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Correlations of skull measurements in the postembryonic development of the house sparrow *Passer domesticus*

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Age-related differences in correlations of 11 skull measurements were analysed for house sparrows of the Białowieża population. Differences were found in the curves of frequency distribution of correlation coefficients for three age-classes. Correlations of skull measurements were lower in house sparrows as compared with mammals. The pattern of skull development in some mammals (lagomorphs, rodents, carnivores, and even-toed ungulates) was characterized by a high correlation of skull measurements in youngest animals, gradually declining with age, thus reaching lowest values in oldest animals. An opposite pattern was found for the house sparrow. The lowest correlations of skull measurements were observed in youngest birds, and higher in older age classes.

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Корреляции между измерениями черепа домашнего воробья *Passer domesticus* в постэмбриональном развитии

Исследована возрастная дифференциация корреляции 11 промеров черепа у беловежской популяции домашнего воробья. Констатирован отличающийся ход кривых распределения коэффициентов корреляции для трех возрастных классов. Констатировано также, что зависимость промеров черепа у домашнего воробья в зависимости от возраста ниже, чем у млекопитающих. По сравнению с млекопитающими у домащнего воробья наблюдаются тенденции к обратной зависимости, то-есть самые низкие коэффициенты корреляции между отдельными измерениями констатировались у самых молодых особей, более высокие в старших группах.

INTRODUCTION

Age-related qualitative changes in skulls of birds have been known for a long time and they consist in increasing pneumatization of the *fornix* bones. Much later it has been realized that they are accompanied by some changes in skull size (LINSDALE 1928, ILYICHEV 1962, RUPRECHT 1968), and *fornix* thickness (DANILOV 1964, WINKLER 1979), coupled with changes in the brain-case (RUPRECHT 1968, WINKLER 1979). Processes of skull growth in birds are very rapid due to an early obliteration of the skull sutures.

Correlations of skull measurements and some postcranial bones were the subject of few morphological analyses (Latimer 1938, Latimer and Asling 1938, Latimer and Wager 1941). Their objective was to assess the degree of relation of skull weight and length to other parts of the skeleton.

The knowledge of age-related changes in skull size and proportions in relation to the degree of skull ossification inclined the author to analyse the effect of this process on the correlations of skull measurements.

MATERIAL AND METHODS

The material consisted of 90 skulls of *Passer domesticus*, including 45 males and 45 females, collected in Białowieża during November 1965 to June 1966. Following the method of Nero (1951), the material was segregated into three age-classes: I — about 43 days old*, II — 124–186 days, and III — more than 240 days of age, represented by 30, 28, and 32 skulls, respectively. The male to female ratio in these age-classes was as follows: I — 15 : 15, II — 17 : 11, and III — 13 : 19. Because differences in skull measurements between the sexes were small and differences in the calculated correlation coefficients were insignificant, the two sexes were combined for further analysis.

