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**Craniometric Variations in Central European Populations
of *Ondatra zibethica* (Linnaeus, 1766)**

[With 8 Tables & 11 Figs.]

Examination was made of the degree of population differentiation in skull measurements and also in the formation of the skull during individual development, on the basis of a collection of muskrat skulls (n=352) from three Polish populations and one Czech population, divided into four age classes. The muskrats from the three populations differ significantly by reason of their larger dimensions and different proportions of the skull, and also the statistical distances of shape and size, from animals from the central part of Bohemia. Differentiation was also found in the correlation structures of skull dimensions of muskrats from different populations. The number of differences found increases with the animals' age, and also with increasing distance in both space and time from the population closest to the place in which the muskrat was originally introduced into Europe. The skull of the muskrat is distinguished by a slight degree of sex dimorphism in dimensions which increases with the animals' age. Intensive increase of the majority of its dimensions ends in the second calendar year of the animals' lives. Age changes in skull dimensions of the muskrat are also reflected in changes in correlation structures corresponding to periods of isometric and allometric growth.

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1. INTRODUCTION

The American muskrat, a nearctic element new to European fauna, was introduced for the first time in Europe in 1905, when several of these animals were set free in the Dobříš area in central Bohemia. The muskrat spread rapidly during the first few years after its introduction into Europe, but interference in this process took place later on due to further introductions and also intensive extermination. In addition to man's artificial settlement of muskrats these animals also spread naturally, both actively and also passively, as the result of individuals being carried from one place to another during floods. The American muskrat spread naturally from Czechoslovakia into Poland in 1924 and by 1958 had settled in different places over the whole of the country (Nowak, 1971). There were fluctuations in the rate at which they spread in Poland, but the process lasted approximately 30 years in all (Nowak, 1966).

It is assumed that the nominative subspecies, *Ondatra zibethica zibethica* (Linnaeus, 1766) — Kratochvíl (1956), Feriancová-Masárová & Hanák (1965) was brought to Europe.

Although there is a very considerable amount of literature on the muskrat, the attention of such authors has been concentrated primarily on the economic importance, noxiousness and control methods, and also ecology, of this species (Hoffmann, 1967). There are few craniometric studies on this animal (Latimer & Riley, 1934; Gould & Kreeger, 1948; Sather, 1956), and only a small number of authors have dealt with the craniological and comparative analysis of variations in the muskrat (Müller, 1951/52, 1952/53; Lavrov, 1953; Cygankov, 1955; Rejmov, 1967; Petrov, 1967; Petrov & Krasnikova, 1970; Pietsch, 1970).

The results of studies on variations in the muskrat from North America (Gould & Kreeger, 1948), Europe (Pietsch, 1970) and Asia (Cerevitinov, 1951; Petrov, 1967, 1969; Petrov & Krasnikova, 1970) and in particular those relating to Eurasia, show that the differentiation which may occur in this species depending on the habitat is very far-reaching. The muskrat is therefore a rodent particularly suitable for

studies on variability of the species in time and space, understood in a wide sense.

The purpose of the present study was therefore to make a comprehensive analysis of the existing degrees of morphological differentiation in the muskrat, from the various parts of its contemporary range in Central Europe, which have come into being at different times. It was assumed that the different rate of spread and different habitat conditions encountered in new areas might to a certain extent influence the morphological variability of this animal, and in this connection comparisons were made between muskrats from Czechoslovakia and series of these rodents from different populations occurring in Poland. In addition the process of shaping of the muskrat's skull was traced in postnatal development, taking into account both the population and species aspects in undertaking a morphological description of the skull of this rodent.

2. MATERIAL AND METHODS

The material available consisted of 352 skulls of muskrats of both sexes and of animals of undefined sex, originating from central Bohemia and Poland, from the collection of Ústav pro výzkum obratlovců ČSAV in Brno, the author's own collection and that of the Mammals Research Institute of the Polish Academy of Sciences, at Białowieża. The majority of the muskrats had been obtained during shoots, mainly in spring, but partly in autumn also.

2.1. Age Classes

A knowledge of the properties of growth and accompanying wear of the surfaces of the molar crowns in skulls of individuals of known age shows that the first molar (M^1) is the most convenient tooth for defining age in the case of muskrats. This tooth is distinguished by relatively lesser variation in dimensions than the other molars and also by a more uniform degree of wear of the tooth crown (Cygankov, 1955). The process of wear of the molar crowns is accompanied in the muskrat by closure of the prismatic part of the tooth resting in the alveolus, and formation of the root, which in the case of M^1 takes place at the age of approximately $2\frac{1}{2}$ months (Cygankov, 1955).

Measurements of the height of the prismatic part of the tooth were made along the sulcus separating the fifth and third salient angle on the buccal side, using a vernier caliper with a device for measuring an inside diameter with accuracy to 0.1 mm. The measurement was made at the end of the sulcus lying on the cingulum of the tooth to the point lying on the margin of the chewing surface of the tooth crown.

Four age classes were distinguished in the material, using Cygankov's method (1955). Extreme values for the respective age classes are as follows:

age class I (9.4—11.3 mm) — 3—5 months

age class II (7.9—9.3 mm) — 6—8 months

age class III (5.6—7.8 mm) — 9—12 months

age class IV (below 5.6 mm) — from 13 months upwards.

It is a remarkable fact that out of the 352 skulls of muskrats only two specimens

had no distinctly separated roots. Part of the animals, although this also applied to young individuals, were found to have M^1 roots formed to a greater or lesser degree.

Division according to age based on the class system was considered most convenient and consequently as reducing the error which might have arisen if a subjective evaluation had been made of the animal's age. This applied particularly to individuals in which the height of the tooth crown of M^1 came within the intermediate ranges between the average values given by Cygankov (1955).

2.2. Character of Local Populations

The muskrat skull material available was divided into 4 populations (Table 1), and in general originated from a small number of localities situated within the range of the given local population, consequently forming a sample corresponding to a definite small area (except for the Białystok area). In the majority of cases the animals had been obtained in a similar period, chiefly between 1959 and 1965.

The animals from central Bohemia had been obtained during the period from 20.5.1959 to 2.12.1959 at Blatná. Several specimens had been collected at Jistebnice, situated about 60 km to the east of Blatná. These

Table 1

List of material in age classes.

Age groups	Czechoslovakia	Kujawy region	Pomerania	Białystok Province	Total
I	14	2	36	1	53
II	39	2	49	3	93
III	5	13	35	25	78
IV	21	20	60	27	128
Total	79	37	180	56	352

two localities are situated to the south of Dobříš, about 50 km from the place in which the muskrat was first introduced. Both Blatná (440 m above sea level) and Jistebnice (570 m a.s.l.) are situated on rivers (Lomnice and Lužnice — left and right tributaries of the Vltava) and lie in the Central Bohemian Highland region forming part of the South Bohemian Upland and Bohemian Massif. There are a great many fish ponds and extensive forests in this area, characterized by acidophilous oak forests and floodplain forests (willow, alder-ash), chiefly in river valleys. This is in general a poor habitat from the food aspect.

Muskrats appeared in the Blatná and Jistebnice areas about 1908—1909, that is, from 3—4 years after their introduction at Dobříš (Kohl, 1913; cited after Nowak, 1971). A factor additionally favouring the rapid spread of these rodents in Czechoslovakia consisted in the numerous rivers which are tributaries of the Vltava, and other lakes and ponds.

The Kujawy population originates from the mesoregion termed the Toruń Valley, which lies in the middle reaches of the Vistula (Kon-dracki, 1955). Muskrats have occasionally been shot in the administrative district of Aleksandrów Kujawski, but mainly in the immediate vicinity of Ciechocinek (52°53' N, 18°48' E) during the period from October 1960 to 21.4.1965.

Ciechocinek is situated mainly on a terrace above flood level, varying in absolute elevation from 48—51 m and relative elevation of 9—12 m in relation to the average water level of the Vistula, although part of it also extends to the flood level.

Muskrats living there also occur in the river bed of the Vistula and the numerous drainage ditches. They made their appearance in the Kujawy region in 1945 (Nowak, 1966).

The Pomeranian population originates from the Iława Lake District and partly also from the mesoregion of the Vistula haughs, that is, the low-lying region of the Vistula delta, part of which is below sea level (up to — 1.8 m). The greater part of this area is protected from flooding by river dykes and there are also numerous small drainage canals (Kon-dracki, 1955).

The haughs area is very fertile, as the soil consists mainly of silt muds. The majority of the animals were obtained during the period from April 1963 to 27.11.1967, from places in the Sztum administrative district (53°55' N, 19°03' E). A small number of skulls were obtained as late as 1969. The muskrat appeared in the haughs in 1944, although it had already occurred in the Gdańsk coastal area in 1940 (Nowak, 1966).

The Białystok population came from areas in three administrative districts — Gołdap (54°19' N, 22°19' E), Suwałki (54°07' N, 22°56' E) and Hajnówka (52°45' N, 23°36' E). In the last case these are single specimens from the Białowieża Primeval Forest (valley of the river Narewka). The remaining muskrats came from the valleys of the Rospuda and Gołdap a rivers and also from Lake Krzywe near Przerośl, and is therefore a river-lake population.

The majority of the animals were shot during the period from 5.6.1959 to 11.5.1965. According to Nowak's data (1966), muskrats appeared in the Białystok region as follows: in the Białowieża Primeval Forest in 1948, in the Suwałki area in 1950 and in the Gołdap area in 1958.

2.3. List of Measurements and Indices

A total of 10 linear measurements were made on each of the skulls (Fig. 1), using a vernier caliper with accuracy to 0.1 mm, and were defined as follows:

1. Condylbasal length (CbL)
2. Diastema length (DL)
3. Maxillary tooth-row length M^1-M^3 ($MxTRL$)

4. Mandibular tooth-row length M_1-M_3 (*MdTRL*)
 5. Brain-case breadth (*BcB*)
 6. Zygomatic breadth (*ZyB*)
 7. Interorbital constriction (*IC*)
 8. Rostrum breadth (*RB*)
 9. Brain-case height between bullae, measured in such a way that *pars basilaris ossis occipitalis* and the surface of the *ossa parietalia* and *os interparietale* were parallel to the arms of the vernier caliper (*BcH*)
 10. Brain-case length (= condyloalveolar length) after Gould & Kreeger, 1948; Fig. 1) (*BcL*)
- In addition to the above the following were also measured:
11. Capacity of brain-case in millilitres, using fine shot \varnothing 1.5 mm and a graduated cylinder with accuracy to 0.1 ml (*BcC*)

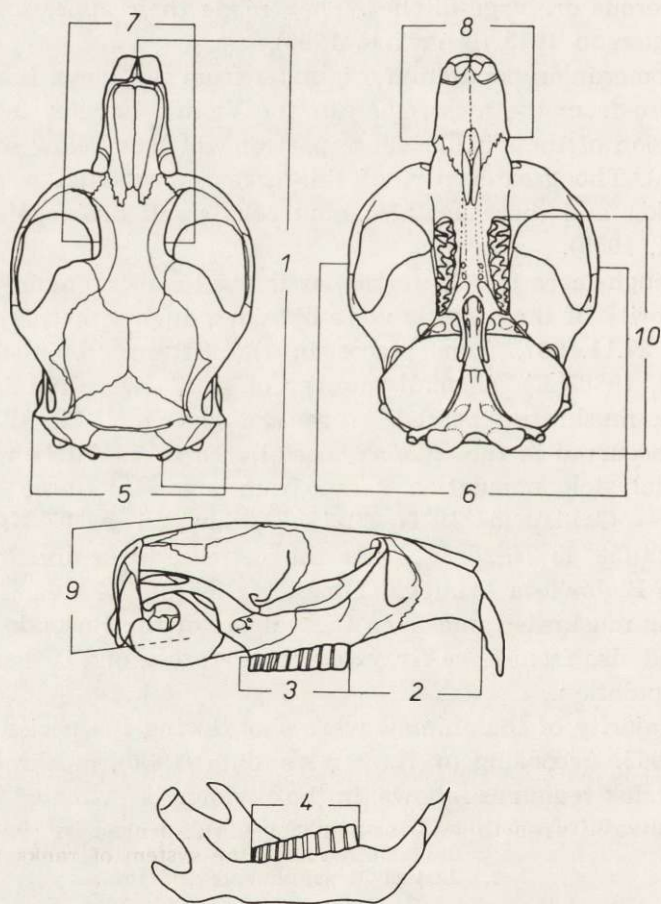


Fig. 1. Explanations of skull measurements in the muskrat.
 1 — Cb length (*CbL*), 2 — Diastema length (*DL*), 3 — Maxillary tooth-row length (*MxTRL*), 4 — Mandibular tooth-row length (*MdTRL*), 5 — Brain-case breadth (*BcB*), 6 — Zygomatic breadth (*ZyB*), 7 — Interorbital constriction (*IC*), 8 — Rostrum breadth (*RB*), 9 — Brain-case height (*BcH*), 10 — Brain-case length (*BcL*).

