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**Correlation Structure of Skull Dimensions in European Hedgehogs**

[With 3 Tables &amp; 7 Figs.]

Variations and correlations of 12 linear measurements, and also variations of the rostral angle and maxillary index of skulls of two species of European hedgehogs — *E. roumanicus* (n=133) and *E. europaeus* (n=74) were examined. Correlation connections between different skull measurements were plotted on Czekanowski's diagrams and the correlation structures of the two species compared by two methods: Terentjev's correlation pleiads and Vyhandu's. Considerable differences were found in the correlation structure of the skull. The indicator-characters of the skull: condylobasal length and zygomatic breadth — exhibit different degrees of connections with the other skull measurements in both of these hedgehogs. Tendencies to intraspecies variation were common in the two forms: montane individuals were larger than lowland hedgehogs. Perhaps these differences are connected with ecological conditions of hedgehog habitat.

## 1. INTRODUCTION

The systematic classification of hedgehogs occurring in Europe is distinguished by the existence of several subspecies, which may be due to the extensive range of these mammals (cf. Ellerman & Morrison-Scott, 1951). The more or less clearly marked variations in the position and shape of the bones of the *viscerocranium* (maxilla, nasal), in the ranges of both the western and eastern hedgehogs have become, in addition to other morphological characters, a basis for differentiating between subspecific forms of a decidedly local character (Barrett-Hamilton, 1900; Stein, 1929/30 and others). As early as 1900 Lönnberg adopted a critical attitude towards the taxonomic characters used at that time, and questioned the usefulness of the shape of *proc. frontalis maxillae*. He simultaneously showed, using as an example the Swedish subspecies, *Erinaceus europaeus typicus* Barrett-Hamilton, 1900, that variations in this character may be very considerable, since he found

three different types of formation of these processes in this subspecies, characteristic of the *typicus*, *occidentalis* and *roumanicus* forms.

The maxillary index points, *inter alia*, to a certain degree of difference in the skull structure of *Erinaceus europaeus* Linnaeus, 1758 and *Erinaceus roumanicus* Barrett-Hamilton, 1900 (Herter, 1938 and 1952; Stein, 1929/30; Rödl, 1966). Recently the result obtained by Rödl (1966) show that in addition to differences in the values of the maxillary index, the skulls of the two hedgehogs also differ concerning the values of the parietal and nasal indices. Rödl (1966) did not, however, obtain complete differentiation of the two species of hedgehog in Czechoslovakia on the basis of the accepted skull criteria despite the fact that karyological analysis subsequently indicated their separate character (Král, 1967). It may be considered that skull indices for the two species of *Erinaceus* possess a relative taxonomic value depending to a considerable degree on their individual variations and the locality from which the study material was obtained. It would also appear that the degree of differences in the taxons compared does in fact seriously affect the practical usefulness of skull indices. This seems to confirm the results obtained by Zaidova (1961) regarding the differences in skull indices in the genera *Hemiechinus* and *Erinaceus*.

In order to define the differences between skull measurements which are not of diagnostic values the correlation structures based on these characters was examined and the degree of their differentiation in two species of hedgehog — the »western« (*E. europaeus*) and the »eastern« (*E. roumanicus*). In addition an attempt was made to estimate the ranges of variations in the skull material of both species of hedgehog by regional analysis.

It would also appear useful to simultaneously employ several ways of presenting differences and similarities in the correlation structures of skull measurements in diagram form (Czekanowski, 1913; Terentjev, 1943, 1960; Vyhandu, 1964). Terentjev's method of correlation pleiads has frequently been applied in craniometric studies from the systematic aspect (Rossolimo, 1962; Kanep, 1967), and also variability aspect (Caboň-Raczyńska, 1964; Gerasimov, 1969). The hierarchical treatment of interrelations between characters makes it possible to choose, from a large number of closely correlated dimensions, the indicator-character which consequently describes the other characters with which it is connected. This arrangement of correlations corresponds, after Terentjev, to intra-pleiad connections. Further degrees of interdependence of characters as their correlation decreases constitute independent groups of mixed and finally interpleiad connections, of which the latter cannot be described by means of their correlation with other dimensions. Accord-

ing to Terentjev there are independent pleiads which, together with dependent pleiads, estimate the taxonomic value of characters.

