja, Ilomantsi, Kitee, Kemijärvi). Sexes pooled, only nine best discriminators.

Function:	1st	2nd	3rd
MI	-0.43	0.03	0.23
RW	0.47	-0.21	-0.37
IW	0.66	0.56	-0.07
FIL	-0.15	-0.48	-0.11
DL	-0.48	0.46	-0.38
MH4	0.61	-0.06	-0.15
MH6	0.55	-0.02	0.26
ML1	0.06	0.27	0.47
ML5	0.45	0.11	0.35
Discrimination (%)	74.1	16.1	9.8

correlate highly with the first canonical function in absolute values; in relative values also *MH5, 6* and *ML5* have high scores (Table 6). The difference between the results of absolute and relative values is evident in the second canonical function. In absolute values the second function can be interpreted as general size of the skull; in relative values this function correlates best with variables showing allometry due to the sex difference in size (see above): mandible length 3, 4, 5, molar index and upper molar row length (Table 6). The absolute size of individuals in Ilomantsi is considerably greater than in Lohja. The classification of the observations in discriminant analysis is more successful in separating the localities (92% hits in absolute values) than the sexes (71% hits).

The small samples of Kitee and Kemijärvi can be included in the locality comparisons when the sexes are pooled (10 and 9 best variables in discriminant function analysis with absolute and relative values, respectively). The discriminations are highly significant and the distribution of discriminating efficiency over three canonical functions (all significant) is rather similar in absolute and relative values. The main results are the same, but because the analysis on relative values is more useful for a comparison of animals from different habitats the following presentation is based on these only.

All the canonical functions are statistically significant. The first function (explaining 74% of the total discrimination) separates Lohja from North Karelia, the second (16%) separates Kemijärvi from other populations, and the third (10%) separates Kitee from the rest (Fig. 8). Clearly the smallest degree of discrimination is found between the two North Karelian populations.

Interorbital width is by far the most important variable in discriminant functions (both in absolute and relative values). It correlates highly with the first two functions; interorbital width discriminates between Lohja, North Karelia and Kemijärvi, but not between Ilomantsi and Kitee (Fig. 8, Table 7). The other variables important in the first canonical function are mandible height 4 and 6, as well as diastema length, rostrum width, mandible length 5 and molar index. The second canonical function, which separates Kemijärvi, correlates best with interorbital width, foramen incisivum length and diastema length; the third function, which discriminates Kitee animals, reflects the contrast of mandible length measurements to diastema length and rostrum width (Table 7). In regard to general differen-

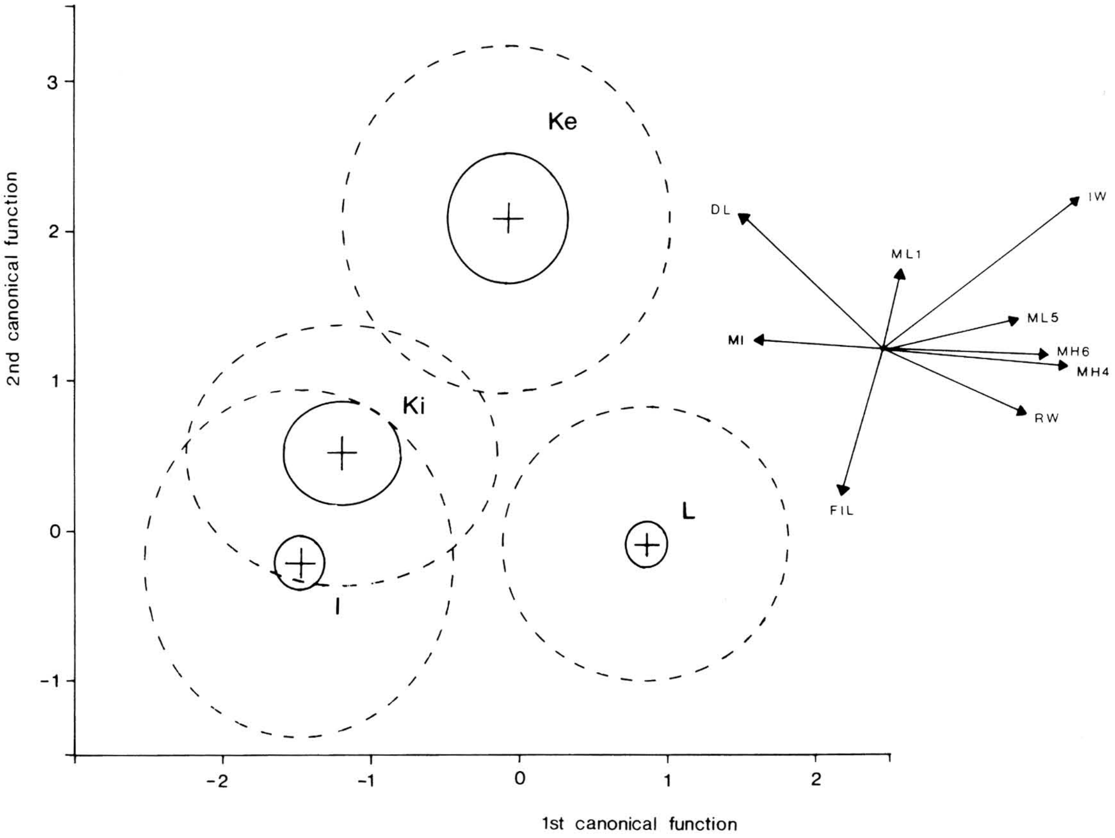


Fig. 8. Discrimination of the four main populations of the study (sexes pooled, 9 variables) according to relative skull measurements. For explanations, see Fig. 3 and text.

ces between localities, Ilomantsi and Kitee samples differ reasonably slightly from each other (Fig. 8), and they can be combined if necessary. By doing this, the classification of the observations (presented for 4 localities in Table 8) is improved as regards North Karelian muskrats (80 % hits).

To summarize the comparisons between the four localities in skull measurements (for population means of the most effective discriminators, see Table 9): The muskrats from Lohja have a short diastema, wide rostrum and high mandibles (*MH4, MH6*). The animals from North Karelia (Ilomantsi and Kitee) have small values in interorbital width (Fig. 9), especially compared with Kemijärvi muskrats, and the mandible height values are lower than in the other localities. Mandible length 1 and 5 are smaller and rostrum width is greater in Ilomantsi than in Kitee populations. In addition to the deviation in interorbital width the muskrats of the Kemijärvi sample have a greater mean diastema length (cf. especially Lohja) and foramen incisivum is short.

Proportions of variance components in one-way analysis of variance between the four localities were calculated according to Sokal & Rohlf (1981) (Fig. 10). Among localities variance component is exceptionally high (41.3 %) in interorbital width, owing to the stability of *IW* in regard to age and sex (see above), i.e., this measurement varies little within each locality. This quality greatly increases the effect of interorbital width in discriminant analysis between localities.

Classification of museum samples. The museum samples from several localities in Finland were used to test the discrimination model. The actual trapping localities of these animals were known and the idea was to test possible geographical trends in the sample:

Table 8. Relationship between actual geographical groups and the grouping from the discriminant function analysis (DFA) in Fig 8.

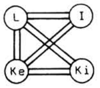
Actual groups	DFA grouping Lohja	Ilomantsi	Kitee	Kemijärvi	Total	Percent hits
Lohja	*266*	28	19	17	330	81
Ilomantsi	19	*111*	22	15	167	67
Kitee	2	3	*22*	3	30	73
Kemijärvi	3	1	1	*23*	28	82

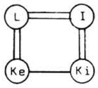
Table 9. Comparison of the 9 best skull discriminators and *CL* between the four localities. The variables are presented in the order of discrimination efficiency from right to left. Both absolute and relative means, *SD*, *n* and *F* of one-way analysis of variance are presented. Significant differences between the localities (Gabriel's method, see Sokal & Rohlf 1981:253) are expressed in lines: single line = $P<0.05$, double line = $P<0.01$ (L=Lohja, I=Ilomantsi, Ki=Kitee, Ke=Kemijärvi).

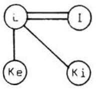
ABSOLUTE VALUES (mm)

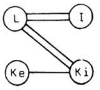
	I W			D L			M H 6			M I (%)			R W		
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Lohja	6.81	0.40	329	21.95	1.02	325	22.13	1.19	326	56.57	10.33	326	12.28	0.59	329
Ilomantsi	6.29	0.43	167	22.73	1.09	167	21.63	1.02	167	62.92	9.58	167	12.13	0.57	167
Kitee	6.38	0.52	30	22.03	0.83	30	21.63	0.86	30	65.82	10.47	30	11.62	0.51	30
Kemijärvi	7.19	0.41	28	22.76	1.17	28	21.61	1.00	28	58.89	10.08	28	11.99	0.40	28
F=	75.25***			23.35***			9.20***			21.59***			14.44***		

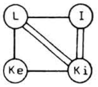
Differences between localities







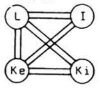


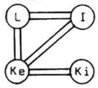


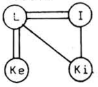
RELATIVE VALUES

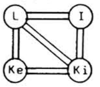
	I W			D L			M H 6			M I (%)			R W		
	Mean	SD	n	Mean	SD	n	Mean	SD	n				Mean	SD	n
Lohja	10.79	0.69	329	34.77	0.92	325	35.05	1.26	326				19.45	0.65	329
Ilomantsi	9.87	0.78	167	35.57	0.92	167	33.85	1.06	167	see			18.99	0.67	167
Kitee	10.18	0.82	30	35.14	0.73	30	34.51	1.05	30				18.54	0.59	30
Kemijärvi	11.44	0.76	28	36.20	1.06	28	34.36	0.95	28	above			19.08	0.67	28
F=	77.43***			41.25***			38.50***						32.05***		