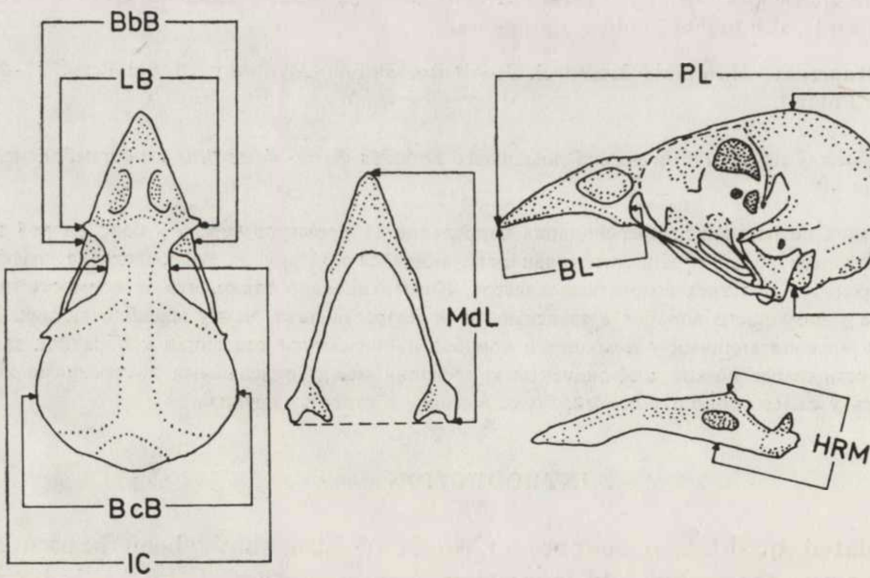

Fig. 1. A scheme for skull measurements in the house sparrow.
PL — profile length, BcB — brain-case breadth, BL — bill length, BbB — bill base breadth, LB — lacrymal breadth, IC — interorbital constriction, BcH — brain-case height MdL — mandible length, HRM — height of *ramus mandibulae*. After RUPRECHT (1968).

* "Age-class I" consisted of birds of the first brood that hatched at the turn of April and then were captured on the same date (June 13, 1966).

A total of 9 linear skull measurements were taken with callipers to the nearest 0.1 mm: 1) profile length (PL), 2) brain-case breadth (BcB), 3) bill length (BL), 4) bill base breadth (BbB), 5) lacrymal breadth (LB), 6) interorbital constriction (IC), 7) brain-case height (BcH), 8) mandible length (MdL), and 9) height of *ramus mandibulae* (HRM) — (Fig. 1), and also two weight-capacity measurements: 10) mandible weight in milligrams (MdWt), and 11) brain-case capacity in millilitres (BcC). These measurements were used as a basis for computing correlation coefficients. They are denoted by the same symbols as in an earlier paper (RUPRECHT 1968). The 11 measurements were correlated in all the possible combinations. For three age-classes they formed three correlation matrices made up of 55 correlation coefficients each. The corresponding pairs of correlation coefficients were compared with each other by means of the formula

$$t = (r_1 - r_2) \cdot \sqrt{\frac{n_1 + n_2 - 4}{1 - (r_1 - r_2)^2}}$$

in age-classes I and II, and II and III, at two significance levels: $P_{0.05}$ denoted by + and $P_{0.01}$ denoted by ++. For a better illustration of the differences in the correlations, the pleiad correlation method of TERENTJEV (1960) was used. It is based on a circle divided into parts the number of which corresponds to the number of measurements, and correlations between these measurement are given by the chord.

RESULTS

Since the number of correlation coefficients in the matrices was high, they were comparatively analysed in three aspects.

Analysis of the frequency distribution of correlation coefficients

The number of statistically significant correlation coefficients in the matrices for three age-classes was 17, 28 and 26, respectively ($P < 0.05$, critical value of $r \geqslant 0.3494$). Correlations of skull measurements for the youngest birds (age-class I) contain the smallest number of significant correlations as compared with those for maturing (age-class II) and adult (age-class III) birds. This is clearly shown by the curves of frequency distribution of correlation coefficients in relation to age (Fig. 2). The largest differences in these curves were found between age-classes I and II.

Analysis of correlation pleiads of TERENTJEV

For age-class I, the pleiad of measurements correlated at the highest level consists of PL, BcH, and MdL, also of BcC and BcB. Thus, all the three measurements of brain-case (breadth, height, and capacity) are highly correlated.

And so are the length measurements. These characters vary synchronously, thus they are correlated to the highest degree. The other characters form independent pleiads comprising BL, BbB, LB, IC, HRM, and MdWt (Fig. 3).