## 2. MATERIAL AND METHODS

The material used consisted of 207 hedgehog skulls (133—*E. roumanicus* and 74—*E. europaeus*) from Europe, originating from collections in the British Museum in London, the Zoological Museum of the Humboldt University in Berlin, the Institute of Zoology, Polish Academy of Sciences in Warsaw, the Institute of Zoology of the Academy of Sciences of the USSR in Leningrad and the Institute of Zoology, Lomonosov University in Moscow. Use was also made of hedgehog skulls from Poland, chiefly those in the collections of the Mammals Research Institute, Polish Academy of Sciences, at Białowieża. It must be emphasised that the material was not at all of a uniform quality, since it had been obtained from different parts of the ranges of these two species and consequently contained specimens belonging to different populations. The material was divided into the two species on the basis of known morphological criteria (Herter, 1938; Rödl, 1966) and analysed only from the aspect of the differences between them.

Among the skulls used for analysis were those of adult and old animals of both sexes and also specimens of unidentified sex, and in this connection it is necessary to bear in mind the possibility of variations in age affecting the correlation structure of skull measurements (cf. Caboń-Raczyńska, 1964).

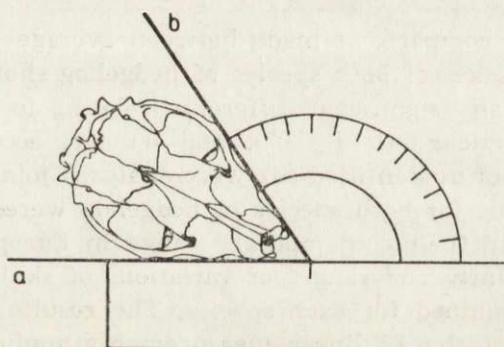


Fig. 1. Method of measuring rostral angle of hedgehog skull.

a — fixed arm, b — movable arm of protractor.

Twelve linear measurements accurate to 0.1 mm were made on the skulls, defined as follows: (1) Cb., (2) length of upper tooth row (from  $I^1$ — $M^3$ ), (3) mandibular length (from the internal margin of alveolus  $I_1$  to the end of *proc. articularis*), (4) mastoidal breadth, (5) zygomatic breadth, (6) maximum breadth of nasals, (7) postorbital breadth, (8) maximum length of nasales, (9) height of skull *per bullae*, (10) height of *ramus mandibulae* (from *inc. praeangularis mandibulae* to apex of *proc. coronoideus*), (11) length of neurocranium (Cb. minus palatine length), (12) palatine length (from incisure on prosthion to staphylion).

In addition the rostral angle of *pars facialis* was measured in the frontal plane by inserting the rostra of the skulls in the opened arms of a suitably modified

protractor. When making this measurement the skull was in contact horizontally with the two arms of the protractor in two places: lateral points on the margins of intermaxillare and the same on *proc. zygomaticus ossis maxillaris* (Fig. 1). Maxillary indices were calculated for the majority of the material, i.e., ratio of length of maxilla on the suture (from the apex of *proc. nasalis ossis intermaxillaris* to the end of *proc. frontalis ossis maxillaris*) and its height (from the apex of *proc. nasalis ossis intermaxillaris* to the external edge of alveolus  $P^1$ ).