Differences between localities





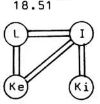


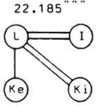


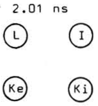
ABSOLUTE VALUES (mm)

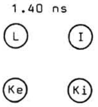
	F I L			M H 4			M L 1			M L 5			C L		
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Lohja	12.79	0.69	329	12.99	0.86	329	31.62	1.14	327	42.43	1.62	328	63.14	2.15	330
Ilomantsi	13.15	0.87	167	12.49	0.69	167	31.84	1.04	167	42.19	1.52	166	63.88	2.03	167
Kitee	12.55	0.65	30	12.15	0.49	30	31.95	0.86	30	42.10	1.40	29	62.69	1.77	30
Kemijärvi	12.21	0.61	28	12.63	0.62	28	31.68	1.08	28	42.02	1.62	28	62.86	2.00	28
F=	18.51***			22.185***			2.01 ns			1.40 ns			6.21***		

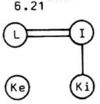
Differences between localities







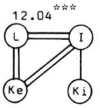


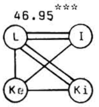


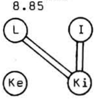
RELATIVE VALUES

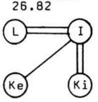
	F I L			M H 4			M L 1			M L 5		
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Lohja	20.25	0.96	329	20.57	1.06	329	50.11	1.19	327	67.21	1.43	328
Ilomantsi	20.59	1.17	167	19.55	0.85	167	49.86	1.09	167	66.06	1.18	166
Kitee	20.02	0.96	30	19.39	0.74	30	50.97	1.04	30	67.11	1.48	29
Kemijärvi	19.43	0.77	28	20.09	0.85	28	50.40	1.06	28	66.83	1.22	28
F=	12.04***			46.95***			8.85***			26.82***		

Differences between localities









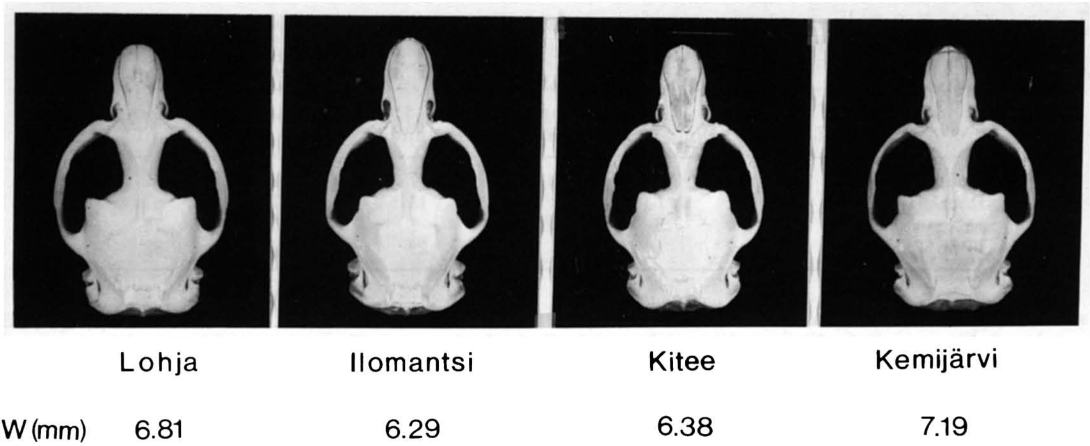


Fig. 9. Muskrat skulls from the four main populations of the study. The individuals are of comparable age; all are females. Notice the difference in interorbital width between the populations.

are the individuals classified by the DFA to belong to the nearest populations? A discrimination function analysis was calculated over the three main localities (Lohja, North Karelia, Kemijärvi; museum animals were omitted from the Lohja sample) by using the same 'best' variables presented above, except molar index. (The use of *MI* is not justified due to unknown age structure of the museum samples and because their trapping dates range over several months of the year, not only spring.) Some support on the hypothesis of hitting a nearby group more often than one further away was found (Fig. 11). 79% of the muskrats in the Lohja museum sample are classified to belong to Lohja group; none is classified to Kemijärvi, which situates 750 km from Lohja. Correspondingly, the Pielisjärvi sample in North Karelia hits the latter group in 64% of the cases. Similar, but more vague trends can be observed in most other samples.

Classification of variables in locality comparisons. The differences among the four localities in skull measurements, as expressed in a one-way analysis of variance, were compared using absolute and relative values (Table 10). Most of the variables showed similar differences among localities, irrespective of whether one used absolute or relative values (group 1 in Table 10). As a rule these are the variables contributing most to the discriminant func-

Table 10. Grouping of skull measurements into three types according to the differences among the four localities in absolute and relative measurements. The figures indicate the between locality variance components (in percentages) in one-way analysis of variance (ns = not significant, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$). Group 1: similar differences between the localities in both absolute and relative values; group 2: significant differences in absolute values only; group 3: significant differences in relative values only.

		Absolute	Relative
Group 1	RW	10.6 ***	23.4 ***
	ZW	1.7 *	16.1 ***
	IW	41.3 ***	42.9 ***
	SSL	0.3 ns	1.2 ns
	FIL	16.0 ***	9.8 ***
	DL	16.6 ***	28.4 ***
	UML	10.8 ***	16.3 ***
	LML	5.5 ***	2.6 *
	MH1	1.2 ns	1.2 ns
	MH2	2.3 *	3.8 **
	MH4	16.8 ***	31.1 ***
	H5	8.3 ***	21.5 ***
	MH6	8.0 ***	27.0 ***
	ML3	2.7 **	4.3 ***
Group 2	BW	6.0 ***	0.4 ns
Group 3	BL	1.1 ns	7.9 ***
	MH3	1.3 ns	6.3 ***
	ML1	0.8 ns	7.2 ***
	ML2	0.8 ns	7.2 ***
	ML4	0.0 ns	14.4 ***
	ML5	0.5 ns	20.4 ***

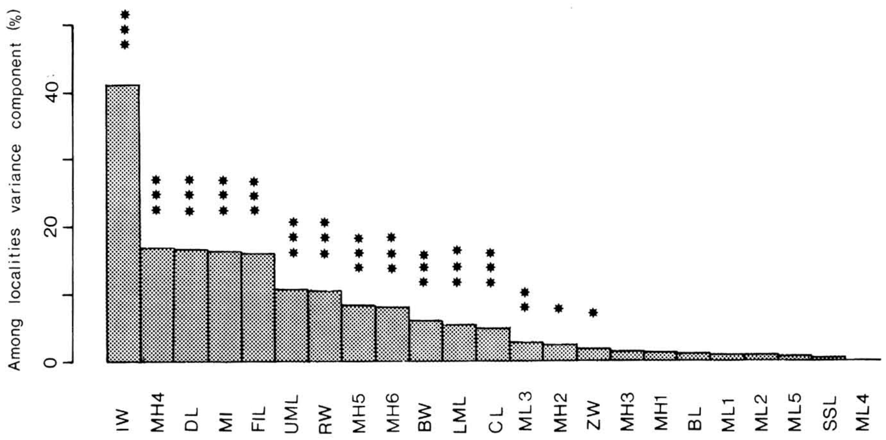


Fig. 10. Proportion of among localities variance component in one-way analysis of variance between the four localities (Table 9; for method, see Sokal & Rohlf (1981:216). The skull measurements (absolute values) are arranged in decreasing order of the "among group" variance components. Asterisks indicate statistical significance between the four localities. Notice that these values are relative, i.e., a high percentage indicates great variation among localities *compared to the total variation*.

tions. Only one variable (braincase width) showed significant differences in absolute values, but not in relative values, thus resembling the general size variable, condylobasal length. In six variables significant differences were observed in the relative values only. These variables (group 3 in Table 10) can perhaps be termed 'important', as their value stays fairly constant in spite of the size differences. Variables describing mandible length (*ML1, 2, 4, 5*) or height (*MH3*) and braincase length belong to this group (Table 10).

3.1.5. Comparison between subpopulations in Lohja

Comparison of the five subpopulations of the Lake Lohjanjärvi has earlier shown that body size and molar index (Pankakoski 1980) depend on habitat factors (Pankakoski 1983). When studying differences in absolute skull measurements between these subpopulations, the same dependence of size on habitat suitability is evident. In relative values the five subpopulations differ much less than the four

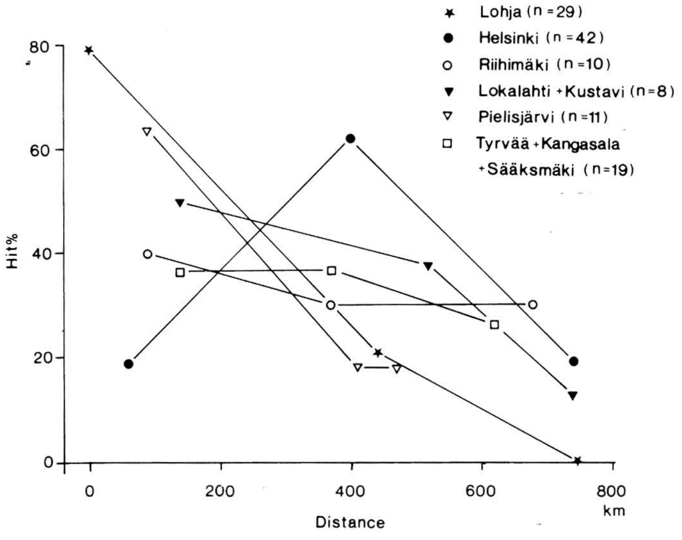


Fig. 11. The dependence of hit-% on the geographical distance in the classification of museum samples according to the discriminatory space of three main populations (Lohja, North Karelia, Kemijärvi).

localities compared earlier, although in the DFA the first two canonical functions are significant (11 best variables only). The classification of observations in discriminant analysis is rather poor (37 % hits). (The museum animals in the Lohja sample were omitted in these calculations because their exact trapping sites were not known.) The analyses of variance of relative values show significant differences between the subpopulations in some traits, but the differences cannot usually be localized by *a posteriori* methods. The muskrats in Puimala (poorest habitat, see Pankakoski 1983) are characterized by high relative means in sagittal suture length, mandible length 4, mandible height 3 and lower molar row length, thus differing from individuals in Ahtiala, especially (Fig. 12).