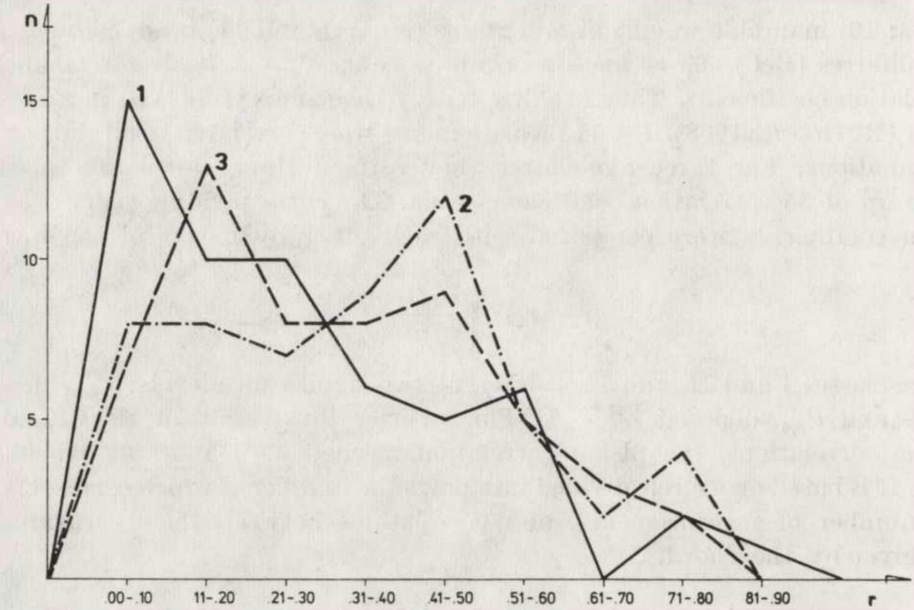

Fig. 2. Frequency distribution of 55 correlation coefficients for different age classes of the house sparrow.
1 — age-class I, 2 — age-class II, 3 — age-class III. Numbers (n) in classes of the variability of correlation coefficient r.

In the next stage of the postembryonic development of house sparrow skulls, that is, in age-class II, three pleiads of highly correlated measurements can be distinguished, with somewhat distinct characteristics. The first pleiad consists of PL, BL, and MdL, the second is made up of BcB, BcH, and BcC, and the third comprises only two components: BbB and LB. For birds with almost completed ossification of the brain-case, the pleiad comprising profile length and mandible length also contains bill length. The pleiad of measurements characterizing the brain-case remains closely correlated in the form of a triangle. A new pleiad is formed, made up of the bill base breadth and lacrymal breadth. The number of independent pleiads is reduced to IC, HRM, and MdWt (Fig. 3).

Age-related changes in the correlation of skull measurements for birds of age-class III, thus with a completely pneumatised brain-case *fornix*, consist in the presence of two independent pleiads of dependent measurements. They are qualitatively similar to the pleiads for age-class II, but differ in the degree of measurement correlation. The first pleiad consists of PL, BL, and MdL, which are correlated in the form of a triangle. The second comprises BcB, BcC, and BcH. In these birds a synchronous growth of the profile length, bill length, and mandible length is continued, and the three measurements of the brain-case are also highly correlated. The third pleiad, containing bill breadth and lacrymal breadth in birds of age-class II, disappears, and, consequently, the number of independent pleiads increases, comprising BbB, LB, IC, HRM, and MdWt (Fig. 3).