Means ( $\bar{x}$ ), standard deviations (*SD*) and coefficients of variation (*C.v.*) were calculated for these craniometric values which were examined for possible sexual dimorphism for each species as well as for differences between populations within the given species. Skull measurement values were subjected to analysis of variance and tested for significance by the *F* Snedecor test at the  $P=.05$  and  $P=.01$  levels. In addition each craniometric measurement was correlated with each of the others, obtaining a correlation matrix for the two species, each of which consisted of 66 coefficients *r*. The correlation matrix was examined for existence of differences in the correlation structures of skull measurements in the two species. Significance of differences between corresponding pairs of correlation coefficients for both species was defined by the usual methods, accepting the two levels of probability stated above.

### 3. RESULTS

#### 3.1. Interspecies Similarities and Differences

The result of the comparisons made between average skull measurements for the two sexes of both species of hedgehog showed that there is only one statistically significant difference relating to the postorbital breadth in *E. roumanicus* ( $.01 < P < .05$ ), and on this account skulls of males, females, and of unidentified sex were analysed jointly.

The series of skulls for both species of hedgehog were obtained from different localities in their contemporary range in Europe. They were, however, treated jointly and ranges of variations of skull measurement characters were examined for each species. The results given in table 1 show that none of the 12 linear measurements applied individually provides a basis for defining the species on account of the almost complete overlapping of ranges of measurements of both forms. The usefulness of the maxillary index was fully confirmed in defining the two species on this basis. The value of the rostral angle (Table 1) may also be of certain, although only supplementary, taxonomic importance.

Comparison of coefficient of variation shows that the study material varies to a slight degree only. The greatest variations in both forms were found with respect to breadth of nasals (*C.v.*=14.04 and 18.38%). The other skull measurements exhibit variation within limits of (*C.v.*=2.88—6.20%), and therefore the material may be considered relatively uniform and treated jointly for purposes of analysing correlation structures of both species. For this purpose calculation was made of the correlation

Table 1  
 Variations in skull dimensions of two species of hedgehog from Europe (data for males and females treated jointly owing to absence of sexual dimorphism).

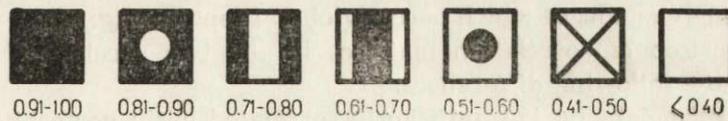
Measurement	<i>Erinaceus roumanicus</i>				<i>Erinaceus europaeus</i>			
	n	min—max	$\bar{x} \pm SD$	C. v.	n	min—max	$\bar{x} \pm SD$	C. v.
1. Cb. length	123	51.0—62.0	57.28 ± 2.07	3.61	66	50.0—65.7	56.94 ± 2.17	3.82
2. Maxillary tooth-row length	123	26.4—30.9	28.68 ± 0.92	3.21	66	25.7—32.4	28.43 ± 0.88	3.10
3. Mandible length	123	38.0—45.9	42.68 ± 1.58	3.70	66	38.4—49.3	42.69 ± 1.56	3.67
4. Mastoid breadth	123	24.3—30.5	27.91 ± 0.93	3.34	66	25.1—32.4	28.17 ± 1.31	4.67
5. Zygomatic breadth	123	30.3—38.0	34.15 ± 1.40	4.10	66	30.4—39.5	34.80 ± 1.67	4.80
6. Nasal breadth	114	1.8—5.1	3.57 ± 0.50	14.04	62	1.4—4.3	2.70 ± 0.49	18.38
7. Postorbital breadth	114	13.4—16.0	14.71 ± 0.46	3.14	62	13.1—15.4	14.32 ± 0.41	2.88
8. Nasal length	114	15.2—21.7	18.14 ± 1.12	6.20	62	14.3—21.3	17.77 ± 0.98	5.54
9. Height of skull	114	17.7—22.4	20.07 ± 0.83	4.13	62	17.6—23.2	20.26 ± 0.92	4.53
10. Height of ramus mandibulae	123	16.0—21.4	19.10 ± 1.01	5.29	66	15.8—21.7	19.38 ± 1.05	5.44
11. Braincase length	114	23.1—28.4	25.89 ± 1.01	3.93	62	21.2—27.4	24.71 ± 1.09	4.41
12. Palatine length	114	27.5—34.5	31.39 ± 1.27	4.05	62	28.8—38.3	32.27 ± 1.29	4.03
13. Maxillary index	113	1.00—1.73	1.25 ± 0.10	8.77	54	0.43—1.01	0.79 ± 0.11	14.47
14. Rostral angle	122	43.0—52.0	47.09 ± 1.75	3.73	58	45.0—57.0	50.90 ± 2.15	4.22