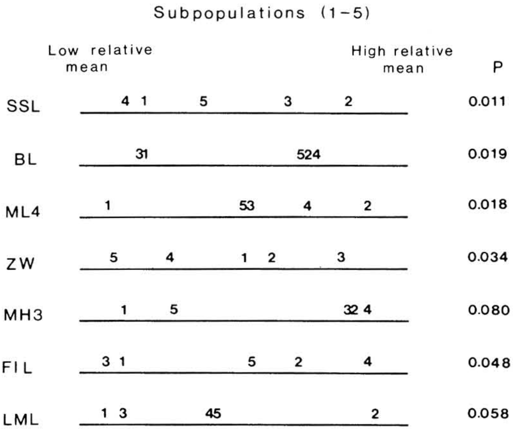


Fig. 12. Comparison of relative skull measurements between the five subpopulations of Lohja. The seven traits showing the greatest differences are presented in order of decreasing discrimination efficiency in DFA. The relative position of each subpopulation is indicated by a figure (1-5) on the horizontal line for the trait. Subpopulations: 1 = Ahtiala, 2 = Puimala, 3 = Paavola, 4 = Seppälä, 5 = Porla. P = probability in one-way analysis of variance.

3.1.6. General trends of skull morphology over larger geographical areas

Mean values of skull measurements in 20 muskrat samples given in the literature or obtained in this study are presented in Table 11. The data covers the main parts of the muskrat's range. Only those measurements of the present study which were also taken by other authors were included in this comparison. (The studies of Hollister (1911), Lavrov (1953), Hoffmann (1958), Pietsch (1970) and Boyce (1980) could not be used here either because the authors do not give means, or because most of the measurements were different.) The results represent animals of as comparable age as possible: only spring animals born during the previous summer ("young", see Pankakoski 1983) represent the Finnish muskrats. Age group III was taken from Ruprecht (1974), animals of 9 and 12 months of age being taken from Cygankov (1955). The results of Gould & Kreeger (1948) were based on muskrats presumably somewhat older than those in other studies. In order to study general trends in muskrat skull morphology, correlation coefficients were calculated from the means in Table 11 between the size (*CL*) and other measurements (Table 12). Because the absolute values are highly dependent on habitat quality (see above and Pankakoski 1983), the correlations with relative values were also calculated.

As expected, the correlation coefficients between absolute values and size (*CL*) are as a rule highly significantly positive (Table 12). Interorbital width and rostrum width with their low correlations form exceptions. Correlations between relative values are either not significant or they are negative. The lower molar row length, braincase length, and interorbital width are relatively smaller in populations with large animals. These three measurements were earlier shown to be rather stable also at the individual level (for age comparisons in Lohja sample, see above), irrespective of the growth in general size.

The amount of variability of skull measurements within separate geographical areas was studied by calculating principal component analysis over the populations in Table 11 (both absolute and relative values). In the analyses the sample from Lohja was divided into five subpopulations. Multiple regression models, based on individual measurements of the Finnish muskrats, were constructed to calculate the substitute values for the missing variables in some populations, using the available sample means as independent variables. PCA was calculated both with five "complete" variables (*CL, ZW, IW, DL* and *UML*, with a replaced mean only in *IW* of Kansas sample) and with nine variables (including also *RW, BW, BL* and *LML*, which contain substitute values). When using absolute measurements, the results of the two first

Table 11. Mean values (in mm) of nine skull measurements in 20 muskrat populations. Figures in parenthesis are substitute values, which were calculated from available sample means (for details, see text). The three samples from the USA represent different subspecies (Kansas and Nebraska: *O. z. cinnamominus*; Louisiana: *O. z. rivalica*) than in other studies (*O. z. zibethica*, see Artimo 1960, Pietsch 1970).

Locality	*n*	CL	RW	ZW	IW	BW	BL	DL	UML	LML
USA										
Kansas[1]	124	62.4	(11.9)	38.3	(6.6)[8]	(26.5)	(36.8)	22.5	15.0	(15.0)
Louisiana[2]	357	65.5	(12.5)	40.9	6.3	(28.0)	38.7	22.5	15.9	(15.4)
Nebraska[3]	96	62.6	(11.9)	38.9	6.2	(26.8)	36.6	22.7	15.1	(15.0)
Germany[4]										
Halle	51	59.9	(11.4)	36.4	6.7	(25.4)	(36.1)	20.1	15.2	(15.0)
Magdeburg	27	62	(11.8)	38	7	(26.2)	(36.9)	21	15	(14.9)
Czechoslovakia[5]	5	57.0	11.9	33.9	6.4	24.3	34.7	19.4	15.0	14.8
Poland[5]										
Pomerania	33	62.2	13.1	37.1	6.3	26.4	37.2	21.9	15.7	15.7
Kujawy	12	61.9	13.0	36.9	6.2	26.0	36.8	22.0	15.5	15.6
Białystok	17	62.7	13.4	38.0	6.5	26.8	37.2	22.2	15.5	15.5
USSR[6]										
Kurgan (9 mo.)	14	61.0	11.0	35.1	5.8	(25.4)	(36.8)	21.2	16.7	(15.6)
Kurgan (12 mo.)	10	63.1	11.5	37.2	6.1	(26.5)	(37.8)	22.7	17.1	(15.8)
Finland[7]										
Lohja	307	62.8	12.2	38.6	6.8	26.7	37.7	21.8	16.4	15.5
Ilomantsi	152	63.7	12.1	38.6	6.3	27.3	37.9	22.6	16.2	15.6
Kitee	27	62.4	11.6	38.1	6.4	26.4	37.4	21.9	16.3	15.1
Kemijärvi	25	62.7	11.9	38.5	7.2	26.6	37.4	22.9	15.9	15.6
Helsinki	37	59.8	11.4	36.2	6.4	24.6	36.0	21.3	15.6	15.2
Lokalahti & Kustavi	5	61.7	11.5	38.7	6.6	26.0	36.6	21.9	15.6	15.3
Riihimäki	7	61.8	12.0	38.0	6.6	26.3	36.9	22.0	15.5	15.1
Tyrvää, Kangasala & Sääksmäki	10	60.2	11.2	37.1	6.7	25.5	35.8	21.3	15.5	15.0
Pielisjärvi	10	61.4	11.5	37.3	6.3	26.3	36.5	21.5	15.7	15.2

Sources:
[1] Latimer & Riley 1934.
[2] Gould & Kreeger 1948.
[3] Sather 1956.
[4] Müller 1952.
[5] Ruprecht 1974.
[6] Cygankov 1955.
[7] Present study.

[8] The original value (8.3) was not used in later calculations, because the technique of measurement is evidently not comparable (see also Gould & Kreeger 1948).

principal components were very similar both with 9 and 5 variables, and only the latter solution is presented here (Fig. 13A). In relative values the use of substitute values in some variables affected the results only a little; the difference between the two solutions was negligible, except that in the four-variable solution Ruprecht's (1974) data set was relatively close to those of Finland and Germany (cf. Fig. 13). As Ruprecht's data did not contain substitute values in either analysis, only the solution based on 8 variables is presented here (Fig. 13B).

In absolute values the first principal component describes the general size of the skull (highest correlation with *CL, ZW* and *DL*), and the second principal component correlates best with *UML* (and *IW*; Table 13). In relative values *IW* has the highest correlation with *PC1*, *RW* with *PC2* and both molar row lengths and *BL* with *PC3* (Table 13). The variance explained by the first two principal components is smaller in the solution based on relative, than on absolute, values, i.e., the populations differ more in regard to general size than to shape of the skull.

Table 12. Correlation coefficients between size (*CL*) and other measurements (absolute and relative values) of the muskrat skulls in the localities in Table 11. Substitute values were not used in the calculations.

Variables	Populations	Correlation Absolute	Correlation Relative
RW	15	+0.319 ns	−0.160 ns
ZW	20	+0.868 ***	+0.321 ns
IW	19	−0.056 ns	−0.544 *
BW	13	+0.948 ***	+0.230 ns
BL	15	+0.966 ***	−0.659 **
DL	20	+0.855 ***	+0.321 ns
UML	20	+0.393 o	−0.387 o
LML	13	+0.797 **	−0.763 **

Table 13. Correlation coefficients of the skull measurements with the first two or three principal components (PC1—PC3). Data from literature (Table 11) and Finnish muskrats (Lohja sample divided into 5 subpopulations in this case).