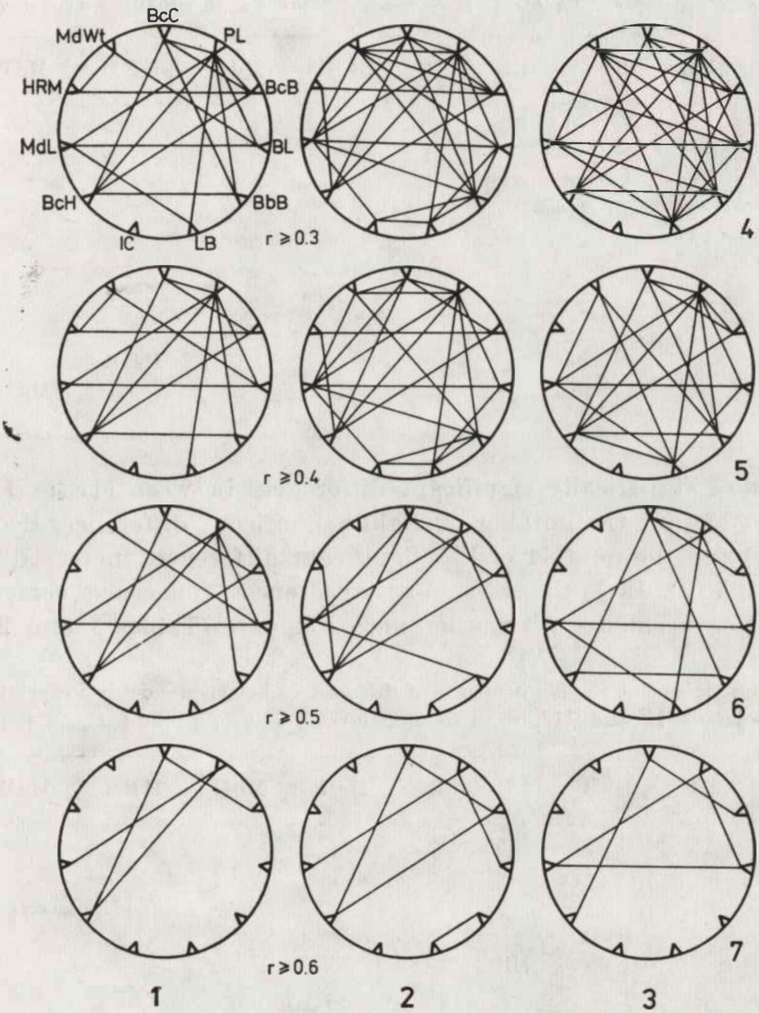

Fig. 3. Correlations of 11 skull measurements in relation to age of the house sparrow. 1 – age-class I, 2 – age-class II, 3 – age-class III, 4–7 – levels of correlation: $r \geqslant 0.3$, 0.4, 0.5, and 0.6. The circle is divided into 11 sections containing skull measurements denoted by the symbols in the described order. For symbols explanation see Fig. 1.

Analysis of age differences

To get a more complete picture of age-related differences, corresponding pairs of correlation coefficients were compared for classes I and II and for classes II and III.

The first comparison revealed 11 differences, including 7 highly significant ($P < 0.01$) and 4 significant ($P < 0.05$) ones (Table 1). In the second comparison

Table 1. A comparison of the significance of differences between correlation coefficients for age-classes I and II. Significance levels: $P_{0.05}$ (+) and $P_{0.01}$ (++)

PL	BcB	BL	BbB	LB	IC	BcH	MdL	HRM	MdWt	BcC
PL										
	BcB									
		BL								
			BbB	++	++	+	+			
				LB	++				+	
					IC		++			++
						BcH		++		
							MdL			++
								HRM		
									MdWt	+
										BcC

the number of statistically significant differences between classes II and III increased to 13, but the number of highly significant differences decreased to 4 ($P < 0.01$) and the number of less significant differences increased to 9 ($P < 0.05$) (Table 2). In both cases most differences concerned correlations of brain-case measurements with other measurements (Tables 1 and 2).

Table 2. A comparison of the significance of differences between correlation coefficients for age-classes II and III. Significance levels: $P_{0.05}$ (+) and $P_{0.01}$ (++)

PL	BcB	BL	BbB	LB	IC	BcH	MdL	HRM	MdWt	BcC
PL					+					
	BcB	+				+				
		BL						+		
			BbB		++	++				
				LB	+	+				+
					IC				+	+
						BcH		++		
							MdL			++
								HRM		
									MdWt	
										BcC

DISCUSSION

Obliteration of the sutures of the skull in birds has an important effect in the process of its development, limiting it basically to early stages of the postembryonic development. This is so because in addition to absorbing mechanical shocks, skull sutures are zones of growth of skull bones (Nikityuk 1965). Further changes in the skulls of birds consist in the ossification of the *fornix* bones, leading to the development of a double (two-layer) *fornix*. Although these changes occur in the already formed skull, their effect can be seen, *e.g.* in an increased thickness of the *fornix* (Danilov 1964, Winkler 1979), also in the total reduction of skull capacity with age (Ruprecht 1968, Winkler 1979), and in a slight increase in other skull measurements (Linsdale 1928, Ilyichev 1962, Ruprecht 1968). The picture of changes in the skull of the house sparrow is completed with changes in the correlations corresponding to the age groups distinguished.

According to Kamshilov (1941) an organism is a system of interrelated complexes, and its evolution is related to two opposite processes: differentiation (associated with specialization of parts or organs) and integration, leading to an increasing interdependence of these differentiated components, subordinated to the organism as a whole. Also Olson and Miller (1958), when introducing the concept of morphological integration, express its actual state by means of the so-called integration coefficient. In their opinion, this coefficient can reflect the phases of both increase and decrease, related to alternate effects of integration systems involved in growth. The phase of increasing effects of integration systems corresponds to the concept of ontogenetic autonomy. According to Yegorov (1979), the increasing autonomy of ontogeny leads to increased correlations among characters within specified morphological systems and, at the same time, to decreased correlations among complexes of characters in later stages of ontogeny. In this way intra-pleiad and inter-pleiad connections are produced, which can be revealed by correlation analysis of different morphological structures, *e.g.* the skull.