12. Mandible weight in grammes with accuracy to 0.01 g (*MdWt*).

Using the values of skull measurements as a basis calculation was made of the following quotient indices:

1. (Brain-case height \times 100) : Mandible weight (after Rossolimo, 1958)
2. (Brain-case breadth \times 100) : Cb length
3. (Brain-case height \times 100) : Cb length
4. (Interorbital constriction \times 100) : Cb length
5. (Diastema length \times 100) : Cb length
6. (Zygomatic breadth \times 100) : Cb length
7. (Brain-case length \times 100) : Cb length
8. (Double height of brain-case) : (Cb length+brain-case breadth) — (after Hrdlička - Kočka, after Pucek, 1963).

Standard body measurements were made on some of the specimens, as follows:
1. body length, 2. tail length, 3. length of hind foot, 4. height of ear and 5. body weight.

2.4. Mathematical Methods

Calculation was made of averages (\bar{x}), standard deviations (SD) and coefficients of variation (C. v.) for the various values of skull measurements, quotient indices and also body measurements.

The method of variance analysis was used for comparisons of the average values obtained. The significance of the effect of the given factor (sex and population) was examined by means of the *F*-Snedecor test, with $P_{0.05}$ and $P_{0.01}$ levels. In order to examine interpopulation differences calculation was made of the statistical distances of size and shape in accordance with the wellknown mathematical method (Penrose, 1954; Sych, msc).

Comparative methods were also used for the matrices of correlation coefficients (r), which reflect the degree of correlation of 12 craniometric characters and form the given correlation structure. Correlations were calculated on the basis of the generally accepted methods. Significance of differences between corresponding pairs of correlation coefficients were checked by means of chi-square statistics, in this case also accepting two levels of significance; $P_{0.05}$ and $P_{0.01}$. In comparisons between pairs of correlation coefficients included in the given correlation structure examination was also made of the possible effect of age and population. In all, 12 matrices of correlations were calculated in four populations divided into four age classes. In the four remaining cases this was impossible on account of the lack of sufficient material (age classes I and II from the Kujawy and Białystok populations). In addition, in order to give a general description of changes taking place with increasing age in the skull of the Central European muskrat, calculation was made of matrices of correlation for four age groups, without taking into consideration division into populations.

In arranging correlation matrices in order use was made, *inter alia*, of Czekański's diagram method (1913), introducing the system of ranks for the ranges of variations in correlation coefficients corresponding to them. On account of the individual order of each diagram, the order of characters differs on the diagrams. This method was used in relation to the correlation matrices characterizing age variations in the muskrat from the species aspect.

Correlation structure of skull measurements in the form of matrices or arranged diagram formed the starting point for its further analysis. Terentjev's method

of correlation pleiads (1943 and 1960) and V y h a n d u's method (1964), distinguished by its simplicity and ease of application, were considered the most convenient in studies of this kind.

3. RESULTS

3.1. Sex Dimorphism in Skull Measurements

Using the method of variance analysis, comparisons were made of average values for dimensions and skull indices and body measurements between the two sexes, simultaneously allowing for the age divisions accepted. Division into populations was not taken into consideration in the comparisons on account of the small numbers of muskrats of known sex.

It was found that differences connected with sex dimorphism became apparent as the animals increased in age, for instance no statistically significant differences between the sexes were found in the two first age classes in respect of any of the craniometric characters examined. Only two statistically significant differences were observed between males and females in age class III in *MxTRL* and *MdTRL* ($0.05 > P > 0.01$). Statistically significant differences in average values for 6 measurements were found in muskrats in age class IV, although these were not highly significant differences ($0.05 > P > 0.01$) and related to: *CbL*, *DL* and *BcL*, and also *BcB*, *BcH* and *MdWt*. Skull dimensions of males were slightly greater than those of females in muskrats in age classes III and IV. Males were also distinguished by significantly greater hind foot measurements ($0.05 > P > 0.01$) in comparison with females. Indices expressing the percentage ratio between: *BcH* and *MdWt* ($0.05 > P > 0.01$), *IC* and *CbL* and *ZyB* and *CbL* were in this case significantly higher in females than in males ($P < 0.01$).

Sex dimorphism in the muskrat is also evident in the different growth rate of the skull in individuals of different sex, the skulls of males being distinguished in nearly all cases by greater increases in percentages than females (Table 2).

It may therefore be said that the muskrat is an animal in which differences connected with sex dimorphism in skull measurements are slight. Although the males are usually larger than the females, these differences were significant only in 11 cases out of 80. As the sex of the individuals was not identified for a large part of the skulls the whole material has been treated jointly in the further part of this study. Table 3 provides information on the sex ratio of the individuals examined and at the same time points to possible burdening of the average values of the measurements analysed, which may be due to differences in the size of

Table 2

Increases in percentages of dimensions and indices of the skull of Central European muskrats in different age groups of males and females.

Skull measurements	♂♂				♀♀				General*		
	II	III	IV	IV	II	III	IV	IV	II	III	IV
1. Cb length	5.28	13.69	16.97	16.97	2.66	10.18	12.10	12.10	3.18	10.83	14.04
2. Diastema length	6.90	17.03	22.76	22.76	2.55	12.54	16.59	16.59	3.26	13.22	18.41
3. Maxillary tooth-row length	1.76	6.32	4.96	4.96	1.01	3.45	3.65	3.65	0.54	4.79	4.05
4. Mandibular tooth-row length	1.37	7.19	4.10	4.10	-0.41	3.36	1.88	1.88	0.13	4.35	2.01
5. Brain-case breadth	7.00	14.13	18.57	18.57	2.23	10.23	12.38	12.38	3.32	10.52	14.01
6. Zygomatic breadth	6.51	15.74	20.22	20.22	2.57	11.32	16.13	16.13	2.77	11.58	16.20
7. Interorbital constriction	0.96	2.23	-1.44	-1.44	0.80	-0.32	2.25	2.25	-0.63	-1.10	-2.66
8. Forstrum breadth	8.42	17.02	23.47	23.47	2.42	11.24	17.47	17.47	3.10	12.24	18.27
9. Brain-case breadth	6.09	13.43	16.29	16.29	0.87	7.37	9.37	9.37	2.25	8.75	11.56
10. Brain-case length	3.90	10.92	12.90	12.90	2.32	7.94	9.29	9.29	2.92	8.97	10.95
11. Brain-case capacity	7.05	19.22	21.41	21.41	0.45	6.80	9.52	9.52	1.13	9.50	11.99
12. Mandible weight	18.45	48.81	63.39	63.39	5.69	34.42	39.56	39.56	7.60	36.68	46.74
Indices											
1. 9 × 100 : 12	-20.45	-31.84	-37.24	-37.24	-9.65	-23.61	-25.42	-25.42	-10.99	-25.15	-29.16
2. 5 × 100 : 1	0.52	0.54	0.75	0.75	-0.62	0.19	0.19	0.19	0.16	0.47	0.35
3. 9 × 100 : 1	-0.32	-0.35	-1.23	-1.23	-2.74	-2.67	3.08	3.08	-1.71	-1.98	-2.68
4. 7 × 100 : 1	-5.00	-11.19	-16.78	-16.78	-3.02	-10.31	-9.95	-9.95	-4.26	-11.12	-15.00
5. 2 × 100 : 1	2.18	4.05	6.35	6.35	0.29	2.78	4.33	4.33	0.52	2.86	4.76
6. 6 × 100 : 1	0.71	1.61	2.15	2.15	0.52	1.52	3.66	3.66	-0.19	1.13	1.97
7. 10 × 100 : 1	-1.57	-2.48	-3.75	-3.75	-0.58	-2.06	2.70	2.70	-0.56	-1.65	-2.85
8. 9 × two : 1 + 5	-2.50	-2.50	-2.50	-2.50	-2.50	-2.50	-2.50	-2.50	-2.50	-2.50	-2.50

* males and females were combined with specimens of unknown sex. Average values for age class I were taken as 100%.

males and females and the not always equal participation of the two sexes in the samples examined. The general sex ratio in the whole collection was 55⁰/₀, which does not significantly differ from the proportions 1 : 1 ($\chi^2 = 2.58$, $\chi^2_{0.05} = 3.84$).

3.2. Interpopulation Differentiation

3.2.1. Variations in Values of Absolute Dimensions and Indices

Variations in the craniological characters of the muskrat were examined from the interpopulation aspect, simultaneously taking into consideration the age division accepted. Among the 12 craniometric characters of muskrats in age class I the most variable character in both the Czech and Pomeranian populations was *MdWt* (C. v. = 15.9 and 18.4⁰/₀). The values of the other skull measurements were distinguished by lesser variability in the Czech population (C. v. = 2.8—7.5⁰/₀) than in the Pomeranian population (C. v. = 3.1—8.5⁰/₀). Quotient indices, with the exception of the ratio of *BcH* to *MdWt*, varied very little in the two populations, as is shown by the range of their coefficient of variation (Table 4).

Table 3

Sex ratio in part of material consisting of animals of known age.

Age groups	I	II	III	IV	Total
	♂:♀	♂:♀	♂:♀	♂:♀	♂♂:♀♀
Czechoslovakia	5 : 9	18 : 21	2 : 3	7 : 14	32 : 47
Kujawy region	1 : —	2 : —	7 : 6	13 : 6	23 : 12
Pomerania	6 : 8	7 : 12	19 : 7	25 : 9	57 : 36
Białystok Province	1 : —	1 : 2	15 : 9	15 : 12	32 : 23
Total	13 : 17	28 : 35	43 : 25	60 : 41	144 : 118

A certain reduction in C. v. value, occurring in both the Czech and Pomeranian populations, can be observed in age class II. The variations in *MdWt* are in this case 12.9 and 11.9⁰/₀ respectively. In the case of other characters of skull dimensions this variation fluctuated in Czech muskrats within limits of 3.0—6.8⁰/₀ and in the Pomeranian animals correspondingly from 3.1—5.5⁰/₀. Variations in indices, apart from the ratio of *BcH* to *MdWt*, which alters markedly with age, increase slightly in age class II (Table 4), which would appear to point to greater changes in skull proportions more clearly manifested in indices than in the values of absolute dimensions.

In age class III *MdWt* was also one of the most variable dimensions. Its relatively low variability in muskrats from the Czech and Białystok populations (C. v. = 6.4 and 8.8⁰/₀) distinguished these animals from those of the Pomeranian and Kujawy populations (C. v. = 12.2 and 14.1⁰/₀). C.v.

values for the remaining measurements in the various populations varied to a lesser (Białystok region and Pomerania) or greater degree (Kujawy and Czechoslovakia) (Table 4). Variations in skull indices in the Czech and Białystok populations were small in comparison with the Pomeranian and Kujawy populations. The differences evident in variations of indices in age class III in four populations point to continuing changes in skull proportions.

In all populations in age class IV a renewed increase can be observed in variability of *MdWt* as compared with class III, forming evidence of age differentiation of muskrats composing that group. The values of C. v. defining the variations of this character are, however, very even (10.0—12.8%). The variations in the remaining characters in the populations compared rarely exceed 5%. Among the indices the greatest variability is found in the ratio of *BcH* to *MdWt* (C. v. = 8.1—9.7%) and *IC* to *CbL* (C. v. = 6.8—9.2%). Variations in the other indices are small and rarely exceed 3% in the Czech, Pomeranian and Białystok populations as compared with the more variable Kujawy population (Table 4). Apart from the fact that variations in an index based on *BcH* and *MdWt* is usually greater, the remainder vary only very slightly in comparison with it, which points to the stabilization of skull proportions in this age group.

3.2.2. Differences in Absolute Values of Measurements and in Indices

Before interpopulation comparisons were made it was necessary to check the age uniformity of the groups by comparing average values for height of *M*¹ crown within the groups. In 11 cases out of the 12 examined the differences were non-significant, only the average for this measurement in the Czech population, in age class III, differing significantly from the other three Polish populations ($P < 0.01$). The cause of this was undoubtedly the small amount of material and exceptionally small variations in height of *M*¹ crown in age class III of the Czech population (C. v. = 1.5%) (Table 4).

Comparison of average values of measurements and indices in individuals from age class I between the Czech and Pomeranian populations revealed 4 statistically significant differences. The Czech muskrats had narrower *IC* and *RB* and smaller *MdWt* ($0.05 > P > 0.01$) and also shorter *MdTRL* ($P < 0.01$) than in the Pomeranian population (Table 4 and 5).

When individuals in age class II from the Czech and Pomeranian populations were compared a total of 11 statistically significant differences were found between them, 8 of which related to skull dimensions, and 3 to quotient indices. Czech muskrats were distinguished by shorter *DL* and *BcL* and narrower *BcB* and *IC* ($0.05 > P > 0.01$). In addition they had

shorter *CbL*, *MdTRL* and also lower *BcH* and smaller *BcC* ($P < 0.01$) than the Pomeranian muskrats (Tables 4 and 5).

In order to distinguish the population most markedly differing from the remainder, as from age class III, two variants were made of comparisons: (1) of all four study populations and separately, (2) three populations from Poland.