	Absolute values		Relative values		
	PC1	PC2	PC1	PC2	PC3
CL	0.98	-0.15	–	–	–
RW	–	–	0.41	0.86	0.29
ZW	0.95	0.30	0.37	-0.10	-0.75
IW	0.19	0.59	0.96	-0.29	-0.01
BW	–	–	0.18	0.30	-0.36
BL	–	–	0.26	-0.32	0.82
DL	0.84	-0.23	-0.31	0.10	-0.24
UML	0.38	-0.73	-0.21	-0.50	0.81
LML	–	–	0.10	-0.03	0.90
Variation explained (%)	84.7	8.5	41.0	27.0	21.8

The following conclusions can be drawn from Fig. 13:

1) In the general size of the skull (*PC1* in Fig 13A) there is considerable overlap of the populations in Finland, Central Europe, USSR and USA: the smallest values are found in Czechoslovakia, the greatest in Louisiana, USA (the latter sample represents older individuals, however; see above). Finnish muskrats are of average size.

2) The two populations from Kurgan, USSR are clearly distinguishable from other populations both in absolute and relative values. The USA population is also reasonably well separated from other populations (especially by *PC3* of relative values, not illustrated here).

3) The Central European populations differ from each other in about the same degree as the Finnish populations do.

4) The variability between the populations in Central European countries (Poland, Germany, Czechoslovakia) is much greater than within these countries (Poland, Germany).

5) In relative values Finnish muskrats most resemble the muskrats in Germany and deviate most from muskrats in Poland and Kurgan, USSR.

6) The variability among subpopulations in Lohja is much smaller than it is over the whole of Finland, but it is only slightly smaller than the variability among the three USA populations, which represent different subspecies of the muskrat.

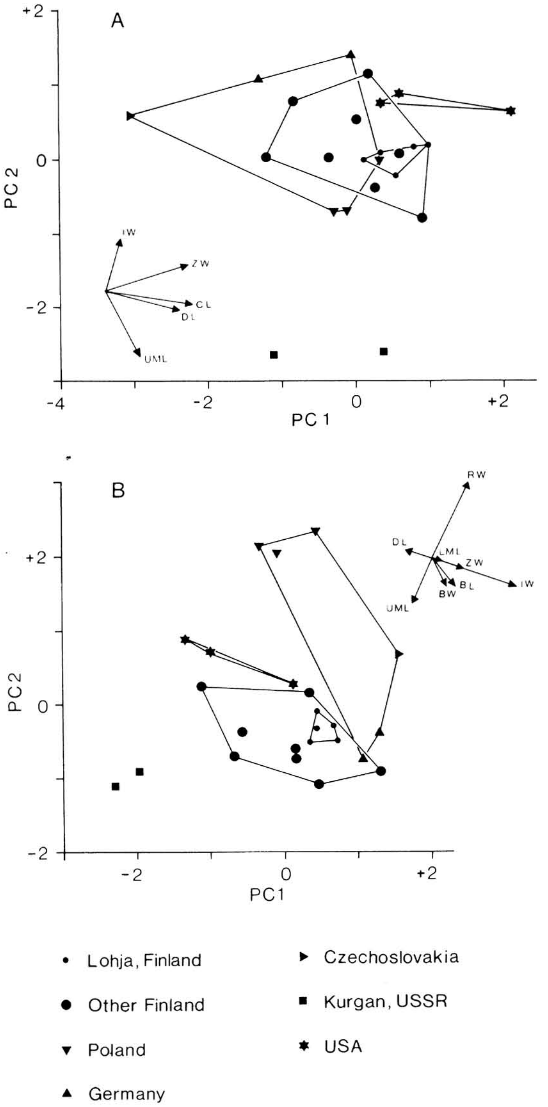


Fig. 13. Comparison of muskrat skull variation between populations in Finland and other countries: principal component solution over the sample means in Table 11 (A = absolute values, B = relative values). The outermost populations within the range of variation in the USA, Central Europe, Finland and Lohja are connected with lines. The Lohja sample is divided into five subpopulations. For details, see text.

3.2. Nerve foramina

3.2.1. Age and sex

The number of foraminal openings of nerves in the bone seems to be independent of

Table 14. Comparison between sexes in numbers of skull foraminal openings (mean ± *SD*, *t* and percent dimorphism). The relationship between foramen numbers and three skull measurements are presented as partial correlation coefficients (the effect of sex is eliminated) for the total sample. (*CL* and *ZW* are evidently the best variables for reflecting skull size (see 4.1.); in *DL* sexual dimorphism was greatest.) Only <1 yr. old individuals, trapped in April and May. Age grouping as in Pankakoski (1983). Number of males = 313-321, number of females = 239-248, r = right side, l = left side.

Foramen	Number of openings			Dimorphism	Partial correlation (*df*=567)		
	Males	Females	*t*	%	CL	ZW	DL
fro r	1.19 ± 0.81	1.27 ± 0.82	1.07	−5.8	−0.06	−0.04	+0.07o
fro l	1.13 ± 0.85	1.18 ± 0.85	0.61	−3.7	−0.05	−0.03	+0.05
max a r	3.53 ± 1.51	3.12 ± 1.31	3.42***	13.3	+0.16***	+0.10*	+0.22***
max a l	3.53 ± 1.46	3.33 ± 1.36	1.67o	6.1	+0.06	+0.09*	+0.14***
max b r	2.10 ± 1.12	1.99 ± 1.33	1.00	5.2	+0.01	+0.06	−0.05
max b l	2.20 ± 1.18	1.97 ± 1.20	2.25*	11.6	+0.05	+0.09*	+0.01
men a r	1.60 ± 0.87	1.65 ± 0.91	0.69	−3.1	+0.03	+0.03	−0.02
men a l	1.46 ± 0.78	1.50 ± 0.79	0.65	−2.9	−0.00	+0.02	+0.05
men b r	3.82 ± 1.23	3.63 ± 1.17	1.89o	5.4	+0.04	+0.07o	+0.07
men b l	3.97 ± 1.28	3.79 ± 1.36	1.57	4.6	−0.01	−0.01	−0.05
Total	24.49 ± 5.06	23.43 ± 5.20	2.40*	4.5	+0.07o	+0.10*	+0.11**

individual age. When the four age groups of the Lohja sample were compared in this respect with discriminant analysis, the result was not statistically significant, as it was with skull measurements (see above). Neither do the sexes in the total muskrat sample differ significantly (P=0.11) in the discriminant function analysis. When the numbers of foraminal openings were compared between the sexes using t-tests, a few differences emerged, however (Table 14). This might be a consequence of greater size in males, because there are significant positive correlations between the foramen numbers and some skull measurements (Table 14).

3.2.2. *Comparison between localities*

In discriminant analysis the differences in foramen numbers are clear among the four localities, although they are not as striking as in skull measurements. All the three canonical functions calculated are significant, explaining 61 %, 23 % and 16 % of the total discrimination. The first canonical function discriminates Lohja from the other samples (Fig. 14). It describes the contrast in f. frontale and f. maxillare b on both sides of the skull (Table 15). The second canonical function (correlations with f. maxillare b right and f. mentale a left) discriminates the Ilomantsi and Kemijärvi populations as the extreme samples. F. maxillare b left and f. mentale a right are best correlated with the third canonical function, which is effective in discriminating the Kitee and Kemijärvi populations from Lohja and Ilomantsi (Table 15). F. maxillare a and f. mentale b (on each side of the skull) did not prove to be essential for locality discrimination.

The three main localities, Lohja, North Karelia and Kemijärvi are all characterized by

Table 15. Correlation coefficients of nerve foramen numbers with the first three canonical functions discriminating between the four Finnish muskrat populations (Lohja, Ilomantsi, Kitee, Kemijärvi; sexes pooled). r = right side, l = left side.

Foramen	Canonical functions		
	1st	2nd	3rd
fro r	-0.54	-0.36	-0.19
fro l	-0.54	-0.10	-0.30
max a r	-0.18	0.23	0.10
max a l	-0.11	0.25	0.19
max b r	0.43	-0.59	0.36
max b l	0.41	-0.19	-0.45
men a r	0.36	0.21	-0.42
men a l	0.22	0.57	0.06
men b r	-0.18	0.02	0.29
men b l	0.11	0.08	0.32
Discrimination (%)	61.4	22.7	15.9

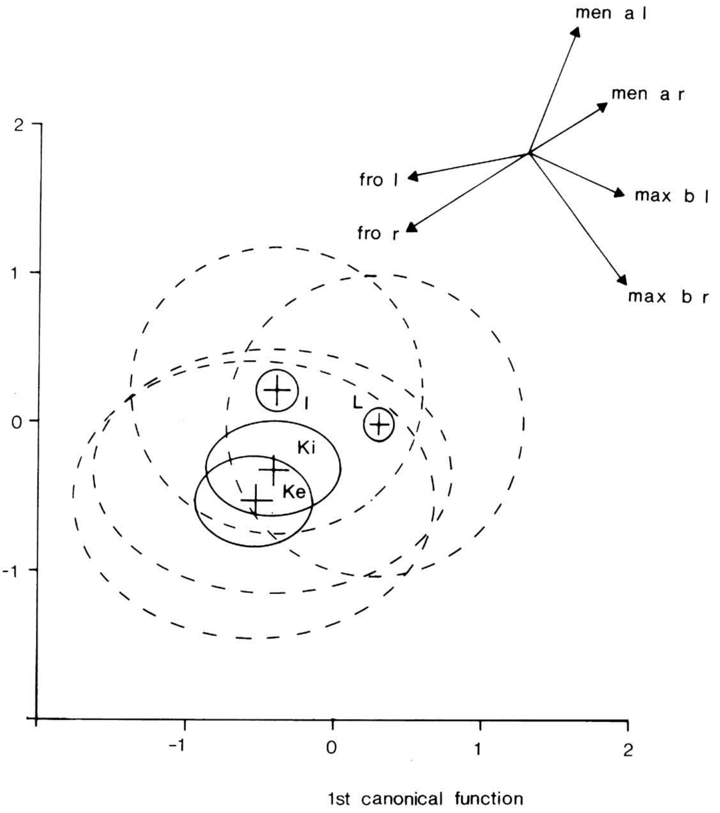
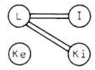
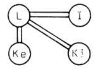
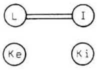
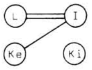
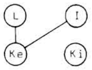
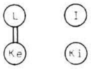


Fig. 14. Discrimination of the four main populations of the study (sexes pooled) according to nerve foramina. For explanations, see Fig. 3 and text.