These is a clear inverse relationship between the degree of correlation of skull measurements in the house sparrow and their percentage increases with age. An example of such a relationship is the so-called dependent pleiads, comprising characters having low percentage increases with age, and, on the other hand the so-called independent pleiads, involving characters with highest percentage increases. The dependent pleiads for compared age-classes usually contain profile length, bill length, mandible length, and measurements of the brain-case. The independent pleiads usually include mandible weight, height of *ramus mandibulae*, interorbital construction, bill base breadth, and lacrymal breadth. The first four measurements of the house sparrow skull are characterized by the highest percentage growth with age, coming up to 24.0, 8.2, 5.6, and 4.2 %, respectively (Ruprecht 1968). Growing so rapidly, these characters do not change synchronously in relation to other skull dimensions. The result is an increasing disproportion between these characters and the other ones, and this is reflected in a small number of high correlations. Thus, the mechanisms of the recorded age-related differences can be explained as follows. A decrease in the number of high correlations in age-class I is the result of uneven, allometric growth (see age-related changes in skull indices by Ruprecht 1968). Skulls of birds of the age-classes II and III seem to grow more evenly, isometrically, producing a large number of high correlations of skull measurements.

Age-related changes in skull growth were well characterized by Sych and Sych (1975). They analysed the effects of the mechanisms of morphological integration, measuring them by the correlation of skull measurements in the steppe leming. They distinguished three categories of situations in terms of the correlation coefficient:

1. no correlation between two characters for all age-classes or a very weak correlation, approaching significance for one or two groups;

2. a high correlation between two characters at least for two age groups, not exceeding 0.70;

3. a correlation between two characters higher than 0.70 at least in one age group.

Thus, some skull measurements are not correlated in the available age groups, reflecting different stages of postembryonic development. An example of such a character is the postorbital breadth of the skull in the mink. Its low correlation with other measurements was explained by Yegorov (1979) to be the result of its earlier formation, while other parts continue their growth. This is related to the effect of a highly specialized nervous tissue of the brain, playing the role of an inductor in the formation of some skull parts.

Differences in skull correlations between mammals and birds consist in a higher correlation of measurements in mammals. First of all they seem to stem from differences in growth rate of the skull in representatives of these two vertebrate classes. Mammal skulls grow longer than bird skulls. Although the age classes distinguished here for house sparrows and the compared mammals correspond to each other, it cannot be excluded that these classes contain groups differing in the degree of their individual development. Sych and Sych (1975) put in question the usefulness of correlation for classification because "... fluctuations in the values of correlation coefficients in different developmental stages lead all attempts at classification to the comparison of analogical age groups, which in practice can rarely be done in view of species-specific differences in life span and in growth rate". Not denying the validity of this reservation it should be stated that, independent of different conditions, skull correlations in lagomorphs, carnivores, rodents, and even-toed ungulates behave in a similar way. The pattern of skull ontogeny in these mammals involves a high correlation of measurements for youngest animals (Fig. 4) which gradually decreases, reaching the lowest degree in oldest animals (CABOŃ-RACZYŃSKA 1964, RUPRECHT 1974, BUCHALCZYK and RUPRECHT 1977, KOBRYŃCZUK and ROSKOSZ 1980). As compared with mammals, correlations of skull measurements for house sparrows show an opposite tendency, that is, the lowest correlations for youngest birds and the highest for older age groups (Fig. 2). This indicates that there must exist some deeper causes of these differences.