It was found that Czech muskrats from age class III differed significantly from the Polish populations in respect of 10 craniometric characters, 2 skull indices and in 3 body measurements. Comparison of aver-

Table 5

List of statistically significant differences at a level of $P=0.05$ (+) and $P=0.01$ (++) , obtained by comparing arithmetical means for populations and age groups by means of variance analysis.

Age groups No. of comparing populations	I	II	III		IV	
	2*	2*	4**	3***	4**	3***
1. Cb length	—	++	++	—	++	—
2. Diastema length	—	+	++	—	+	—
3. Maxillary tooth-row length	—	—	—	—	++	—
4. Mandibular tooth-row length	++	++	++	—	++	—
5. Brain-case breadth	—	+	++	—	++	—
6. Zygomatic breadth	—	—	++	—	—	—
7. Interorbital constriction	+	+	—	—	—	—
8. Rostrum breadth	+	—	++	—	++	+
9. Brain-case height	—	++	++	—	++	—
10. Brain-case length	—	+	++	—	+	—
11. Brain-case capacity	—	++	+	—	+	—
12. Mandible weight	+	—	++	—	++	—
Indices						
1. $9 \times 100 : 12$	—	—	++	—	++	—
2. $5 \times 100 : 1$	—	—	—	—	—	—
3. $9 \times 100 : 1$	—	+	—	—	+	+
4. $7 \times 100 : 1$	—	—	—	—	++	—
5. $2 \times 100 : 1$	—	—	—	—	—	—
6. $6 \times 100 : 1$	—	+	—	—	++	++
7. $10 \times 100 : 1$	—	—	++	—	++	—
8. $9 \times \text{two} : 1 + 5$	—	+	—	—	+	—

* results of comparisons of Czech with Pomeranian populations, ** results of comparisons of all four populations, *** results of comparisons, omitting the Czech population.

age absolute measurements shows that skulls of Czech muskrats are distinguished by smaller *BcC* ($0.05 > P > 0.01$), shorter *CbL*, *DL*, *MdTRL* and *BcL*, and in addition smaller *ZyB*, *BcB* and *RB*, and also lower *BcH* and *MdWt* ($P < 0.01$) in comparison with the Polish individuals (Table 5). In respect of body measurements the Czech muskrats had shorter ears ($0.05 > P > 0.01$) and tail and lower body weight ($P < 0.01$) than those of the remainder (Table 4). Among Polish populations the Białystok muskrats from age class III were significantly larger than the animals from

the Kujawy region only in respect of tail length and height of ear ($0.05 > P > 0.01$) (Table 4).

Comparison of four populations of muskrats from age class IV showed that there are statistically significant differences between them in respect of 9 skull measurements, 4 indices and 4 body measurements (Table 4 and 5). Czech muskrats were characterized by shorter *DL* and *BcL*, and also by smaller *BcC* ($0.05 > P > 0.01$). They also had shorter *CbL*, *MxTRL* and *MdTRL*, narrower *RB* and *BcB*, lower *BcH* and smaller *MdWt* ($P < 0.01$) than Polish muskrats (Table 5). In respect of body measurements the Czech muskrats differed from the Polish individuals in respect of shorter tail, hind foot and ear and also smaller body weight ($P < 0.01$).

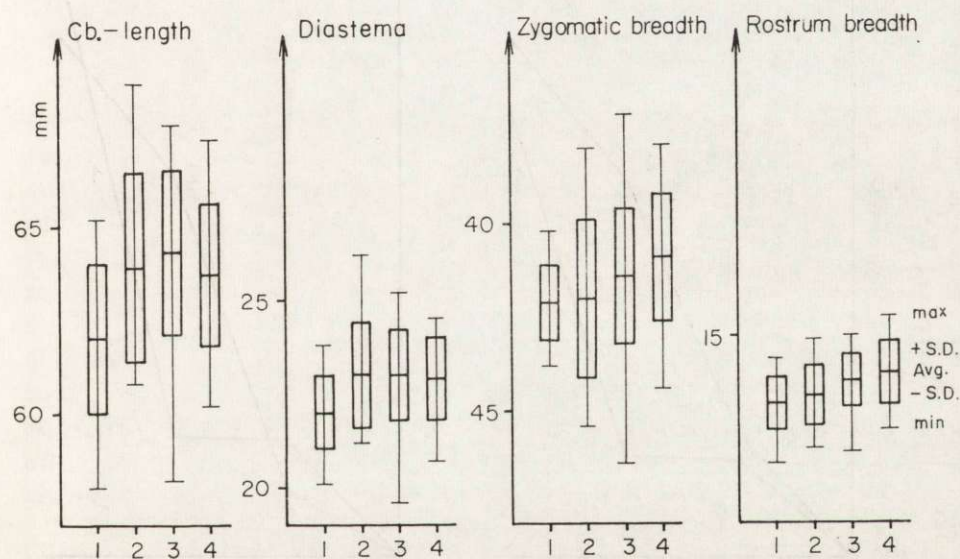


Fig. 2. Variations in certain skull measurements (differing significantly) in the muskrat from the population aspect. Extreme and average values are given, with standard deviations. All data refer to age class IV only. 1 — Czechoslovakia, 2 — Kujawy, 3 — Pomerania, 4 — Białystok region.

(Table 4). Among the three Polish populations in age class IV the Białystok animals had wider *RB* ($0.05 > P > 0.01$) than the other two populations, and in addition the Białystok muskrats were larger than those from the Kujawy region in respect of height of ear ($0.05 > P > 0.01$), but smaller in respect of length of hind foot ($P < 0.01$) (Table 4).

The results of comparisons thus point to considerable differentiation of muskrats from the Czech population, expressed in generally smaller skull dimensions than in the other three populations from Poland (Fig. 2).

In addition to interpopulation differences in absolute values of measurements, differences were also found in the average values of the various quotient indices which do not become evident until age class II. The skulls of Pomeranian muskrats were relatively higher in this class, but zygomatic breadth was narrower than in the Czech animals. In age class III *BcH* in animals from the Czech population formed a higher percentage of *MdWt* than that for Polish muskrats. Czech muskrats had relatively longer *BcL* than that for the three Polish populations. In age class IV the skulls of Pomeranian and Białystok muskrats were relatively higher than

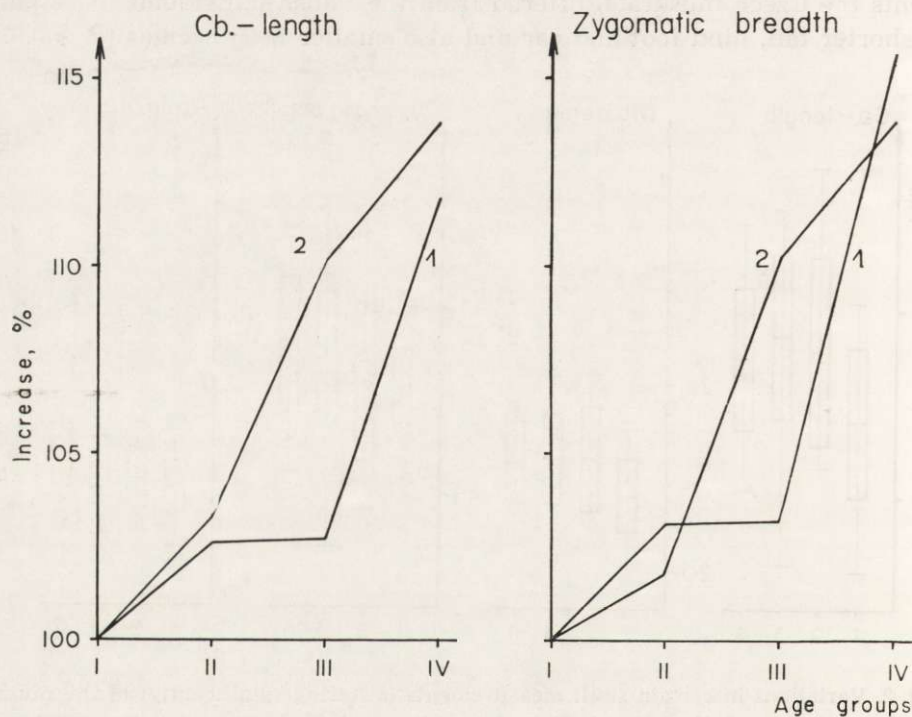


Fig. 3. Comparison of increases in percentages of two skull dimensions in muskrat populations from Czechoslovakia (1) and Pomerania (2).

the Kujawy and Czech skulls, and also in age class IV Czech muskrats *BcH* formed a higher percentage of *MdWt* than in Polish populations. In addition the skulls of Czech muskrats were relatively wider at the zygomatic arches than the Kujawy and Pomeranian animals, had a broader *IC* than the Pomeranian animals and longer *BcL*. Of the Polish muskrat populations, that from the Białystok region was distinguished by the fact that the skulls were relatively higher than in those from Kujawy and wider in *ZyB* than the Kujawy and Pomeranian skulls (Tables 4 and 5).

These data show that there are population differences in skull proportions in the corresponding age groups.

The values of indices were dependent on the individual rate of growth of the various measurements, and therefore the finding of significant differences in the indices within different populations must form evidence of the different growth rate of these same measurements under different conditions. Comparison of the growth rate of the two basic skull measurements for the Czech and Pomeranian populations did in fact show that both *CbL* and *ZyB* increased intensively in muskrats from the Pomeranian population (Fig. 3). The different growth rate of certain skull dimensions in individuals from the various populations is thus one of the causes of formation of different skull proportions.

3.2.3. Differences in Correlation Structure of the Skull

The comparisons made below were intended to grasp the influence exerted by the place of the population's origin on the correlation structure of the muskrat's skull, examined in groups of uniform age. The curves of distribution of frequency for values of correlation coefficients are distinguished by a very varied distribution within different populations (Fig. 4). It is only rarely that they had three peaks, permitting of making a division among correlation coefficients and distinguishing among them groups of intrapleiad, mixed and interpleiad connections (Fig. 4). They were therefore not used for this purpose, but only as an indication of the existence and extent of interpopulation differences in correlation matrices. Analysis of the distribution of curves does not supply an answer to the question — in which combinations of craniometric characters is this differentiation most strongly marked?

These questions are unequivocally explained by analysis of the correlation cylinder, divided into parts, the circular bases of which are treated as correlation circles — levels of interrelation of characters. Although interpopulation differences are evident in correlation circles from the very start, in further discussion we shall limit ourselves only to analysis of the highest level of relations taken by us as $r \geq 0.8$ (Fig. 5).

In age class I there is one large pleiad including the majority of the characters, connected with each other by lines defining the degree of their interrelation, for the Czech and Pomeranian populations. In both these populations, however, the capacity of the pleiad grouping the related characters is different and decidedly greater in the case of muskrats from the Pomeranian population. Independent pleiads, on the other hand, are formed in the Czech population by *MxTRL*, *MdTRL* and *IC*, and in Pomeranian population by only the first two of these characters (Fig. 5).

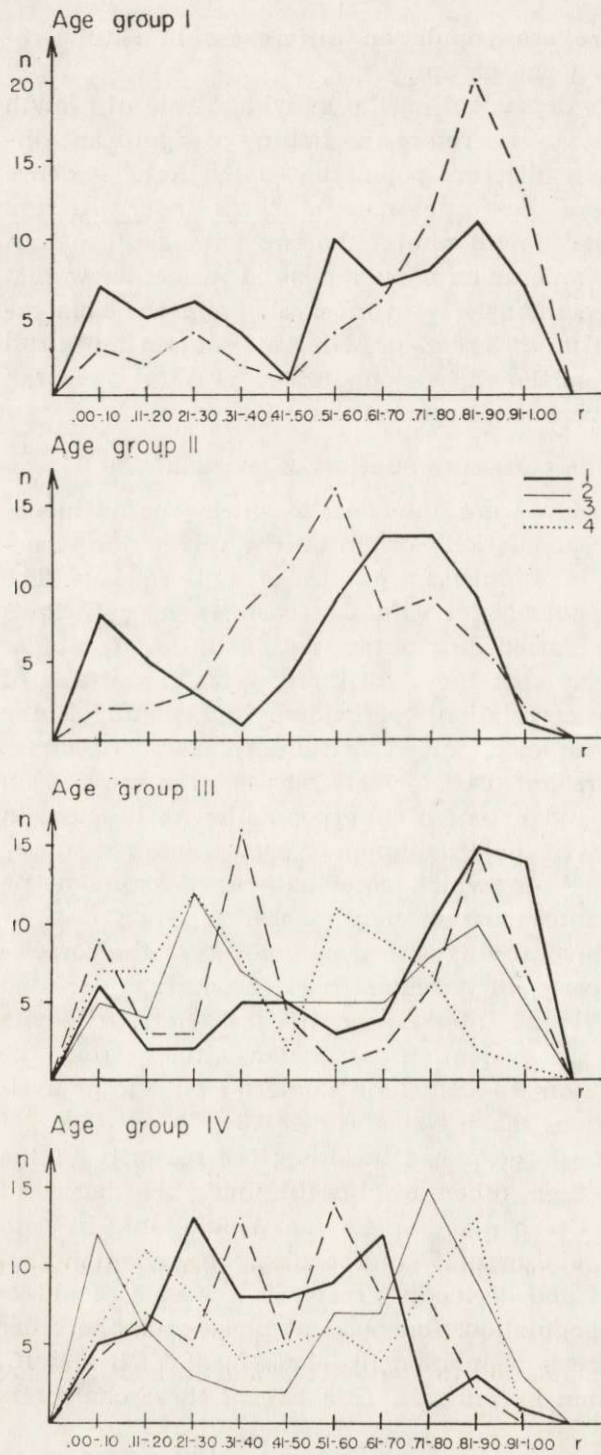


Fig. 4. Frequency of 66 correlation coefficients for skull dimensions in the muskrat from the age and population aspects. 1 — Czechoslovakia, 2 — Kujawy, 3 — Pomerania, 4 — Białystok region.