Table 16. Comparison of nerve foramen numbers of the six best discriminators between the four localities. For explanations, see Table 9.

	F. frontale						F. maxillare b						F. mentale a					
	Left			Right			Left			Right			Left			Right		
Locality	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Lohja	1.01	0.774	355	1.08	0.751	355	2.26	1.284	353	2.21	1.345	350	1.51	0.763	357	1.72	0.933	358
Ilomantsi	1.27	0.873	168	1.29	0.864	168	1.89	0.938	168	1.71	0.945	167	1.51	0.826	168	1.55	0.803	168
Kitee	1.50	1.106	30	1.57	1.006	30	2.37	0.928	30	1.80	0.714	30	1.23	0.504	30	1.70	1.119	30
Kemijärvi	1.33	0.894	36	1.56	0.998	36	1.83	1.248	35	2.38	1.409	32	1.14	0.425	36	1.22	0.485	36
F =	6.81^{***}			7.61^{***}			5.02^{**}			7.55^{***}			3.70^{*}			4.16^{**}		
Differences between localities																		

low values in one pair of nerve foramina: f. frontale in Lohja, f. maxillare b in North Karelia and f. mentale a in Kemijärvi (Table 16). In each case the differences are almost similar on both left and right sides of the skull.

Classification of observations in discriminant analysis of nerve foramen numbers is much less successful than in skull measurements: 43.4 % hits (73.7 % in relative skull measurements). The percentage of hits is highest in Kemijärvi (58 %), lowest in Ilomantsi (40 %).

The classification of museum samples according to the discriminant analysis of nerve foramina was rather haphazard, in contrast to the classification based on skull measurements (see above). Neither did the five subpopulations of Lake Lohjanjärvi differ significantly in regard to foramen numbers.

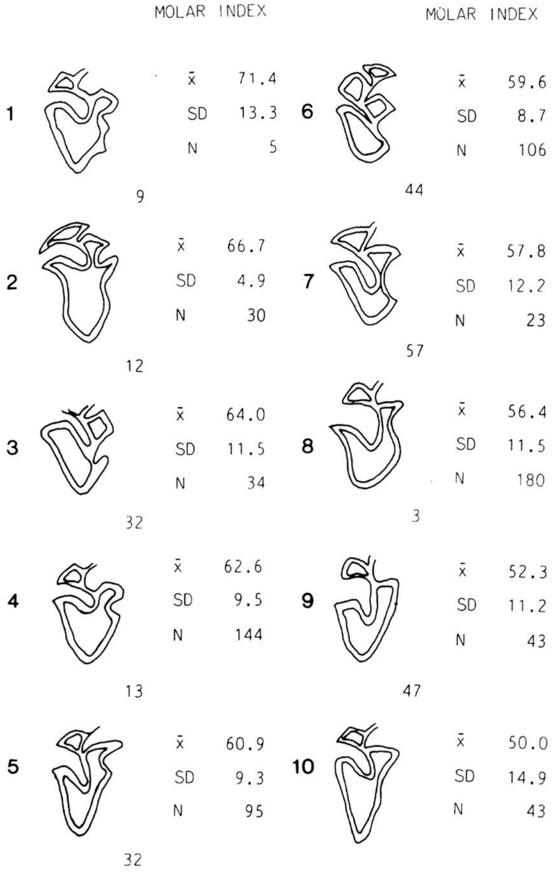


Fig. 15. Patterns of the third upper molar (M^3) of Finnish muskrats arranged according to tooth wear (molar index). Low tooth wear = high molar index. The figures between consecutive patterns indicate statistical significance (*P* in %) between the molar index values (*t*-tests). The combination of the types (1+2+3), (7+8) and (9+10) was based on these *P*-values and sample size (in order to get enough observations in each type).

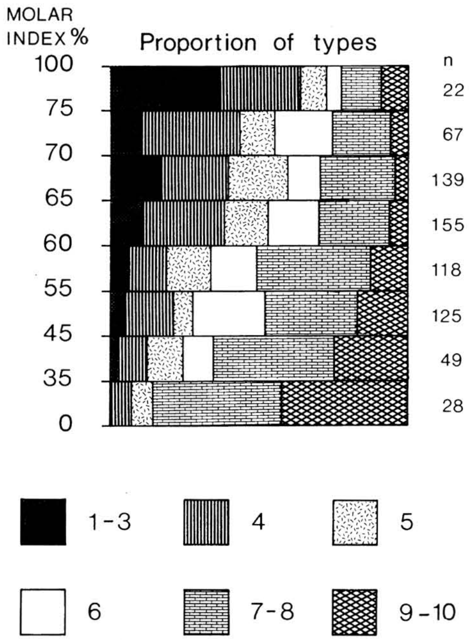


Fig. 16. Change of M^3-pattern types according to molar wear. For molar pattern classification according to molar wear, see Fig. 15.

3.3. Variation in molar patterns

The patterns of the third upper molar (M^3) were classified into ten types according to the shape of the enamel loops. As the molar patterns were quite symmetric, the results on right M^3 only will be presented. Because the degree of molar wear affects the patterns (Ognev 1963) the ten types were arranged according to the average molar index of the types (Fig. 15). Mean values of the molar index, which reflects molar wear, differed highly significantly between the molar pattern types ($F=12.43^{***}$, $df=9;693$). Due to the small number of individuals in some pattern types, adjacent types were combined for later comparisons: 1+2+3, 7+8 and 9+10. The frequency distribution of the resulting six groups clearly changed with animal age (= molar index; Fig. 16).

Because the sexes differ as regards molar wear (Pankakoski 1980, 1983), the comparison of frequencies in molar pattern types between the sexes must be based on individuals with as similar a molar index as possible. Within molar index groups of 5 %, the distribution of molar patterns did not differ between the sexes (χ^2-tests). Although the sexes could thus be pooled for comparisons between populations, only the samples from Lohja and Ilomantsi were sufficient for a reliable comparison, because only individuals with a similar level of molar wear could also be used in this case (for the differences in molar wear between localities, see Pankakoski 1983). In all the molar index groups that were large enough for statistical treatment, the distribution of molar pattern types differed between Lohja and Ilomantsi (Fig. 17). The sample from Ilomantsi

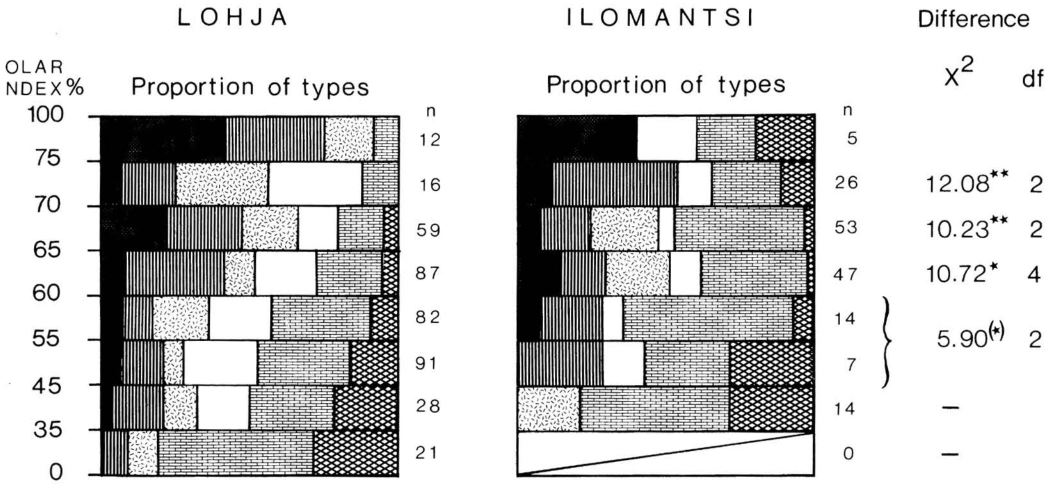


Fig. 17. Comparison of M^3-pattern types between Lohja and Ilomantsi in comparable classes of molar wear. For symbols, see Fig. 15.

was characterized by a lower percentage of types 5 and 6 and higher proportions of type 7+8 than the Lohja sample.