	Nasal breadth	Postorbital breadth	Height of skull	Mastoid breadth	Height of ramus mandibulae	Zygomatic breadth	Palatine length	Cb. length	Mandible length	Maxillary tooth-row length	Braincase length	Nasal length
	6	7	9	4	10	5	12	1	3	2	11	8
6												
7	.061			●		⊗		⊗	⊗			
9	-.104	.296		■	●	■	●	●	■	⊗	⊗	
4	.028	.521	.625		■	■	■	■	■	⊗	■	●
10	.002	.289	.609	.617		■	■	■	■	●	●	⊗
5	.097	.465	.660	.754	.747		■	■	■	●	■	⊗
12	-.011	.386	.597	.646	.710	.709		■	●	●	●	■
1	.011	.412	.581	.722	.696	.762	.918		●	●	●	■
3	-.056	.417	.642	.669	.724	.791	.843	.876		■	■	●
2	-.004	.347	.441	.487	.552	.539	.866	.837	.749		●	■
11	.036	.350	.426	.649	.518	.653	.603	.870	.714	.607		⊗
8	-.080	.340	.384	.555	.506	.424	.648	.633	.541	.625	.466	

ERINACEUS ROUMANICUS

Fig. 2. Correlation structure of

	Nasal breadth	Postorbital breadth	Height of ramus mandibulae	Height of skull	Mastoid breadth	Zygomatic breadth	Mandible length	Cb. length	Palatine length	Maxillary tooth-row length	Braincase length	Nasal length
	6	7	10	9	4	5	3	1	12	2	11	8
6												
7	326		X				●	●	X	X	●	
10	021	434			●				●	●		
9	.098	.614	700			○						
4	103	.617	594	692		○		○				X
5	235	.663	754	846	818		○	○				X
3	028	.565	.747	.803	.806	.857			○	○		X
1	129	.556	726	753	.842	861	.923			○		●
12	007	.443	.592	641	766	725	867	911		○	X	●
2	.040	489	539	621	720	668	.822	.885	879		●	X
11	262	539	684	671	680	779	705	805	.487	.607		X
8	.106	357	242	.388	435	468	459	560	536	.509	.413	



*ERINACEUS EUROPAEUS*

skull dimensions in the hedgehog.

coefficient of each linear measurement of the skull in relation to each of the other measurements, separately for *E. europaeus* and *E. roumanicus*. Due to the different number of skulls (*E. roumanicus*  $n=121$ , *E. europaeus*  $n=70$ ), among the 66 coefficients 11 were not significant in *E. roumanicus* when  $P=.05$  was accepted ( $r \geq .1946$ ). In the case of *E. europaeus* 8 coefficients ( $r \geq .2319$ ) were not significant at  $P=.05$  level, and the significance of 3 coefficients came between  $P_{.05}$  and  $P_{.01}$  ( $r \geq .3017$ ).

A total of 55 highly significant  $r$  values ( $P < .01$ ) were found for both species, which forms 83.3% of all coefficients in the correlation matrix, and thus the skull dimensions examined for the two species of hedgehog are reciprocally highly correlated.

### 3.1.1. The Czekanowski Diagram Method

The correlation matrix of skull measurements for the two species, arranged on diagrams in order of their decreasing and increasing values, clearly reveals the similarities and differences within the correlation structures of the two forms. Due to the individual arrangement of each diagram the order differs in which the examined characters occur (Fig. 2). Both species are distinguished by a different order in the arrangement of the various dimension characters on the diagrams which correspond to defined  $r$  values. Although the same number of significant correlation coefficients ( $n=55$ ) with  $P < .01$  was found for both species, the skull of *E. europaeus* is characterized by measurements correlated to a greater degree than *E. roumanicus*.