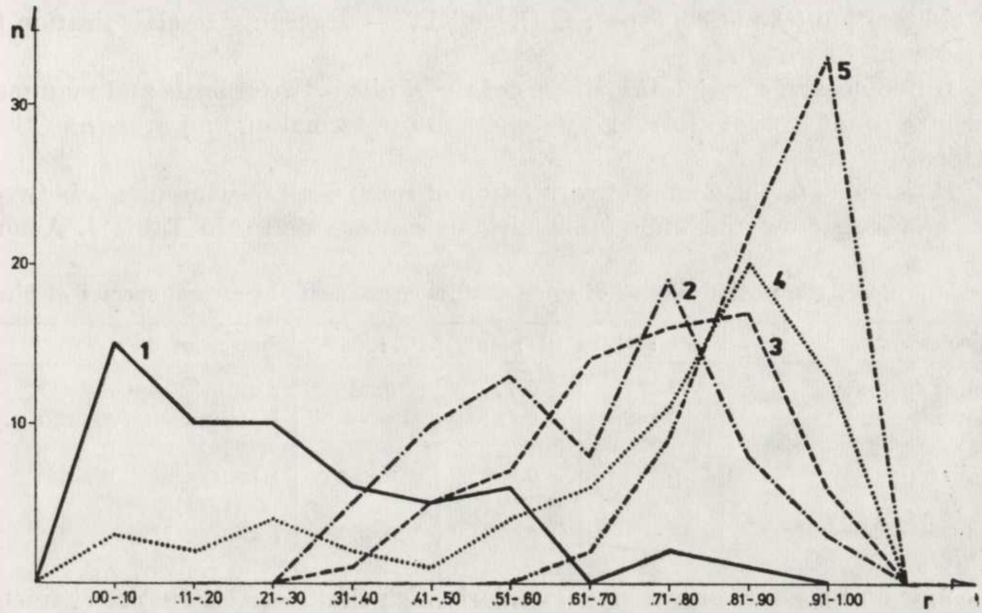

Fig. 4. Frequency distribution of correlation coefficients in age-class I for the house sparrow (1) as compared with the frequency distribution of correlation coefficients for the youngest age classes of some mammals: european hare (2) — after CABOŃ-RACZYŃSKA (1964), common polecat (3) — after BUCHALCZYK and RUPRECHT (1977), muskrat (4) — after RUPRECHT (1974), and european bison (5) — after KOBRYŃCZUK and ROSKOSZ (1980).
The correlation matrix for the house sparrow consists of 55, and those for each mammal species of 66 correlation coefficients.

Distinct correlation patterns for birds and mammals were also obtained by other authors. LATIMER and ASLING (1938), who analysed correlations between skull weight and the weight of six long bones in the mourning dove, obtained mean $r = +0.473$, as compared with $r = +0.8$ for mammals (the muskrat and skunk). LATIMER and WAGER (1941) found a similar regularity when comparing analogous correlations for the mallard and cat.

Although the mammals compared with the house sparrow represent rather distant taxonomic units, their correlations are very similar in the youngest age groups. According to NIKITYUK (1965), the reason for this convergence lies in the fact that they represent the same obliteration type III, which is characterized by the preponderance of longitudinal over transverse suture obliteration.

Both the european hare and the european bison belong to the subtype A, in which *sutura sagittalis* is most obliterated, and the degree of its obliteration increases from the anterior to the posterior parts of the skull. The muskrat and the common polecat represent the subtype B, in which *sutura metopica* is most obliterated, and the degree of obliteration of *sutura sagittalis* increases from the posterior to the anterior parts of the skull. Further studies are needed to explain skull correlations for other mammal species, depending on the type of obliteration (the other types: I, II, and IV — according to classification by Nikityuk 1965).

Differences in correlation patterns of the skulls between birds and mammals seem to result first of all from differences in the formation and growth of their skulls.

Differences in the degree of correlation of some skull measurements between the house sparrow and some other bird species are shown in Table 3. Among

Table 3. Correlation coefficients *r* of some skull measurements in several species of birds

Species	PL : BL	PL : MdL	PL : MdWt	Source of data
house sparrow	0.61	0.77	0.38	Author's own data
mourning dove	0.369	0.481	—	Latimer and Asling (1938)
mallard	0.983	0.980	0.814	Latimer and Wager (1941)
red-tailed hawk	—	0.823	0.660	Latimer (1938)

the four bird species compared, particularly high skull correlations are characteristic of the mallard and the red-tailed hawk. As compared with them skulls of the house sparrow and mourning dove show a lower correlation of the measurements analysed here.