4. Discussion

4.1. Choice of size variable

For studying the shape (allometry) of animal organs generally one single measurement of each individual is chosen to reflect animal size (however, see Humphries et al. (1981) and Bookstein (1984) for criticism and a more advanced method). Usually this is some metric measurement (preferably not body weight) with a rather large mean value, like the condylobasal length of the skull used in this study. Mosimann & James (1979) emphasize that there is no reason to expect similar size — shape associations for the different choices of a size variable. In the present study some parallel discrimination analyses were calculated both with condylobasal length and zygomatic width representing muskrat size. Zygomatic width has sometimes been used even for age determination of the muskrat (e.g., Alexander 1951), due to its continuous growth. The results were rather similar with either measurement as a size variable. *CL* has also been used as a basis for allometric comparisons in earlier muskrat studies (Gould & Kreeger 1948, Pietsch 1970, Ruprecht 1974).

4.2. The effect of age on skull morphology

4.2.1. Discrimination of age groups

A sample from only one locality (Lohja) was used for age comparisons in order to eliminate the errors in age grouping, which originate from differences in molar wear between localities (Pankakoski 1983). However, differential wear on molars in different habitats in lake Lohjanjärvi is responsible for the almost total overlap of age classes II and III in discrimination analysis. In the poor habitats molar wear was extensive and the muskrats were classified as older than individuals of the same true age in better habitats. Because most of the present material was trapped in spring and is composed mainly of animals born during the previous summer (Pankakoski 1980, 1983), the number of individuals in the youngest and oldest age groups (I, IV) remains low. These two extreme age groups are also clearly separable, however, in spite of the habitat effect.

4.2.2. Change of skull measurements according to age

The general size of the muskrat skull increases according to age, but the growth differs in separate variables. In this study growth was the greatest in diastema length and zygomatic width. In contrast, braincase size (particularly its length) grows more slowly. As regards age, the most stable measurements in the muskrat skull are interorbital width and molar row lengths. These results agree with earlier studies on skull growth in the muskrat (Gould & Kreeger 1948, Cygankov 1955, Pietsch 1970, Ruprecht 1974) as well as in other rodent species (e.g., Kubik 1952, Wasilewski 1960, Haitlinger 1962, 1969, Gębzyńska 1964, 1967, Gerasimov 1969, Carleton 1985).

The percentages of growth in skull measurements from age groups I to IV are smaller in the present material than the ones calculated by Ruprecht (1974) in Central European muskrats. The reason for this difference is the different age grouping of the animals. However, the order of size in the growth percentages of separate skull variables is almost identical in the present and Ruprecht's (1974) data. The correlation coefficient in growth percentages between the nine measurements that are common in both studies is very high: $r = +0.90^{***}$ ($df = 7$). In other words, the growth patterns of the skull are similar in Finnish and Central European populations of the muskrat.

According to Ruprecht (1974) certain dimensions of the viscerocranium are distinguished by continuous increase, whereas the dimensions of the neurocranium are fairly rapidly attained. As regards braincase length and width in the present study, the growth is smaller than the growth of general size, indicating that during the growth stages studied here the period of intensive growth in braincase dimensions has already been passed.

The stability of molar row length is a general feature of rodents (in muskrat, see Gould & Kreeger 1948, Pietsch 1970, Ruprecht 1974; in other species, e.g., Haitlinger & Rüprecht 1967, Haitlinger 1969). The size of the teeth is already determined during the early phases of ontogenesis and thus later changes in other measurements of the skull do not affect teeth (Gould & Kreeger 1948). In some rodent species molar row length has been observed even to decrease with age (*O. zibethica*: Gould & Kreeger 1948; *Apodemus sylvaticus*: Haitlinger 1969). One reason for this observation in the muskrat is perhaps molar wear, which slightly shifts the points of measurement according to wear of the tooth crown and simultaneous protusion of the narrower tooth neck from the tooth alveole.

The stability of interorbital width in muskrats of different age (see also Gould & Kreeger 1948, Cygankov 1955, Ruprecht 1974) implies the possibility that this measurement is closely connected with the sense of sight. This is indicated by the generality of this observation in microtines: *IW* does not change according to age in *Microtus agrestis, Lagurus lagurus* and *Pitymys subterraneus* (Gębzyńska 1964, 1967, Wasilewski 1960). *IW* is also stable with age in the fox (*Vulpes vulpes*; Huson & Page 1980). In other rodent species the heritability of this measurement has been shown to be rather high ($h^2=0.42$ in the rat (Atchley et al. 1981), 0.56 in mice (Leamy 1974). According to Ruprecht (1974) the small decrease observed in *IW* with age in the muskrat is probably connected with the formation of a crest on the frontal bone. In several mustelid species it has been shown that the postorbital constriction (which is located slightly more posteriorly to the interorbital constriction in these species) decreases with age (e.g., Buchalzyk & Ruprecht 1977, Wiig 1982). Wiig (1982) explains this by the resorption of bone in the postorbital area, which gives room for an increase of the temporal muscle with age and thus increases the force in the fully opened jaw. Diminution of *IW* with age in the muskrat may be connected with a corresponding strengthening of the temporal muscle, which runs rostralwards from the roof of the braincase, bends ventralwards at interorbital constriction and runs caudally of the eye to the lower jaw (van Vendeloo 1953). The decrease of interorbital width with age has also been observed in *M. agrestis* (Gębzyńska 1964).

The information on the growth processes in the mandibles of the muskrat is scanty in the literature. Ruprecht (1974) has weighed the mandibles of his muskrats, but does not present linear measurements, so the comparison is restricted to the cranium only. The relative growth in the weight of muskrat mandibles is higher than in any metric measurement of the skull (Ruprecht 1974), but evidently this is due to the thickening of the bone and consequently exponentially increased mass of the mandibles (see also Gould & Kreeger 1948, Cygankov 1955). In the present study mandible lengths grow in accordance with general size or even more slowly. Mandible height measurements have a tendency to override mandible lengths in growth, resulting in greater height/length ratios in older animals.

In several rodent species morphological differences have been observed between the spring and autumn generations (e.g. Haitlinger 1962, 1965, Schwartz et al. 1964, Adamczewska-Andrzejewska 1971, Zejda 1971, Klevezal et al. 1984). However, in the muskrat the time of birth of the individual probably has less influence on skull dimensions (Ruprecht 1974). Although in the present study the individuals born during the early and late parts of the breeding season were not analysed separately, this has evidently not had any greater effect on the results. On the contrary, habitat influences are much more difficult to rule out.

4.2.3. Change of correlations during ageing

The positive correlations between the variables in Finnish muskrat skulls usually decreased with age, as was also observed by Ruprecht (1974) in the muskrat, Caboń-Raczyńska (1964) in *Lepus europaeus* and Gerasimov (1969) in *Clethrionomys glareolus*. In the present study the decrease was greatest in *IW* and *RW*, as was the case also in Central European muskrats (Ruprecht 1974). The decrease of the correlation coefficients was explained by Caboń-Raczyńska (1964) as being due "to the inhibition of the growth of some cranial elements, with the remaining elements still increasing. Some additional differences may result from a wide range of individual variation in particular measurements ..., or they may be effected by the differentation of certain morphological types of skulls (long and narrow skulls, short and broad skulls, etc.)." Correspondingly, the increase in the correlation coefficients with age, which was most evident in sagittal suture length in the present study, is a consequence of either decreased variation or increased growth in the oldest individuals. In the muskrat *SSL* grows less than *CL*, but in *A. sylvaticus SSL* even decreases with age (Haitlinger 1969).

4.2.4. Epigenetic characters and age

Ageing affects the two types of epigenetic characters investigated in the present study, nerve foramina and molar patterns quite differently. The effect of age on the nerve foramina was not significant, but was so on molar patterns. The nerve foramina are affected by maternal effects (Howe & Parsons 1967, Thorpe 1981), e.g., by stress during ontogeny, but after the muskrat leaves the nest the constellation of the nerve foramina evidently remains rather unchanged (see also Pankakoski 1985). Some differences due to individual age in foraminal constellation have been observed in *A. agrarius* (Sikorski 1982) and in *Sorex araneus* (Hanski & Kuitunen 1986).

Age-dependent variation in molar patterns, particularly in the first molar of the mandible, M_1 (Ognev 1963), is pronounced in the muskrat (see also Cobert 1963 and Sikorski & Bernshtein 1984 for similar results in *C. glareolus*). Molar wear is chiefly responsible for the differences in molar patterns. Thus, separate types of molar patterns predominantly reflect transverse sections at different heights of the tooth.

4.3. Sexual dimorphism in skull morphology

In most muskrat studies males have been found to be larger than females (for references, see Pankakoski 1983). In the present data the linear measurements of the skull averaged 1.3% more in the males than in the females (equally weighed variables). The difference in body weight is 13% (individuals born during the previous summer, Pankakoski 1983). As weight generally scales to the third power of linear measurements, the cube roots of weights were taken. The degree of sexual dimorphism is even then greater in body weight than in the skull measurements of the same individuals (both body and carcass weight 4.2% : $t=4.20^{***}$; $df=21$), possibly due to the proportionally heavy musculature in males.

Sexual dimorphism in muskrat skulls has been observed by Gould & Kreeger (1948), Sather (1956), Hoffmann (1958), Ruprecht (1974) and Boyce (1978), while Hollister (1911) and Pietsch (1970) did not notice differences between the sexes in skull measurements. However, no single measurement of the skull distinguishes between the sexes (see also Gould & Kreeger 1948), as opposed to, e.g., the mink (*Mustela vison* ; Wiig & Lie 1980). The general size of the skull depends so strongly on habitat quality (Pankakoski 1983) that it also fails as a criterion for sex identification. Sexual selection for large size in male combats (Ralls 1977, Halliday 1978) has been suggested as an explanation for sexual dimorphism in the muskrat (Pankakoski 1983).