Increase in the number of independent pleiads connected with decrease in the capacity of pleiads grouping characters of a high degree of reciprocal correlation can be observed in muskrats in age class II in both these populations. In this case the number of independent pleiads was smaller in the Czech population and included only 5 characters (*MxTRL*, *MdTRL*, *IC*, *BcH* and *BcC*), whereas in the Pomeranian population 6 in-

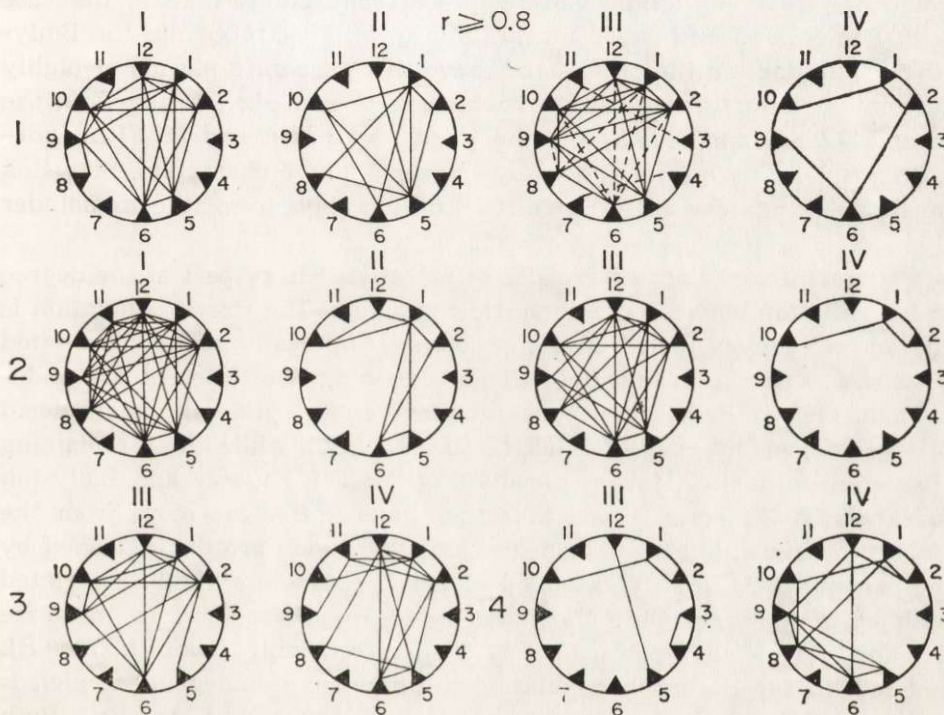


Fig. 5. Correlation structures of skull dimensions in the muskrat from the age (I-IV) and population aspects. Dotted line indicates correlation coefficients not significant with $P_{0.05}$ level.

1 — Czechoslovakia, 2 — Pomerania, 3 — Kujawy, 4 — Bialystok region. Symbols: 1 — Cb length (*CbL*), 2 — Diastema length (*DL*), 3 — Maxillary tooth-row length (*MxTRL*), 4 — Mandibular tooth-row length (*MdTRL*), 5 — Brain-case breadth (*BcB*), 6 — Zygomatic breadth (*ZyB*), 7 — Interorbital constriction (*IC*), 8 — Rost- rum breadth (*RB*), 9 — Brain-case height (*BcH*), 10 — Brain-case length (*BcL*), 11 — Brain-case capacity (*BcC*), 12 — Mandible weight (*MdMt*).

dependent pleiads occurred, including in their scope *RB* in addition to the above-mentioned characters. The pleiad of related characters is characterized by greater capacity in the Czech population (7 characters) than in the Pomeranian population (6 characters), and in addition these characters exhibit a higher number of connections with the other components of the pleiad in Czech muskrats (Fig. 5).

Animals in age class III in the Czech population were characterized by a pleiad grouping highly reciprocally correlated characters, and possessing maximum capacity, so that no independent pleiads were distinguished here at all. The Pomeranian and Kujawy populations are distinguished by the presence of four independent pleiads formed by *MxTRL*, *MdTRL*, *IC* and *BcC*. The pleiad of related characters in the Kujawy population has, however, a smaller number of reciprocal connections than is the case with Pomeranian and Czech muskrats (Fig. 5). Muskrats from the Białystok population, on the other hand, have three separate pleiads of highly correlated characters, the first of which takes in *CbL*, *DL* and *BcL*, the second — *BcB* and *MdWt*, and the third — *MxTRL* and *MdTRL*. Independent pleiads are formed here by the remaining 5 characters. Białystok muskrats in age class III thus differ considerably from the remainder (Fig. 5).

Muskrats in age class IV are also differentiated in respect of the degree of interrelation between craniometric characters. The Czech population is characterized by a pleiad of 5 characters, reciprocally highly correlated (*CbL*, *DL*, *ZyB*, *BcH* and *BcL*). The remaining 7 characters are independent pleiads. Pomeranian muskrats have an exceptionally small pleiad of three dependent characters (*CbL*, *DL* and *BcL*), while the 9 remaining characters form independent pleiads (Fig. 5). The Kujawy and Białystok muskrats in age class IV, on the other hand, differ far more from the first populations. Muskrats from the Kujawy region are distinguished by the presence of a greatly extended pleiad of characters highly correlated with each other grouping the majority of the characters. In this case independent pleiads are formed by 3 characters only (*MxTRL*, *MdTRL* and *IC*). In the Białystok population the number of independent pleiads includes not only all the above mentioned characters but also *BcC*. Both the Kujawy and Białystok population, despite their apparent similarity, differ from each other in respect of the number of connections within the related pleiads. In the case of the Kujawy muskrats the group *CbL*, *DL*, *BcC* and *MdWt* can be considered as the »core« of the dependent pleiad, whereas in the analogical pleiad for the Białystok muskrats it is the group — *BcB*, *ZyB*, *RB*, *BcH* and *BcL* which occupies first place (Fig. 5).

It can be seen from the data given that interpopulation differentiation in the muskrat applies not only to absolute values of measurements, but also of indices and degree of correlation of the various dimensions of the skull.

Examination was next made of the significance of differences between correlation coefficients of the corresponding pairs of craniometric characters in these animals from different populations in comparable age groups. To start with the matrix of average values of correlation coef-

ficients was obtained and its homogeneity tested by means of the chi-square test. Table 6 contains a list of statistically significant differences throughout the four age groups in 16 cases out of 66. In turn examination was made of interpopulation differentiation of these 16 correlation coefficients within the various age classes, when it was found (Table 6) that there are 4 significant differences in age class I connected with a different relation — *BcC* and *CbL*, *DL* and *ZyB*, and also *MdTRL* and *MdWt*.

Table 6

List of statistically significant differences ($P=0.05$ (*), $P=0.01$ (**)) of the correlation coefficients for craniological characters of muskrats from different populations. Statistically significant differences through all age groups have been given, as the result of testing the homogeneity of average matrices for correlation coefficients by means of test χ^2 .

Cb length	1	*	**	*	**1	*
Diastema length	2	*		**	**1,4	**
Maxillary tooth-row length	3					
Mandibular tooth-row length	4					**1 *
Brain-case breadth	5			*		**
Zygomatic breadth	6			**	*	**
				**1	**3	
Interorbital constriction	7					
Rostrum breadth	8					
Brain-case height	9					
Brain-case length	10				*	
Brain-case capacity	11					
Mandible weight	12					

Differences between populations have been indicated; 1, 3, 4 indicate I, III, and IV age classes, respectively.

No statistically significant differences were found in age class II. In age class III and IV it was found respectively that only the relation *ZyB* and *MdWt* and *DL* and *BcC* differ significantly.

It may therefore be said that in general the correlation structures of skull measurements in the muskrat are distinguished by a small number of statistically significant population differences between given pairs of correlation coefficients. This does not, however, mean that in 100% of cases there are no real interpopulation differences in correlation struc-

tures. It is possible that they were not made clearer in the present study only on account of the numbers in the various groups being too small. It is worth mentioning here that the method used for comparing correlations is more »sensitive« to differences between high than low correlations, due to the fact that the error of the calculated correlation is significantly dependent on the correlation itself (in particular when $r = 1$, the error is zero and a correlation of this kind always differs significantly from others).

3.2.4. Interpopulation Differences in Statistical Distances

Statistical distances were calculated in relation to 12 skull dimensions for muskrats in age class IV from four populations analysing them in units of standard deviation.

The greatest differences in skull size were found between the Czech and Kujawy populations (47.53). Twice smaller differences appeared when the Kujawy population was compared with the Białystok one (18.75). The following populations differed from each other to a very similar degree: Kujawy and Pomeranian (11.29) and Czech and Pomeranian (12.48). The Czech and Białystok populations were divided by a distance of 6.57, while the skulls of muskrats from Pomerania and the Białystok region are almost identical in size (0.94). In respect of distance in shape the greatest interpopulation differences of similar order were found between the Czech and Kujawy populations (49.23), and between the Czech and Białystok populations (50.22). A slightly smaller difference was found between Czech and Pomeranian populations (38.97). Differences of similar size occurred between the Kujawy and Pomeranian populations (9.65), and also between the Pomeranian and Białystok populations (11.69). The smallest differences in shape of skull were found between the Kujawy and Białystok populations (4.92).

Although when using the method of distances in size and shape the results obtained are slightly different from those when using variance analysis and differences in matrix of correlation, the difference of the Czech population from the others would appear to be fully proved. The use of the statistical distance method made it possible to highlight interpopulation differences and to define their extent in the case of apparently uniform muskrat skull material from Poland.

3.3. General Craniological Characteristic of Central European Muskrats

Taking as a starting point the assumption that Polish populations of muskrats probably originated from the Czech populations, despite the interpopulation differences shown above it was decided to make a general craniological characteristic of the Central European muskrat. By omitting

division into populations a larger amount of material was obtained in the different age classes (cf. Table 1).

Analysis was first made of the rate of increase in dimensions and changes with age in skull indices. Table 2 shows that *DL*, *RB* and *MdWt* change most intensively with age in the muskrat, increases being respectively of the order of 18 and 46%. *MxTRL* and *MdTRL* change only to a minimum extent with age (2–4%), and also *IC*, which even decreases slightly in the older animals. Decrease in *IC* is probably connected with the formation with age of a crest on the frontal bone in these