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STRESZCZENIE

[Wiekowa zmienność zależności korelacyjnych wymiarów czaszek *Passer domesticus*]

Do analizy użyto 90 czaszek *Passer domesticus* — 45 samców i 45 samic z Białowieży, zebranych w okresie od listopada 1965 do czerwca 1966 r. Na podstawie metodyki NERO (1951), materiał podzielono na trzy klasy wieku: I — około 43 dni ($n = 30$, w tym 15 samców i 15 samic), II — 124–186 dni ($n = 28$, w tym 17 samców i 11 samic), III — ponad 240 dni ($n = 32$, w tym 13 samców i 19 samic). Na każdej z czaszek wykonano 9 pomiarów liniowych z dokładnością do 0,1 mm: 1 — długość profilu (PL), 2 — szerokość puszki mózgowej (BcB),

3 — długość dzioba (BL), 4 — szerokość podstawy dzioba (BbB), 5 — szerokość lakrymalna (LB), 6 — szerokość międzyoczodołowa (IC), 7 — wysokość puszki mózgowej (BcH), 8 — długość żuchwy (MdL), 9 — wysokość *ramus mandibulae* (HRM) — ryc. 1, oraz dwa pomiary wagowo-objętościowe: 10 — ciężar żuchwy w miligramach (MdWt) i 11 — pojemność puszki mózgowej w mililitrach (BcC). Ze względu na niewielki stopień zróżnicowania dymorficznego wymiarów czaszek *P. domesticus* i nieistotne różnice płciowe w obliczonych współczynnikach korelacji, obie płci w dalszych rozważaniach traktowano łącznie. Kolejność, określenia i sposób wykonania pomiarów są takie same jak we wcześniejszej pracy (Ruprecht 1968).

Wartości 11 pomiarów korelowano na zasadzie każdy z każdym, zestawiając dla trzech klas wieku 3 macierze współczynników korelacji liczące po 55 współczynników każda. Porównując krzywe rozkładu frekwencji współczynnika korelacji w trzech klasach wieku, stwierdzono maksymalną liczbę wysokich współczynników *r* u ptaków z II i III klasy wieku (ryc. 2). Analiza najwyższego poziomu zależności badanych cech ($r \geqslant 0,6$) przy użyciu metody plejad korelacyjnych Terentjeva wskazuje, że we wszystkich trzech klasach wieku w skład tzw. plejad cech zależnych wchodzą zawsze: PL i MdL oraz trzy wymiary puszki mózgowej (BcB, BcH i BcC) — ryc. 3. Cechy te odznaczają się jednymi z najniższych przyrostów procentowych z wiekiem, co jednocześnie wskazuje na zasadnicze ich ukształtowanie we wczesnym etapie ontogenezy. Natomiast, cechy tworzące tzw. plejady niezależne, jak: MdWt, HRM, IC i BbB wykazują największe przyrosty procentowe z wiekiem. Wzrost ich połączony jest ze zmianą proporcji względem cech pozostałych (allometryczny), co bezpośrednio uwidacznia się w obniżeniu liczby wysokich zależności korelacyjnych (ryc. 3). Realność różnic wiekowych między parami współczynników korelacji odpowiadających klasom wieku została potwierdzona wykazaniem 11 statystycznie istotnych różnic z porównania I i II klasy wieku (tabela 1) oraz 13 z porównania II i III klasy wieku (tabela 2).

Wymiary czaszek wróbla domowego są skorelowane odmiennie niż u ssaków. U ptaków najmłodszych (I klasa wieku) obserwuje się małą liczebność wysokich współczynników korelacji, która wzrasta u ptaków starszych (II klasa wieku) i dorosłych (III klasa wieku). U ssaków pochodzących z różnych rzędów obserwuje się jako prawidłowość tendencję odwrotną (ryc. 4).

Porównując ze sobą korelacje niektórych wymiarów czaszki (długość profilu z długością dzioba, żuchwy z ciężarem żuchwy) u przedstawicieli wróblowatych, gołębi, blaszkodziobych i drapieżnych, stwierdzono dość duże różnice w stopniu wzajemnego skorelowania tych cech (tabela 3), wskazujące na istnienie między przedstawicielami tych rzędów specyficznych odrębności.