In relative values (measurements related to *CL*) males tended to be larger than females only in regard to diastema length, which also grows most with age (Fig. 4). In females the relative but not the absolute values were greater in several mandibular dimensions and both molar row lengths. In *A. sylvaticus* sexual dimorphism was of a lesser degree in molar row lengths (Haitlinger 1969). Mandibular measurements (including molar row lengths) are presumably adaptively "important" for the muskrat, especially because they are all associated with feeding. This suggests a similarity of the diets in both sexes, and indeed no intersexual differences in food selection have been reported in the literature. Feeding structures are nearly sexually monomorphic also in the house sparrow (Johnston & Fleisher 1981).

Sexual dimorphism in epigenetic characters is not thought to be extensive (Deol 1955, Wiig & Lie 1979, Thorpe 1981, Hanski & Kuitunen 1986), which is true also in the muskrat (foramen numbers and molar patterns). Some sexual dimorphism in epigenetic characters has been observed in *A. agrarius* (Sikorski 1982), and also in laboratory mice (McLaren & Michie 1954, Thorpe 1981). The tendency of the males to show greater mean foramen numbers in some variables of the present study is perhaps connected with their greater size. According to Hartman (1980) the appearance of epigenetic characters to some extent depends on animal size.

4.4. Geographical variation in muskrat skull morphology

The muskrat populations of four main localities in the present study are clearly distinguishable on the basis of skull measurements. The most efficient discriminator between the populations is interorbital width, which has the lowest means in the North Karelian, and the highest in the Kemijärvi populations. The populations can also be distinguished on the basis of the number of nerve foramina in the skull, but the differences between populations in this respect are smaller than for metric measurements. There also exists significant interpopulation variability in molar patterns. The muskrats from five subpopulations of Lake Lohjanjärvi are of different size due to habitat effects. Size variation is accompanied by small differences in relative skull measurements between these subpopulations. Subpopulations do not differ in regard to epigenetic characters.

4.4.1. Differentiation after introduction of the species

Because the muskrat is an introduced species in Europe, the founder principle, the restricted gene pool of the few individuals introduced to a certain place, may have had a considerable effect on the early populations. This phenomenon is clearly demonstrated in the differences between the house mouse populations of the Faroe Islands (Berry et al. 1978; cf. Williamson 1981). The morphological differences of Faroe mice are evident even in regard to populations on islands recently (less than 40 years ago) colonized by mice. According to the authors, "this emphasizes the stochastic nature of the founder effect in being able to produce 'instant sub-speciation'" (Berry et al. 1978; see also Davis 1983). Pietsch (1970) has shown in Central European muskrats that in spite of the restricted gene pool of the introduced individuals, the isolated new population rather rapidly reaches about the same degree of phenotypic variability that is present in the donor population. The great diversity in the skull morphology of European muskrat populations is interpreted by Pietsch (1970) as a consequence of genetic recombination. However, Atchley et al. (1981) pointed out the risk of assuming phenotypic changes in the population to directly reflect changes in the genotype (see also Atcheley & Rutledge 1980, Atchley 1983). Nei et al. (1975) have shown that if the rate of population growth is very high (as was the case in the muskrat after introduction, at least in Finland) a relatively high level of heterozygosity can be maintained even if population size goes through an extreme bottleneck. On the other hand, the average number of alleles per locus is reduced by the bottleneck phase because genetic drift eliminates many low frequency alleles.

Pietsch (1970) was able to follow changes in skull measurements in Central European muskrats beginning from the initial locality of release (Prague). He observed the differences to increase in the descendant populations, when the geographical distance from Prague increased. A similar tracking of the differentiation after introduction is not possible in Finnish muskrats, because here muskrats were released at about 300 localities situated all over the country (Artimo 1960).

4.4.2. Environmental effects on skull measurements

The population means of absolute interorbital width did not correlate with average individual size in the Holarctic sample studied, but relative *IW* decreased with increasing animal size (Table 13). This result indicates that *IW* is a fairly stable measure of the muskrat skull, which the environment may influence only a little, while general size probably depends on habitat factors. *IW* is relatively stable also within populations, as shown by the low correlation between *IW* and *CL* in Lohja (Fig. 5). If the variation of *relative IW* depends on the variation in general size only, habitat quality should be directly expressed in its value. Evidence for and against this prediction is found, when the scanty habitat quality data of the literature samples are compared with the first principal component (which reflects relative *IW*) in Fig. 13B. According to Ruprecht (1974) the samples from Czechoslovakia and Pomerania (in Poland) originate from a poor and a fertile habitat, respectively. Indeed, Czechoslovakian muskrats have the greatest relative value of *IW* (=*PC1* in Fig. 13B) of all the populations studied; muskrats in Pomerania have a much lower value. In Kurgan, USSR (Cygankov 1955), the relative *IW* is the smallest of all the populations compared. There is other evidence suggesting that this area is favourable to muskrats: tooth wear proved to be much lower in Kurgan than Lohja (Pankakoski 1980). Of the Finnish populations, Ilomantsi and Kitee represent animals that live in favourable habitats (Pankakoski 1983) and these populations indeed are projected as extreme points of the Finnish populations in Fig. 13B. The other extreme, high relative *IW*, is shown by the Kemijärvi population. The dependence of relative *IW* on habitat quality is, however, not valid when the Lohja subpopulations are compared. If the growth index (Pankakoski 1983) is used as a criterion of habitat quality, some subpopulations of poor habitats in Lohja (Puimala and Porla, especially) should show a greater relative *IW* than Kemijärvi. Even more importantly, despite the marked habitat differences between the Lohja subpopulations, all the data points of Lake Lohjanjärvi are projected near each other (Fig. 13B), perhaps because gene flow between the subpopulations may prevent their substantial differentation.

Because IW was the most effective discriminator between the Finnish populations in *absolute* values too, these differences cannot be direct consequences of habitat quality and general muskrat size. The four populations differed clearly except that the geographically closest populations of Ilomantsi and Kitee had about the same mean value. Within the populations individual variability of *IW* was low. These differences between populations could be connected with sight of the muskrat, but this suggestion is doubtful. Interorbital width does not show clinal variation in a south-north -direction, which should be the case, if this measure is directly dependent on the amount of light. Neither does water clarity correlate with the population means of *IW* (e.g., Lakes Lohjanjärvi and Kiteenjärvi are very similar in this respect; see also Pankakoski 1983).

Snell & Cunnison (1983) observed that the dimension of interorbital width of *Microtus pennsylvanicus* depended on climatological factors. In their analysis of six cranial measurements of 38 vole populations *IW* contributed best with the second principal component (*PC1* was general size). Climatic factors explained 42.1 % of the total variance in *PC2*. *IW* was narrow in areas with a low minimum temperature (both in winter and summer), low annual rainfall and high annual number of days with frost. The last mentioned factor was the best single variable for explaining variation in *IW*.

It is noteworthy that among the skull variables interorbital width is exceptional both during the course of individual life and on an interpopulation level. The absolute *IW* is greatest in the youngest and smallest individuals (Fig. 4.; *IW* also has the lowest correlation coefficients among skull measurements, Fig. 5.). The possibility that these two phenomena are linked together cannot be completely ruled out. Perhaps muskrats in poor habitats have difficulties in completing their ontogenesis during the icefree period of the year, and *IW* remains at the juvenile level (high means). In good habitats lush vegetation provides the animals with sufficient food for rapid growth. If Petrov's (1969) observation that the growth of young muskrats is accelerated in the northern latitudes (where the icefree period is short) is applicable to severe conditions in general, this idea is not tenable, however. According to Schwarz (1962) rodent skull dimensions differ between groups of the same size but with different growth rates. He found, however, that *IW* was smaller in slowly growing animals, while in our material the smallest *IW*:s were found in populations with high growth index (Pankakoski 1983).

It is possible that the heterogeneous introduction background is reflected in interorbital width. In relative *IW* the North Karelian populations resemble the populations in the USA (note the different subspecies); the Kemijärvi population falls near the German and Czechoslovakian populations in this respect (*PC1* in Fig. 13B). Finnish muskrats have been introduced precisely from these three donor countries (evidently all introductions with *O. z. zibethica*, Artimo 1960), and the differences between the founders might still be perceptible in the present populations. However, it is not possible to tell the origin of the founders on a locality scale in Finland.

MH4 was the second best discriminator (after *IW*) between the Finnish localities: high relative means in Lohja, low in North Karelia. The effect of *MH4* in discriminating these populations from each other parallels the effect of the molar index (first canonical function; arrows in Fig. 8). The differences in molar index between localities reflect a different tooth wear that depends on habitat quality (Pankakoski 1983). In the best habitats (North Karelia in this case) molar wear is low, evidently because of soft food. In the rat the hardness of food has also been shown to affect the development of masticatory muscles and mandibular morphology (Moore 1965). It is possible that habitat differences have some influence on mandibular morphology of the muskrat, as in *Peromyscus maniculatus* (Hollbrook 1982; see next section, however).

The size of the rostrum, as expressed in rostrum width and diastema length, differs sharply between the four main Finnish populations. According to Petrov & Krasnikova (1970, see also Ruprecht 1974) diastema length is reduced and rostrum width increased from south to north, because of increasing length of the period during which the muskrat lives under ice. This explanation does not hold true in Finnish muskrats: the rostrum is shortest and widest in the southernmost population from Lohja. Similarly, in Fig. 13B the second principal component, which correlates best with relative *RW*, does not align the European muskrat populations in south-north order. Evidently rostrum shape is not clearly determined by climatological factors.