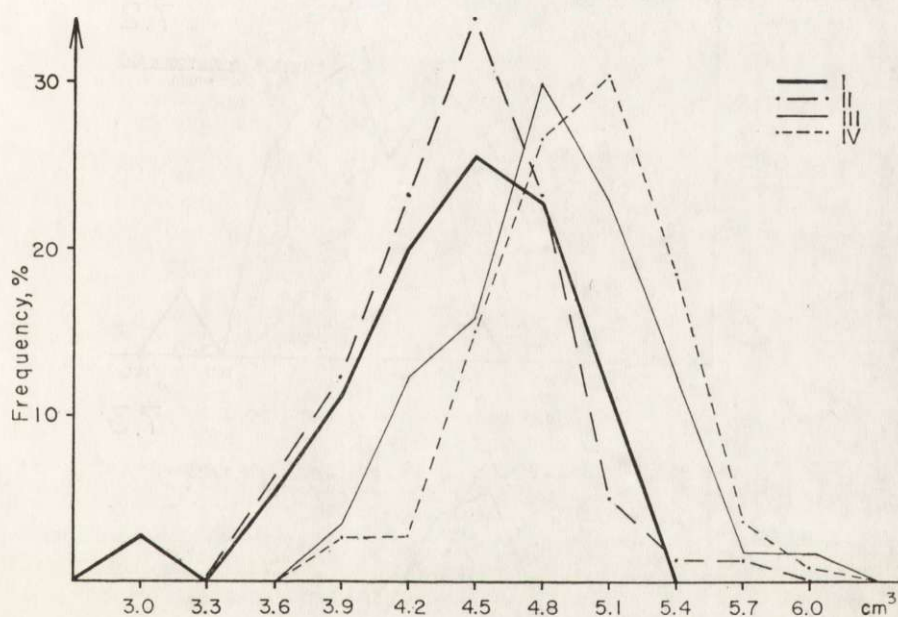
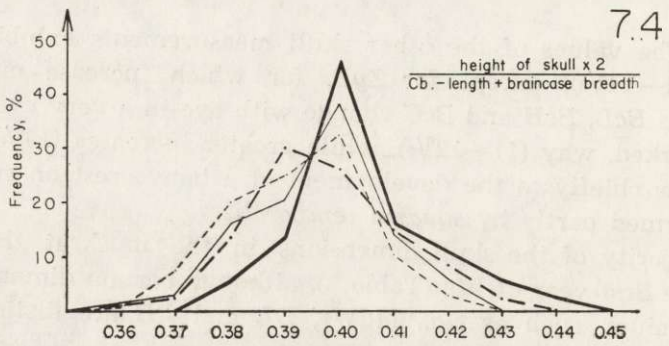
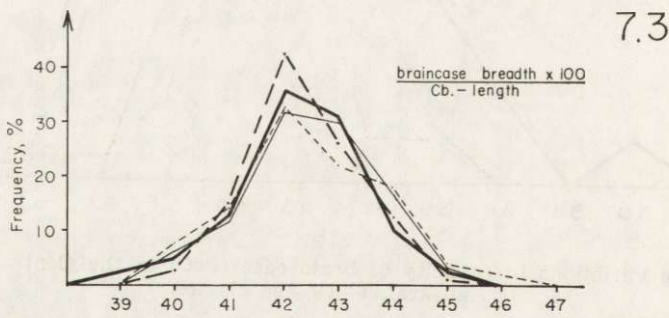
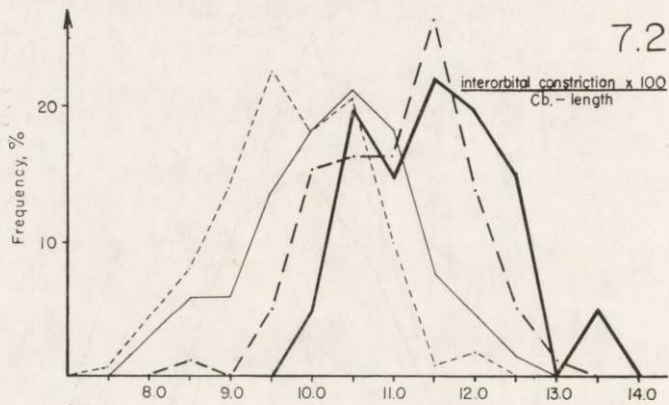
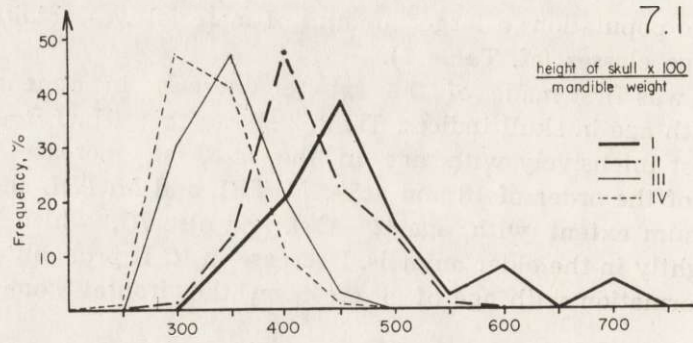


Fig. 6. Age variations in capacity of brain-case (*BcC*) in the Central European muskrat. I–IV age classes.

animals. The values of the other skull measurements exhibit slight increases (11–14%), except for *ZyB*, for which increase exceeds 16%. Dimensions *BcL*, *BcH* and *BcC* change with age in a very even, although not so marked, way (11–12%), while greater increases (14%) are found in *BcB* due chiefly to the development of a bony crest on *sutura lambdoidea*, formed partly by *squama temporalis*.

The majority of the skull dimensions in the muskrat thus increase during the first year of life (Table 2), although certain dimensions of the viscerocranium, such as e.g., *MdWt*, *DL* and *RB* are distinguished by



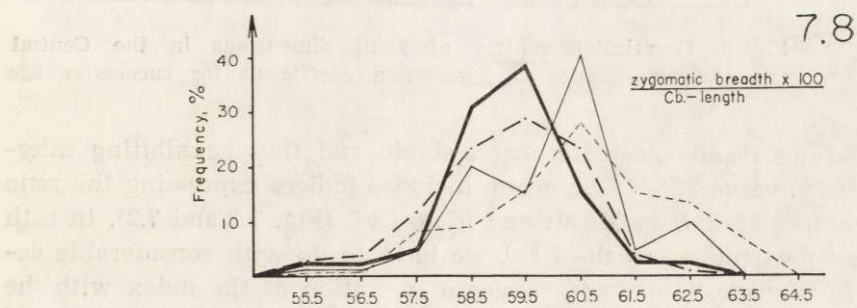
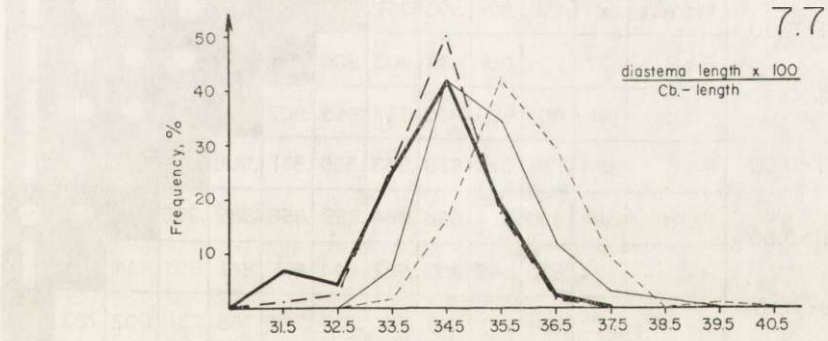
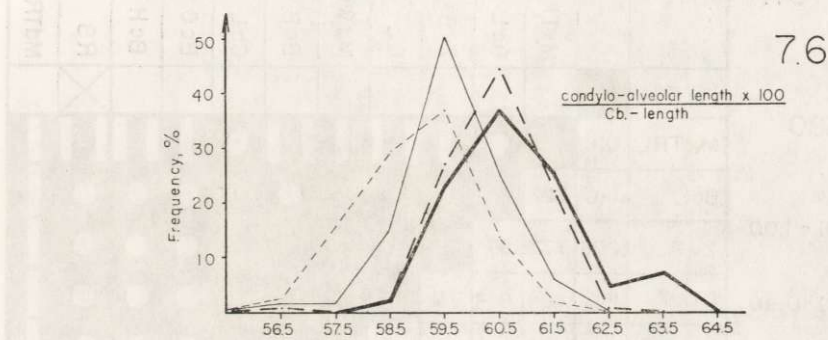
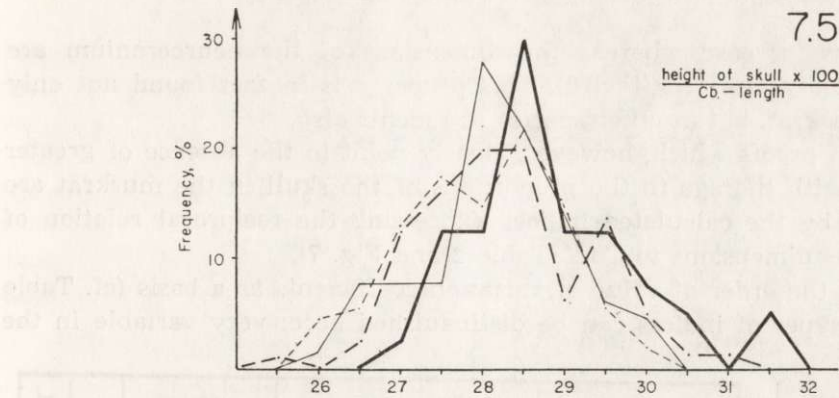


Fig. 7. Age variations in skull indices of Central European muskrat. I—IV age classes.

continuous increase whereas the dimensions of the neurocranium are fairly rapidly attained (Fig. 6). This property is in fact found not only in the muskrat, but in other species of rodents also.

Indirect proofs which, however, clearly point to the absence of greater changes with the age in the proportions of the skull in the muskrat are provided by the calculated indices expressing the reciprocal relation of its various dimensions to *CbL* (Table 2 and Fig. 7).

Taking the order of value of variation coefficients as a basis (cf. Table 4) three types of indices can be distinguished here: very variable in the

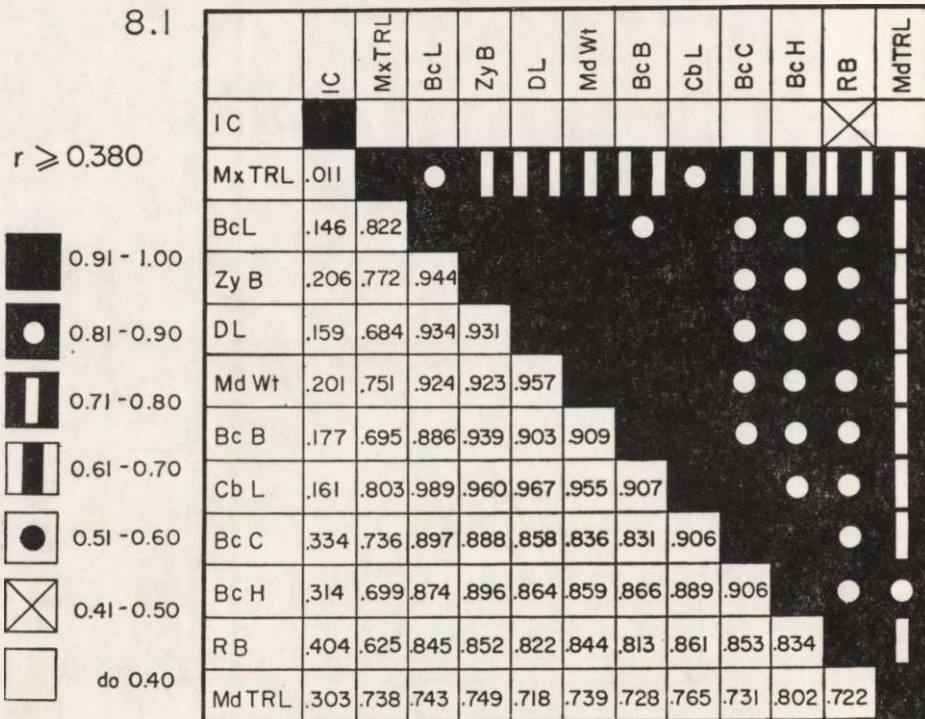


Fig. 8. Correlation matrix of skull dimensions in the Central. The extreme value of significance of correlation coefficient for successive age

sense of ranges and age differences, stable and those exhibiting intermediate C. v. values. The first group includes indices expressing the ratio in percentages of *BcH* to *MdWt* and *IC* to *CbL* (Fig. 7.1 and 7.2). In both cases, and particularly in the first, we have to do with considerable decreases in average values and ranges of variation of the index with the animals' age. This is due to the relatively small increases in *BcH* and considerable increases in *MdWt* (cf. Table 2).

Index *BcB* to *CbL* (Fig. 7.3) is exceptionally stable. It has the lowest coefficient of variation (Table 4) and almost unchanging ranges in the various age groups.

The other indices belong to averagely variable (their C. v. fluctuates in age class IV from 1 to about 4%). The ranges of their variation for the different age classes do not differ basically (Fig. 7.4—7.8), for instance distributions of variation for index *ZyB* to *CbL* (Fig. 7.8) differ only slightly and the age of the animals cannot be judged from them. Both

8.2

$r \geq 0.231$

	IC	MxTRL	MdTRL	BcH	RB	MdWt	BcL	CbL	DL	ZyB	BcB	BcC
IC												
Mx TRL	-267		●		⊗	●	●	●		●	⊗	
Md TRL	.110	.569			⊗	●	●	●	⊗	●	●	⊗
Bc H	.185	.352	.609					●	●			
RB	-.007	.456	.499	.532								●
Md Wt	-.008	.584	.633	.615	.780		●	●				⊗
Bc L	-.176	.657	.637	.566	.720	.825				●		
Cb L	-.188	.536	.576	.585	.770	.824	.937			●	●	
DL	-.136	.332	.405	.551	.734	.731	.763	.913		●	●	
Zy B	-.150	.519	.507	.629	.725	.753	.808	.845	.812		●	
Bc B	-.074	.496	.548	.615	.766	.775	.793	.860	.805	.842		
Bc C	.094	.249	.457	.743	.506	.478	.612	.663	.623	.653	.604	

European muskrat from the age aspect. I—IV age classes. classes, with $P_{0.05}$ level, is given on the left side of each diagram.

ZyB and *CbL* increase evenly with the animals' age. It would therefore appear that the importance of *ZyB* has hitherto been overestimated as a character assisting in identifying the age of muskrats. A low taxonomic value is a character common to all quotient indices calculated in the present study. The linking of curves of distributions of variation for the different indices in different age classes is evidence of the early formation of the skull in the muskrat and the relatively slow increase in its

dimensions over the age of 3 months. It would therefore appear that skull indices based on any skull dimension characters of the muskrat are of no diagnostic value when identifying the age of older animals.

Age changes accompanying the process of growth of the skull in these animals is, however, very clearly evident in the qualitative differentiation of correlation structures corresponding to age classes.

The matrix of correlations for skull dimensions of muskrats in age class I is distinguished by a large number of high values for correlation

8.3

$r \geq 0.287$

	IC	RB	Bc B	Zy B	Md Wt	DL	Cb L	Bc L	Bc H	Bc C	Md TRL	Mx TRL
IC												
RB	-.018		●	●	●	●	●	■	■	●	⊗	
Bc B	-.005	.827		●	●	●	●	■	■	●		
Zy B	-.072	.811	.880		●	●	●	●	●	●		
Md Wt	-.023	.827	.868	.896		●	●	●	●	●	⊗	⊗
DL	-.051	.802	.866	.894	.920		●	●	●	●	⊗	⊗
Cb L	-.081	.812	.890	.899	.910	.953		●	●	●	⊗	⊗
Bc L	-.081	.774	.871	.870	.866	.877	.971		●	●	⊗	●
Bc H	-.037	.707	.792	.857	.813	.833	.829	.815		■	⊗	
Bc C	.306	.554	.556	.590	.520	.507	.513	.499	.729		■	
Md TRL	.059	.424	.395	.343	.440	.392	.445	.459	.408	.398		■
Mx TRL	.038	.320	.407	.346	.437	.308	.451	.529	.361	.398	.722	

Fig. 8. Continued.

coefficients. The majority of the measurement characters of the skull are reciprocally very closely connected, forming a compact block, with the sole exception of IC (Fig. 8.1). This also becomes clearly marked on that part of the curve corresponding in this age class to intrapleiad connections (Fig. 9). In the youngest animals we have to do with one, exceptionally widely extended pleiad of higherly correlated characters and with one independent pleiad — IC (Fig. 10). In addition CbL is a central character grouping 5 characters in a radiating pattern round it (Fig. 11). The high

correlation of skull dimensions in age class I can be explained by the fact that growth in the various parts of the skull takes place synchronously without causing any great changes in reciprocal proportions. The majority of the characters are thus distinguished by isometric increase.

In age class II there is a clearly visible change in reciprocal relations between the various dimensions of the muskrat's skull. This is expressed in reduction in the number of high coefficients of correlation in favour of increase in medium and low coefficients. A high degree of correlation

8.4

$r \geq 0.205$

	IC	Bc C	Bc B	Bc H	Zy B	R B	Md Wt	DL	Cb L	Bc L	Mx TRL	Md TRL
IC												
Bc C	.272		●	■	■	■	■	■	●	●	×	
Bc B	.010	.566		■	■	■	■	■	■	●		
Bc H	.056	.619	.673		■	■	■	■	■	●		
Zy B	.103	.614	.749	.724		■	■	■	■	■		
R B	-.007	.408	.732	.716	.702		■	■	■	■		
Md Wt	.034	.421	.645	.751	.768	.799		●	■	■		
DL	.010	.523	.695	.697	.774	.721	.788		■	■		
Cb L	-.097	.524	.695	.698	.744	.743	.801	.905		■		
Bc L	-.142	.484	.593	.569	.644	.644	.703	.677	.904		×	
Mx TRL	-.269	.078	.188	.211	.183	.275	.382	.180	.367	.482		■
Md TRL	-.154	.171	.251	.253	.153	.250	.378	.135	.278	.381	.695	

Fig. 8. Continued.

in muskrats in age class II is exhibited only by *CbL*, *DL* and *BcL* and *ZyB* and *BcB* (Fig. 8.2). The peak of the curve corresponding to intra-pleiad connections has clearly shifted in the direction of lower values of correlation coefficients (Fig. 9). In addition a certain »thinning« of a correlation relationships of craniometric characters can be observed on the correlation circle. The pleiad of strongly correlated characters decreases in capacity, taking in only 6 of them in its scope. This is accompanied by the formation of 6 independent pleiads (Fig. 10). The sequence of cor-

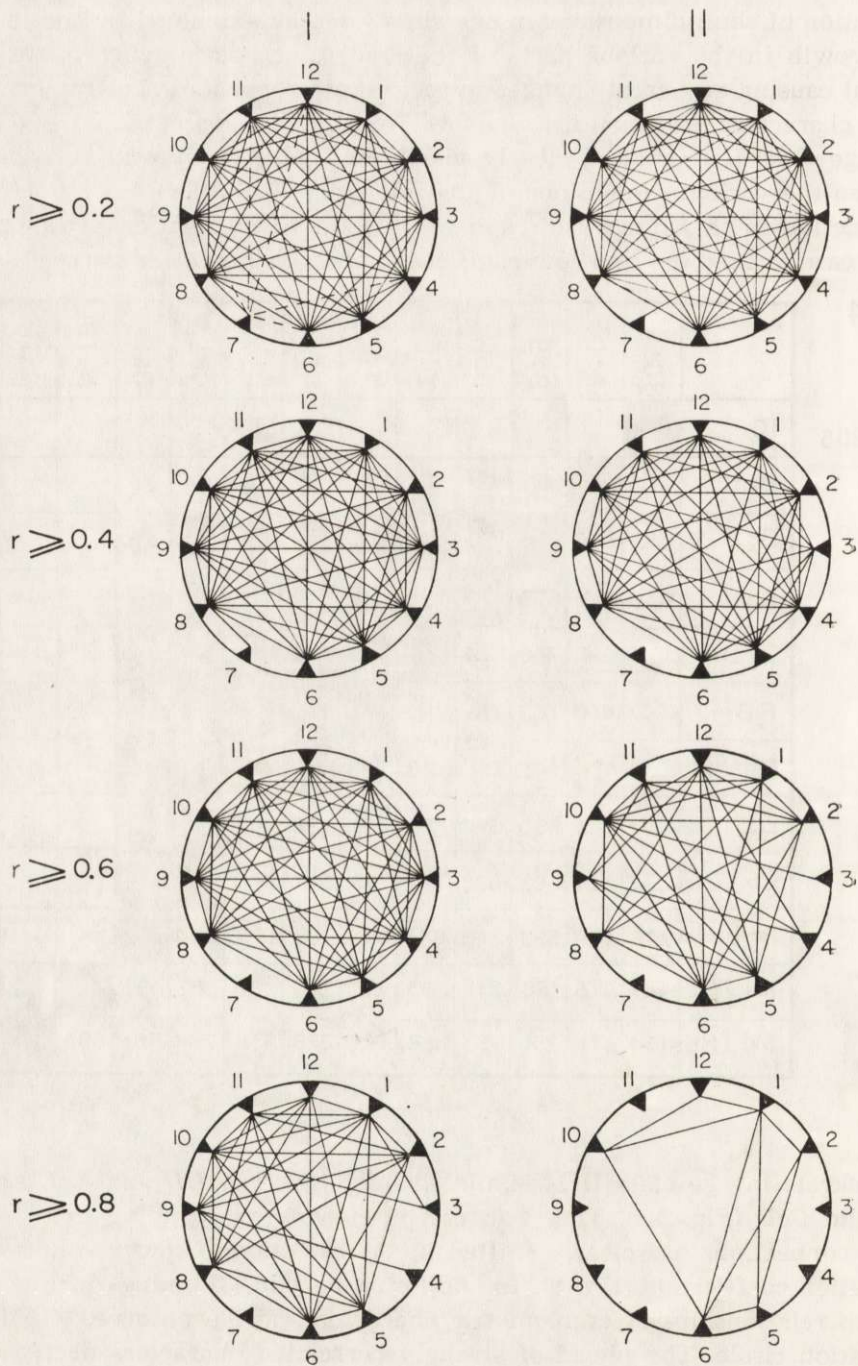
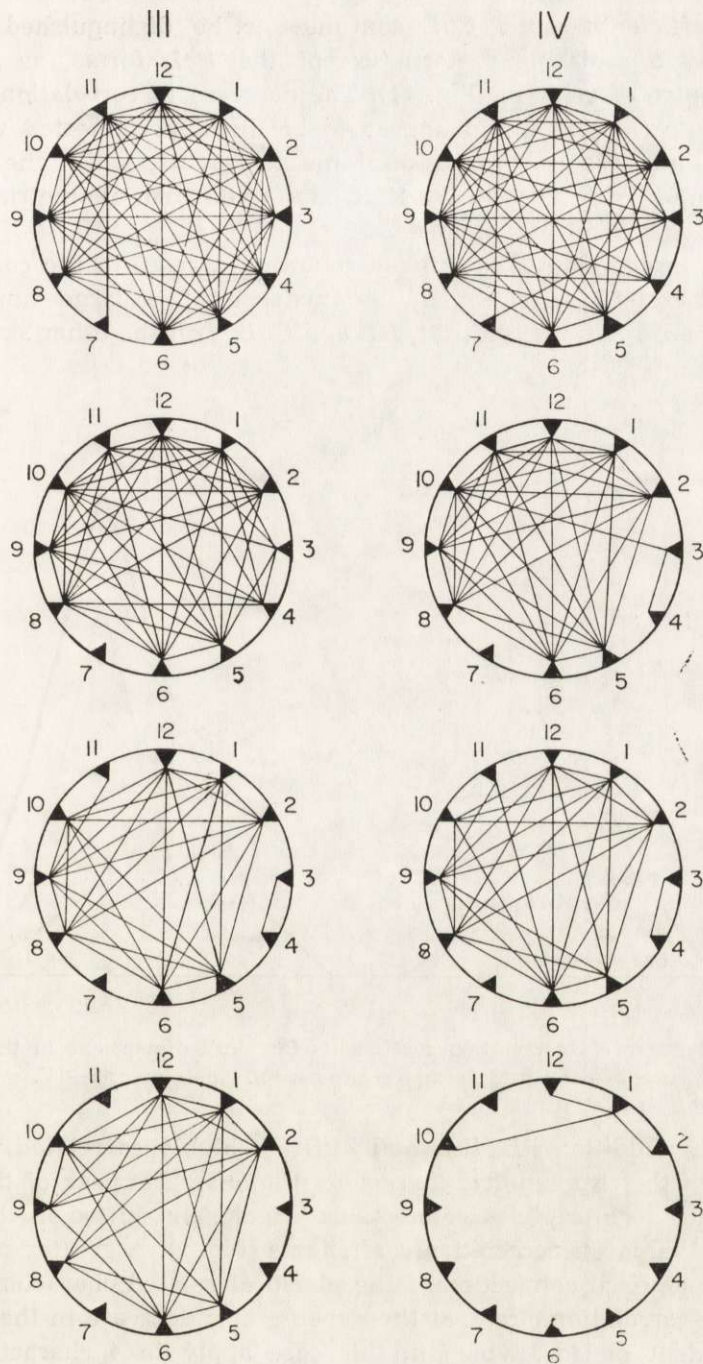


Fig. 10. Age variations in correlation structures of skull dimensions in the Central European muskrat presented in correlation circles with increasing levels of cor-



relation of the characters. Dotted line indicates correlation coefficients not significant when $P_{0.05}$. Symbols as for Fig. 5.

relation coefficients round *CbL* continues to be distinguished in this age class by a radiating pattern, except that *BcL* forms, as it were, a second centre of relation (Fig. 11). The decrease in correlation of characters in age class II would appear to be directly connected with the more rapid increase in certain skull measurements, while the rate of growth of others slows down. We thus have to do with allometric growth involving a change in proportions.

Muskrats in age class III exhibit a renewed increase in the correlation of skull dimensions, expressed in the existence of a large number of high degrees of relation — *MdWt*, *DL* and *CbL* with the other skull mea-

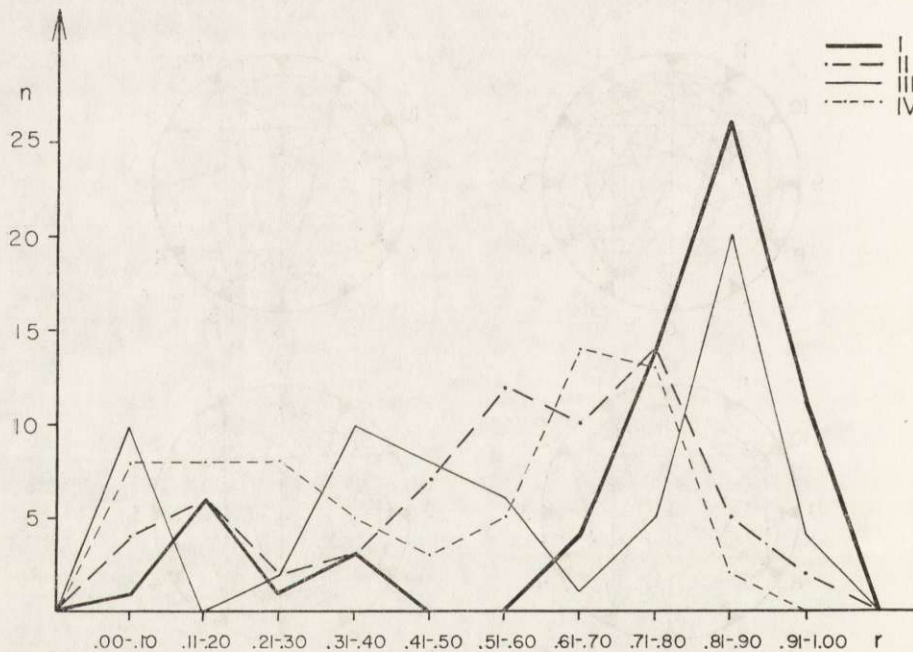


Fig. 9. Frequency of 66 correlation coefficients for skull dimensions in the Central European muskrat from the age aspect. Age classes I—IV.

surements. In addition *RB*, *BcB* and *ZyB* are highly correlated with the remainder of the craniometric characters (Fig. 8.3). The peak of the curve corresponding to intrapleiad connections has clearly shifted in the direction of high values of correlation coefficients (Fig. 9). A greater scope and degree of reciprocal connection of the pleiad of related characters can be seen on the correlation circle, at the expense of a decrease in the number of independent pleiads, which in this case apply to 4 characters only (Fig. 10). The correlation structure of skulls in muskrats in age class III is distinguished by disappearance of the radiating pattern in the order of

sequences of correlation coefficients. Although *CbL* continues to be a central character, it groups only 4 components round it (Fig. 11). The rise in correlation of the characters of muskrat skulls in age class III indicates that there is a renewed and synchronous increase in its various parts.