Boyce (1978) has proposed connections between climate and muskrat body size. Animals are largest in regions of high annual precipitation and low seasonality in rainfall. Highly variable precipitation patterns result in low rates of germination and survivorship for preferred aquatic plants, which in turn reduces the average total food availability for muskrats. In large individuals nutritive demands may exceed supply; thus, selection favours smaller body size in areas of low food availability (Boyce 1978). Comparing the four main Finnish muskrat populations, the differences in precipitation are evidently not responsible for differences in average size, because the areas are rather similar in this respect. On the other hand, habitat quality has a considerable effect on muskrat size (Pankakoski 1983).

4.4.3. "Important" skull dimensions

Barnett (1977) observed in North American *Sciurus carolinensis* a regular cline in the size of most skull features as predicted by Bergmann's rule. However, no clines could be demonstrated in mandibular features and upper molar row length. According to Barnett (1977), this result suggests that structures related to feeding experience intense stabilizing selection that overrides thermoregulatory or other factors generating a size cline in other features of the skull. Similarly, in the comparison between absolute and relative measurements in analyses of variance (four localities, Table 10) most mandibular *lengths* proved to be geographically constant, i.e., stable independently of the observed habitat differences. This was also observed in braincase length (see also Table 12). The stability of these measurements may imply that they are important in the muskrat's ecology (see above: sexual dimorphism). Similarly, in the red-winged blackbird a relatively constant wing/tail ratio was assumed to be important in flight (Mosimann & James 1979).

Molar row lengths (*LML*, especially) also seem to belong to the "important" variables, although in our analyses of the Finnish populations (Table 10) this could not be demonstrated. In literature data from the Holarctic region (Table 13), as well as in comparisons between the subpopulations of Lake Lohjanjärvi (see below), the stability of molar row lengths was evidently independent of the absolute size of the individual. However, among the structures connected with feeding, molar row length is possibly less canalized than other measurements. This is supported by the discovery of Atchley et al. (1981) in comparisons of the proportions between genetic/environmental effects on skull measurements of the rat that *LML* has the highest coefficients on the environmental vector compared to the low genetic coefficient.

4.4.4. Epigenetic characters

The epigenetic skeletal patterns of animal populations have often been considered to characterize the natural populations genetically (e.g., Berry 1963, Rees 1969, Berry et al. 1978, Hartman 1980, Andersen & Wiig 1982, Sikorski 1982, Hanski & Kuitunen 1986), although in some laboratory studies the heritabilities of epigenetic characters have proved to be rather low (Thorpe 1981). In addition to the evident genetical component in epigenetic character regulation, some environmental factors may be important as well (Berry & Searle 1963, Thorpe 1981). For example, Howe & Parsons (1967) recorded that much of the variation in epigenetic characters in mice is genetic in origin, but that also certain environmental factors, such as the physiological state and the diet of the mother, are of importance. According to Hartman (1980) and Hanski & Kuitunen (1986) the occurrence of epigenetic characters in the skull depends to some extent on the individual size. Thus, besides genetical differences, habitat effect (acting through individual size) may also have had some influence on the observed differences between localities in foramen numbers. At least *asymmetry* of foramen numbers (difference between the right and left side of the skull) was highly dependent on habitat quality, as demonstrated with these same individuals by Pankakoski (1985).

Variation in the molar patterns has also been considered to reflect genetic differences among populations (Zejda 1960, Guthrie 1965), but environmental factors have proved to affect them, too. For example, Stein (1958) observed in *M. arvalis* that a tooth pattern of the "simplex"-type in M^3 is more common in individuals living in poor habitats. Similarly, the quality of food affects the molar patterns of *Arvicola terrestris* (Nikolaeva 1982). Because there is a clear difference in habitat suitability between Lohja and Ilomantsi (Pankakoski 1983), it is possible that the observed significant difference in molar patterns between these two localities is partly due to habitat effects.

4.4.5. Differences between subpopulations

The effect of habitat quality on muskrat size was evident in the comparison of the five subpopulations of Lake Lohjanjärvi (Pankakoski 1983). The relative skull measurements differed only to a rather small degree among the subpopulations, the differences mainly arising from high relative values in some measurements of the Puimala sample. Puimala is a poor muskrat habitat, a fact reflected in the general size and animal condition of this sample (Pankakoski 1983). Habitat differences are presumably responsible for the differences in relative skull measurements also between subpopulations. Some "important" skull dimensions must attain certain levels even in poor habitats. Consequently, variables describing these dimensions (in Puimala *LML, ML4*, especially) grow relatively more in small individuals than in large ones.

The skull variables that contribute most to the discrimination between the subpopulations are not the same as those discriminating the main study localities in Finland. For example, interorbital width, the most effective discriminator between localities, is not essential in separating subpopulations of Lake Lohjanjärvi (see also Fig. 13). This points to the possibility that if differences among subpopulations are due to habitat differences, particularly because of the gene flow among the subpopulations, variation among the localities is caused not only by habitat suitability differences but also by genetic differences. Similarly, if nerve foramen constellations are considered to reflect genetic differences among populations, it is quite reasonable that only minor differences exist between subpopulations, although interpopulation variability is clear.

4.4.6. General trends in muskrat variability over larger geographical areas

When comparing skull measurements from the literature, possible differences between the author's measuring methods may affect the comparisons. In the present study this concerns above all the sample from Kurgan (USSR), which deviated clearly from other populations in all analyses. On the other hand, rejection of *IW* values taken by Latimer & Riley (1934) of the Kansas muskrats was evidently the only possibility, although the use of a substitute value in PCA has forced the projection of the Kansas sample towards the Finnish populations.

The same variables that were effective in discriminating the European populations from each other do not separate the three USA populations, although they represent different subspecies of the muskrat (Fig. 13; this also concerns other combinations of principal components 1—3). Pietsch (1970) observed the differences in skull measurements between some Central European muskrat populations to be almost as great as between the subspecies in the USA. Evidently this observation, which is now supported by the present results, reflects the rapid differentiation in the introduced populations (Pietsch 1970). Of course, the data also suggests that splitting of the North American muskrats to subspecies, based (in decreasing order of importance) on size, fur colouration, skull measurements and tail length (Hollister 1911:12), has perhaps been excessive, as judged by the skull measurements.

The differences in skull measurements (as well as in epigenetic characters) are reasonably small on the subpopulation level (Lohja; *DFA* and *PCA*), although subpopulations live in habitats of different quality. In every combination of the first three principal components the populations of Lake Lohjanjärvi are projected very close to each other. This indicates a homogeneous genetic background for these animals. The differences between the Finnish populations are much greater than those between the subpopulations. Correspondingly, variation is even greater between different countries. Generally, geographically distant populations differ more from each other than nearby populations.

Geographical clines in the size of muskrat skulls presented in the literature are somewhat contradictory in different areas. In North American and Central European muskrats Pietsch (1970) observed skull size to increase from north to south, i.e., against Bergmann's rule. On the other hand, in Czechoslovakia and Poland the size of the muskrat skull grows from south to north (Ruprecht 1974). Gould & Kreeger (1948) found the skull size of Louisiana muskrats (*O. zibethica rivalica*) to increase from east to west, but the shape of the skull does not change. In the Soviet Union the muskrats are largest in the central regions, and decrease in size towards the south and north (Petrov & Krasnikova 1970).

The study of clinal variation is difficult because the effect of habitat differences cannot be completely eliminated (Ruprecht 1974, Pankakoski 1983). In the discrimination analysis of Finnish muskrats some museum samples were classified as belonging to the nearest populations, which suggests that clinal patterns might exist. However, in the principal component analysis of the literature data (Fig. 13B) no evident geographical clines could be demonstrated. The southern Finnish populations were projected between North Karelia and South Lapland (Kemijärvi), although this is not the case on a map. Similarly, the Kemijärvi sample, the northernmost population of the present study, most resembles the German populations (in relative values), but differs markedly from the Polish ones. Genetic differences between the introduced individuals and differentiation after introduction, on which chance effects in small initial populations may have had a strong influence, are more probable models of explanation than environmental factors varying geographically. This also concerns epigenetic characters, at least foramen numbers.

4.5. Prospects

Based on the results of the present study and Pankakoski (1983), it can be concluded that habitat differences are clearly reflected in the general size of the individual muskrat, both in body weight and skull measurements. It would be interesting to develop methods to exclude the effect of habitat from the size variation and thus be able to study the direct influence of, e.g., genetics and climate on muskrat size variation. Correction coefficients, in which the condition of the animal or population is taken into consideration using growth indices or condition factors (Pankakoski 1983) or by applying the amount of fat (see, e.g., Dozier 1945) as an index, could be useful.

A decisive explanation for the reasons for the variation of the main discriminator between the Finnish populations, *IW*, could not be attained in the present study. Samples from natural populations at regular intervals along a transect connecting the localities of extreme means of *IW* (North Karelia — Kemijärvi) would be informative and tell whether *IW* changes geographically abruptly (which indicates genetic differences) or clinally (which indicates an environmental influence on the difference). Further studies on *IW* might also otherwise be fruitful, in order to discover the ultimate reasons for its stability. Although differences in the genetic background of the populations seemed to be a more probable reason for population differences in IW than environmental factors, crossing experiments in cages (although difficult in the muskrat) should be made in order to confirm this suggestion. Crossings could resolve the proportions of genetic and environmental variance components (Atchley et al. 1981) in other characteristics as well, including epigenetic features.

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