Musk rats in age class IV, that is, animals over one year old, and older animals, are distinguished by a correlation structure of the skull exhibiting renewed reduction in the correlation of characters. The maximum degree of correlation with the remaining skull dimensions in the oldest animals is exhibited by: *MdWt*, *DL* and *CbL*. Similarly, but to a lesser degree, *RB ZyB* and also *BcB* and *BcH* are still correlated with the other characters (Fig. 8.4). The peak of the curve corresponding to intrapleiad connections

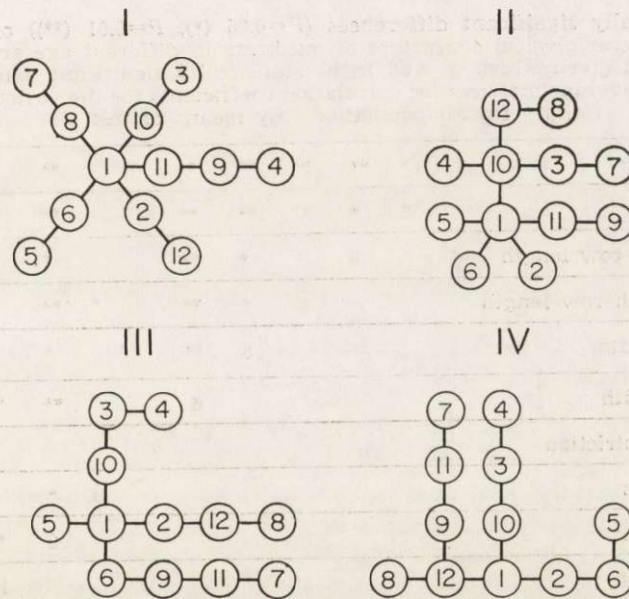


Fig. 11. Age variation in correlation structures of skull dimensions in the Central European muskrat, presented in the form of chains, after V y h a n d u (1964). Symbols as for Fig. 5.

has shifted in the direction of low values of correlation coefficients (Fig. 9). A pleiad of related characters of exceptionally small scope, taking only four characters (*CbL*, *DL*, *BcL* and *MdWt*) can be seen on the correlation circle corresponding to muskrats in age class IV. The other craniometric characters form independent pleiad (Fig. 10). In the oldest muskrats, in comparison with age class I there is considerable increase in the number of independent pleiads, resulting in decrease in the capacity of the pleiad of related characters, whereas the reverse situation is found in age class I. In age class IV disappearance of characters grouped round

CbL continues and *MdWt* becomes the second central character (Fig. 11). A change in the relations between skull measurements in the oldest animals shows that in the case of the muskrat the skull exhibits a constant, although slow growth, particularly clearly marked in *MdWt* and *CbL* (Table 2).

Age differentiation in the correlation structures of skull measurements in the muskrat has also been confirmed by the existence of a certain number of statistically significant differences between corresponding pairs of correlation coefficients compared through all age groups (Table 7). No significant differences were observed only in the degree of cor-

Table 7

List of statistically significant differences ($P=0.05$ (*), $P=0.01$ (**)) of correlation coefficients for craniological characters of muskrats in different age groups. Differences have been given which proved to be statistically significant when tested for homogeneity of average matrices for correlation coefficients for the various age groups (jointly for all populations) by means of test χ^2 .

Cb length	1	*	**	**	**	**	**	**	**	**	
Diastema length	2	*	**	**	**	**	**	**	**	**	
Maxillary tooth-row length	3			*	**	*	*	**	*		
Mandibular tooth-row length				4	*	**	*	**	*	*	
Brain-case breadth					5	**	*	*		**	
Zygomatic breadth						6	**	**	**	**	
Interorbital constriction							7				
Rostrum breadth							8	*		**	
Brain-case height								9	**	**	
Brain-case length									10	**	
Brain-case capacity										11	
Mandible weight											12

relation of *IC* with the other characters of the skull. Only three significant differences were found in the correlation of *RB* with *MdTRL* and *BcH* and with *BcC*. The degree of correlation of the other craniometric characters in the muskrat in the age aspect were more or less significantly differentiated (Table 7).

To sum up it may be said that differentiation in the correlation structures of skull dimensions in the muskrat from both the age and population aspects is manifested in the following forms:

1. In the different pattern of curves for correlation connections (Fig. 4 and 9);
2. In the different order in which characters leave the pleiad as the level of their relation rises and in the consequent different number of related and independent pleiads, and also their qualitative composition (Fig. 5 and 10);
3. In the different order of distribution of relations of characters in the form of a chain (Fig. 11);
4. In statistically significant differences between coefficients of correlation (Table 6 and 7).

4. DISCUSSION

4.1. Influence of Seasonal Generations and Sex Dimorphism on Body Size

At least two kinds of factors — differences between generations and differences connected with sex dimorphism — may affect the dimensions of animals forming a given age class within a given population.

The influence of the generation is particularly clearly evident in the morphological differentiation of the spring and autumn generations in *Micromammalia* (Adamczewska, 1959; Adamczewska-Andrzejewska, 1971; Haitlinger, 1962, 1965; Schwarz *et al.*, 1964; Kubik, 1965; Zejda, 1971 and others). This phenomenon has also been observed in amphibious rodents. Panteleyev & Terehina (1968) found this in *Arvicola terrestris* (Linnaeus, 1758) and, *inter alia*, Smirnov & Schwarz (1959) and Petrov (1967) in the muskrat.

It is difficult to give an exact reply to the question as to what extent these factors may affect skull size in the muskrat. The results of studies on captive individuals of *Microtus gregalis* Pallas, 1779, showed that differences in body and skull proportions occurred between animals of uniform size but born at different times of the year (Schwarz, 1959). It is known that the relation between skull size and body length is to a very great degree directly proportional in the aquatic-terrestrial forms of rodents. Its value expressed in correlation coefficient is $r = 0.82$ (Gould & Kreeger, 1948) in the muskrat and $r = 0.95$ in *Arvicola terrestris* (Kubik, 1957). This would point to the possibility of the body dimensions of these animals being directly conditioned by habitat influences, which are also evident in skull size.

In Wasilewski's opinion (1960) the skull is less plastic than the internal organs and its dimensions may be affected by conditions acting chiefly during the period of juvenile development and for a relatively

short time. It may therefore be considered that if there is in fact a generation influence on the muskrat's skull dimensions, it is probably not so strongly marked under the conditions of a temperate climate. It may also be partially effaced by heterogeneity of the material composing the given age class. Generally speaking the variations in craniometric characters (C. v.) in our material are slight, which justifies the conclusion that it is fairly homogeneous.

Sex dimorphism in the muskrat's skull measurements is only faintly marked. In the first two age classes no differences at all were found in skull size between males and females, and in the case of adolescent and fullygrown muskrats in age groups III and IV only the average values of certain of the skull measurements were significantly higher in males.

Author's opinions are divided on the subject of sex dimorphism in the muskrat's skull dimensions. Gould & Kreeger (1948), who examined numerous series of muskrats in Louisiana, found slight but statistically significant differences in the larger skull dimensions of males. Similarly Sather (1956) found higher average values for male skull dimensions. Pietsch (1970), on the other hand, did not find dimorphic differences in skull measurements of muskrats from either North America or Europe. Neither Lavrov (1953) nor Cygankov (1955) refer to sex differences in the muskrat's skull measurements.

It is likely that the degree of differentiation in skull dimensions depending on sex changes with age in the muskrat. Increase in the number of differences between the sexes depending on age is also known to occur in the skull of *Apodemus flavicollis* (Melchior, 1834) — Adamczewska (1959), whereas in the case of *Citellus suslicus* (Gueldenstaedt, 1770) sex dimorphism in skull dimensions is evident from an early age onwards (Surdacki, 1958).

The muskrat's skull is thus distinguished by a slight degree of differentiation in dimensions depending on sex, and this degree depends to a great extent on the quality of the given sample. This is most certainly a characteristic feature of all voles, in some of which no dimorphic differences are found in skull dimensions (Wasilewski, 1956a, b; Gęb-czyńska, 1964, 1967).

4.2. Growth Rate of the Skull in Muskrats and Other Species

Differences in the size and duration of the life span in different species of rodents, and also different ways of classification according to age, make it impossible to carry out exact comparisons of changes in their skulls with growth.

A character which alters very intensively with age in the muskrat is *MdWt*, in which there is a 46% increase in age class IV. This is confirmed

by earlier data, which show that in the muskrat the skull increases its mass with age (Gould & Kreeger, 1948) and its bones gradually thicken (Cygankov, 1955).

Characters exhibiting less intensive age increase are for instance *DL* and *RB* (18⁰/o), and then in turn *ZyB* (16⁰/o) and *BcB*, and also *CbL* (14⁰/o). The dimensions of the brain-case of the muskrat increase in a very similar and even manner (11⁰/o). A feature which they have in common is the small range of variation and continuous way in which this process takes place. Of the four dimensions of the brain-case it is only *BcB* which is distinguished by the greatest increases, which to a great degree is dependent on development of the bony crest on *sutura lambdoidea*. The formation of angularities on the skull with age is known to occur in other species of voles also (Wasilewski, 1956a, b; Gębczyńska, 1964, 1967). In the muskrat *BcC* increases successively as the animals age, and a similar tendency to increase as the muskrat ages is observed in the weight of the brain (Rejmov, 1966). The minimal range of variations in Hrdlička-Kočka's index would also appear to point to the considerable stability of brain-case dimensions in the muskrat (Fig. 7.4), although this index in *Soricidae* was subject to considerable seasonal fluctuations in connection with flattening of the brain-case in these mammals during the autumn-winter period (Pucek, 1963). The slight flattening of the skull in rodents with age, which is particularly clearly marked in *Pitymys subterraneus* (de Sélys Longchamps, 1835) — Wasilewski (1960), does not occur in the muskrat.

The other skull dimensions in the muskrat change very slightly with age, within limits of 2—4⁰/o, this applying to both *MxTRL* and *MdTRL*. Age changes in length of tooth rows, which in the muskrat are minimal, are more distinct in mice of the subgenus *Sylvaemus* Ognev & Vorobiev, 1923, in which it is even possible to observe a tendency to decrease in their length with age (Haitlinger & Ruprecht, 1967; Haitlinger, 1969). The skulls of representatives of *Lagomorpha*, on the other hand, are distinguished by considerable increases with age in the tooth rows (Empel, 1957; Caboń-Raczyńska, 1964b). The small changes taking place in *IC*, which decreases with age in the muskrat, are confirmed by the earlier data given by Cygankov (1955). This character is also proper to the skull of other species of rodents, both *Muridae* (Adamczewska, 1959; Dynowski, 1963; Haitlinger, 1962, 1969) and *Microtidae* (Wasilewski, 1952, 1956a, b; Gębczyńska, 1964, 1967; Haitlinger, 1965).

The variations within C. v. found for the majority of the craniometric dimensions in the muskrat are similar to those observed earlier in other species of mammals (Yablokov, 1966). A character of the skull in the

youngest animals are the relatively high values of the coefficient of variation, which decreases with age. High C. v. values characterizing skull dimensions in the youngest animals should, in Yablokov's opinion, be explained as due to lack of uniformity in conditions for growth and development of the various individuals composing this age class.

According to C y g a n k o v (1955) the basic growth in the majority of skull measurements in the muskrat ends when the animal reaches the age of 18 months. S m i r n o v & S c h w a r z (1959) and also P e t r o v (1967) consider that young muskrats cease growing in the second year of life. It would therefore appear justifiable in our case to accept a similar age, or even slightly younger, as the lower limit for age class IV. Regardless of the above finding, the assumption put forward by G o u l d & K r e e g e r (1948) that the muskrat's skull, like that of other species of rodents (cf. also S e r a f i ń s k i, 1955) is distinguished by age changes, certain of which would appear to be continuous, would appear to be correct. The results of studies made on captive voles show that the period of intensive increase in skull measurements in *Microtus agrestis* (L i n n a e u s, 1761) lasts from 9—10 months, and in *Lagurus lagurus* (P a l l a s, 1773) up to 8 months. Certain skull dimensions in these voles, such as CbL and ZyB, however, increase throughout the animal's life (G e b c z y ń s k a, 1964, 1967).

The general pattern of age changes in voles' skulls is similar to that in *Dipodidae* and *Muridae*. The slight age differentiation in average values for CbL and absence of age changes in ZyB and dimensions of the brain-case have been found both in *Sicista betulina* (P a l l a s, 1778) and in *Micromys minutus* (P a l l a s, 1778) — K u b i k (1952a, b). This shows that the basic growth of the skull in these animals takes place rapidly within a relatively short time.

To sum up it may be said that changes with age in the skull of representatives of both *Lagomorpha* and *Rodentia* are similar in general outlines, and correspond to the pattern given for the skull of voles (V i n o g r a d o v, 1921), according to which in voles the skull, during the process of ontogenetic development, exhibits only slight changes in the dimensions connected with growth of the brain, while dimensions depending on growth of the viscerocranium are subject to greater changes.

4.3. Age Differentiation in Correlation Structures of Skull Measurements

In discussions on age changes which accompany the process of formation of the skull in the ontogenesis of the given species, it is difficult to omit the question of their possible effect on the correlation structure of the skull. From earlier publications by other authors (C a b o ń - R a c z y ń -

ska, 1964a; Gerasimov, 1969), and the results presented above it can be seen that a high degree of correlation of skull dimensions occurs in young animals, but this decreases considerably in older individuals. Caboń-Raczyńska (1964a) considers that significantly high coefficients of correlation in the group of young hares can be explained by the fact that the various dimensions of their skulls are subject to a process of intensive growth to a uniform degree during this period. Reduction in correlation coefficients when the skull has taken shape in older animals may be due to inhibition of growth of certain elements of the skull with simultaneous continued increase in others.

In the case of the muskrat we have to do with a certain cyclic character of age changes taking place in the skull. Even increase in the majority of skull dimensions takes place in age classes I and III, whereas there appears to be disturbance of synchronized increase in classes II and IV, which is also evident in the reduction in strength of correlation connections.

A check was made to see whether this phenomenon is connected with differences in the growth rate of seasonal generations, such as are known to occur in other rodents (Adamczewska, 1959; Schwarz *et al.*, 1964; Adamczewska-Andrzejewska, 1971; Zejda, 1971 and others). Muskrats in age class II (92% of all individuals) were obtained during the period from September to December, and were thus animals from the early spring litters. Muskrats from age class III, on the other hand (79% of all individuals) were obtained during the period from April to May, and were thus animals from 9–12 months old and originated from the spring-summer period, that is, from a similar period to that of muskrats from age class II. It would therefore be difficult to connect changes in correlation structures of skull measurements, which are the expression of differences in rate of growth of the various dimensions, with the period in which the animals were born.

4.4. Interpopulation Differentiation

The most comprehensive possible analysis of the degree of differentiation in the muskrat's skull shows that there are certain differences which can be connected with the place of origin of the given animals. The greatest differences were found when comparing populations from Czechoslovakia and Pomerania. In addition to the smaller skull dimensions generally characteristic of Czech muskrats over the range of all age classes, a character differentiating them from the other Polish populations was also formed by its different proportions evident as from age class III. The number of interpopulation differences was in direct proportion to the animals' age and applied, in addition to differences in dimensions and

proportions of the skull, also to differences in correlation structures and statistical distances — shape and size.

The range of the differences found was similar to *e.g.* interspecies differences in correlation structures of the skull dimensions of 6 species of voles of the genus *Microtus* (K a n e p, 1967) or of two species of hedgehogs of the genus *Erinaceus* (R u p r e c h t, 1972).

Thus the differentiation found in skull sizes and proportions in muskrats applies to a great extent to differences between the Czech and Polish

Table 8

Ranges of variations in skull and body dimensions of muskrats in age class IV from Poland (Skull dimensions — given jointly for the Kujawy, Pomeranian and Białystok populations. Body measurements — for the Kujawy and Białystok populations jointly). Average values of dimensions for the various populations are given in Table 4.

Measurements	n	Min. — Max.
Cb length	91	58.2 — 68.8
Diastema length	102	19.6 — 26.2
Maxillary tooth-row length	105	14.0 — 17.2
Mandibular tooth-row length	107	13.8 — 16.7
Brain-case breadth	95	23.8 — 30.3
Zygomatic breadth	95	33.6 — 42.9
Interorbital constriction	105	5.4 — 7.4
Rostrum breadth	97	11.9 — 15.5
Brain-case height	95	16.0 — 19.5
Brain-case length	94	34.7 — 40.0
Brain-case capacity	88	4.0 — 5.8
Mandible weight	95	3.70 — 6.90
Body length	42	270.0 — 346.0
Tail length	41	208.0 — 280.0
Hind foot	42	55.0 — 74.0
Ear	25	20.0 — 27.4
Body weight	25	750.0 — 1450.0

populations, and tend in a definite direction. The size of skulls increases from south to north. G o u l d & K r e e g e r (1948) reached similar results in their studies on the muskrat from Louisiana, revealing the existence of changes with direction, expressed in increase in absolute skull dimensions from east to west. These authors assume that the differences they found may be due to habitat differences connected with changes occurring in the degree of salinity of marshes, relative abundance and kind of food and number of predators.

Skull dimensions in both Czech and Polish muskrats are clearly smaller than those of North American individuals in respect of both average values and ranges of variation (Table 4 and 8). Our results also provide

confirmation for Müller's earlier data (1952/53) relating to comparative studies on skull size in muskrats from Germany and North America.

The results given by Petrov & Krasnikova (1970) also point to the existence of population differences in this species, as they show that body weights and skull dimensions of this species from the central regions of the Soviet Union are distinguished by maximum values, whereas skull dimensions decrease in northern and southern regions. The differences evident in the case of skull proportions also, consisting *inter alia* in reduction in the index of diastema length and increase in index of rostrum breadth from south to north, is caused in Petrov & Krasnikova's opinion by increasing length of the period during which the muskrat lives under ice. Taking the degree of differences found between populations it is now possible to distinguish three forms of muskrat in the Soviet Union: subarctic, central and southern.

The results of craniometric studies presented here show that the muskrat's skull is subject to considerable changes over the current geographical range of this species. Authors of various studies most often limit themselves to establishing the presence of certain differences, without attempting to explain their possible genesis. Unfortunately in the majority of cases there were no complex ecological studies aimed at tracing the possibility of individual and joint influence of various habitat factors on the animal's organism and linking them with the results of morphological studies.

When attempting to interpret these differences it is necessary to take into consideration the degree of isolation of a given population, the food resources of the habitat and the effect of climatic factors and of vertical distribution. The small dimensions and different proportions of the skull in muskrats from the Central Bohemian Highland region are accompanied by the highland character of the area and the poor habitat from the food aspect. This population has remained, in relation to Polish muskrats, under the influence of some degree of isolation and in comparison with the latter exhibit greater morphological differences. Muskrats from lowland areas, living in the fertile valley and the estuary of the Vistula, are larger. These two populations are less isolated and consequently exhibit smaller reciprocal differentiation. The more isolated Białystok population living, in comparison with the remainder, under conditions of far longer winters, is accompanied by a greater number of differences in skull proportions and increased rostral breadth.

Differences between populations from Czechoslovakia and Pomerania are also evidenced in the greater percentages of increases in the skull dimensions of the latter population. Our results thus confirm the data given earlier by Petrov (1967, 1969) and Petrov & Krasnikova

(1970), who found that the rate of growth in young muskrats increases from south to north.

Pietsch (1970) considers that climate may be a decisive selective factor in the directional changes in the muskrat's skull size, but the trends observed do not follow Bergmann's rule.

Cerevitinov (1970) is of the opinion that both temperature and food are factors affecting variations in body dimensions in introduced species during their adaptation to new conditions. Studies on the muskrat in different parts of the Soviet Union have shown that this animal attains maximum body dimensions in zones where the average January temperature is from -18° to -19°C . In very cold and in warm regions the muskrat's body size decreases, in accordance with what is known as Terentjev's optimum rule. The temperature factor may thus play a part in extensive regions with a wide variety of climatic conditions.

In discussions on the possible effect of ecological conditions on morphological variations in the muskrat landscape variation also deserves mention. According to Pantel'ev (1968) »landscape variation is a particular form of variations in animals in space, manifested typologically in different landscape populations during the process of adaptation to a similar habitat«. A »landscape population« thus reflects its typological adaptations to the complex of similar conditions occurring both in different geographical regions and also in parts of the same region. The body size of different populations of *A. terrestris* is connected, according to Pantel'ev (1968), with the different degree of their connection with a water habitat. The greater the degree of this connection, the greater the animal's dimensions and *vice versa*.

It would appear that similarity of habitat conditions may be the reason why slight interpopulation differences occur. In our case this certainly applied in the two Vistula populations of muskrats from the Kujawy and Pomeranian regions. The other two populations — Czech and Białystok — came from more differentiated habitats, which was simultaneously manifested in their greater morphological differences.

It is difficult, on the other hand, to look for the genesis of differences in skull size of muskrats from the various populations, in our case, in the different degree to which water plays a part in the habitats in which they live. The muskrat is an animal sufficiently closely connected with a water habitat for this connection to limit the range of its occurrence.

To sum up it may be said that the morphological differences shown above in the skull of muskrats from different populations depend to a great degree on the complex effect of habitat factors, the degree of differentiation of the habitat and its isolation. The length of time which elapsed from the moment of the muskrat's original introduction to the

time these rodents made their appearance in a new habitat may also be of some significance here. The increasing number of differences found in our studies with increasing distance from the initial population and invasion of new areas would appear to be primarily due to adaptational changes.

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ZMIENNOŚĆ KRANIOMETRYCZNA ŚRODKOWOEUROPEJSKICH POPULACJI
ONDATRA ZIBETHICA (LINNAEUS, 1766)

Streszczenie

Na kolekcjach czaszek piżmaków, *O. zibethica* z czterech środkowoeuropejskich populacji ($n = 352$) zbadano wpływ dymorfizmu płciowego i miejsca pochodzenia zwierząt na wymiary (Ryc. 1) i proporcje czaszki. Badano także związki korelacyjne wymiarów czaszki w aspekcie wiekowym i populacyjnym. Jako miarę różnicowań populacyjnych przyjęto odległość statystyczną — kształtu i wielkości, wyrażoną w jednostkach odchylenia standardowego badanych cech.

Czaszka piżmaka odznacza się niewielkim zróżnicowaniem wymiarów związanym z dymorfizmem płciowym, zwiększającym się z wiekiem zwierząt. Średnie wartości pomiarów absolutnych samców były istotnie większe tylko w 8 przypadkach na 48, zaś średnie wskaźników czaszkowych były w 3 na 32 istotnie wyższe u samic. Z wyjątkiem jednego indeksu wykazane różnice nie były wysoko statystycznie istotne ($0.05 > P > 0.01$).

Piżmaki pochodzące z trzech polskich populacji różnią się w porównaniu ze zwierzętami z Czech środkowych istotnie większymi rozmiarami (Ryc. 2), intensywniejszym tempem wzrostu (Ryc. 3) i wynikającymi stąd odmiennymi proporcjami czasz-

ki. Stwierdzono także odrębności w strukturach korelacyjnych wymiarów czaszki u zwierząt pochodzących z różnych populacji (Ryc. 4 i 5), jak i zróżnicowania w odległościach statystycznych. Liczba stwierdzonych różnic rośnie z wiekiem zwierząt i w miarę przestrzennego i czasowego oddalenia od populacji z Czech — najbliższej miejsca pierwotnej introdukcji piżmaka w Europie (Tabela 4, 5 i 6).

Zmiany wiekowe przejawiają się w stosunkowo niewielkich przyrostach w obrębie mózgowcaszki (Ryc. 6, Tabela 2) i znacznie silniej w trzewioczaszce.

Intensywny wzrost większości wymiarów czaszki kończy się w drugim roku kalendarzowym życia zwierząt, z tym jednak że pewne z nich, takie jak: ciężar żuchwy, długość diastemy, Cb oraz szerokość rostrum i jarzmowa odznaczają się jeszcze przyrostami w IV klasie wieku. (Tabela 2, Ryc. 7).

Zróżnicowane tempo wzrostu wymiarów czaszki piżmaka znajduje swe odzwierciedlenie w zmianach współczynnika zmienności (Tabela 4) oraz w strukturach korelacyjnych, odpowiadających grupom wieku. W klasie I i III obserwujemy znacznie wyższe współzależności wymiarowe cech niż w II i IV (Ryc. 8, 9, 10 i 11). Świadczy to o przemienności okresów bardziej synchronicznego wzrostu czaszki i pewnej jej stabilizacji. Synchroniczny wzrost czaszki odpowiadałby wzrostowi izometrycznemu, a okresy stabilizacji odznaczałyby się wzrostem allometrycznym, pociągającym za sobą zmiany w proporcjach czaszki.