In *E. roumanicus* the compact block of characters most highly correlated with the remainder is formed by: Cb. (1), and mandibular length (3), length of upper tooth row (2) and length of braincase (11), while a second block is formed by: zygomatic breadth (5), height of *ramus mandibulae* (10) and mastoidal breadth (4).

In *E. europaeus*, on the other hand, the analogous block is formed by: Cb. length (1), palatine length (12), upper tooth row length (2), and length of braincase (11). The second block consists of mandibular length (3), zygomatic breadth (5), mastoidal breadth (4), and skull height (9). In principle therefore the arrangement of characters correlated to the highest degree can be considered as one two-winged block in *E. europaeus*, the connecting element of which is condylobasal length (Fig. 2).

Comparison of correlation matrices in the two species of hedgehogs showed the following differences:

1. Skull height (9) is significantly correlated with: postorbital breadth (7), and zygomatic breadth (5) — ( $P < .01$ ), as well as with mandibular length (3), Cb. (1) and braincase length (11) — ( $.01 < P < .05$ ).

2. Mastoidal breadth (4) is significantly correlated ( $.01 < P < .05$ ) with the mandibular length (3), upper tooth row length (2), and with Cb. length (1).

3. Nasals length (8) and height of *ramus mandibulae* (10) are significantly correlated in both species ( $.01 < P < .05$ ).

It must be emphasised that the maximum numbers of interspecific differences were found in braincase height and breadth which were significantly correlated with other skull parameters in both species (Table 2). Heretofore differences between the two species of hedgehog have been found mainly within the splanchnocranium (Herter, 1938; Röd l, 1966).

Table 2

Significance of differences between corresponding pairs of correlation coefficients in skull dimensions of the hedgehog at the .05 (\*) .01 (\*\*) level.

Measurements	1	2	3	4	5	6	7	8	9	10	11	12
1 Cb. length		×		*					*			
2 Maxillary tooth-row length			×	*								
3 Mandible length				*					*			
4 Mastoid breadth			×		*							
5 Zygomatic breadth				×					**			
6 Nasal breadth					×							
7 Postorbital breadth						×						
8 Nasal length							×					
9 Height of skull								×		*		
10 Height of <i>ramus mandibulae</i>									×		*	
11 Braincase length										×		×
12 Palatine length												×

### 3.1.2. Terentjev's Correlation Circle Method

Correlation matrices arranged on Czekanowski diagrams permit plotting frequency curves in classes of correlation coefficients for the two species. These distributions (Fig. 3) are bimodal. The group of correlation coefficients ( $r \leq .20$ ), which would correspond to interpleiad connections, is very distinct. The group of mixed connections is not distinguished in any way. Both curves gradually pass into a clearly distinguished large group including both mixed and interpleiad connections (terminology after Terentjev, 1943).

In order to avoid subjective treatment when dividing the curves into three groups of connections (Fig. 3), I used a modified form of Teren-

tjev's method (1960), in accordance with which the correlation coefficient matrix illustrating the correlation structure of a given object can be imagined as a cylinder. This cylinder is divided into parts, the bases of which form correlation circles to which increasing degrees of interdependence of characters correspond (e.g.,  $r \geq .2$ ,  $r \geq .4$ ,  $r \geq .6$  and  $r \geq .8$ ). In determining the lower limit of the range of  $r$  values of correlation coefficient significances were considered for both species (Fig. 4).

It is possible to observe species differentiation in various order and degree to which characters fall away from the pleiads as the level of interdependence of characters increases. Various correlation pleiads became separate on the level of  $r \geq .8$ , but in such cases interspecies differences were visible from the lowest levels (Fig. 4).

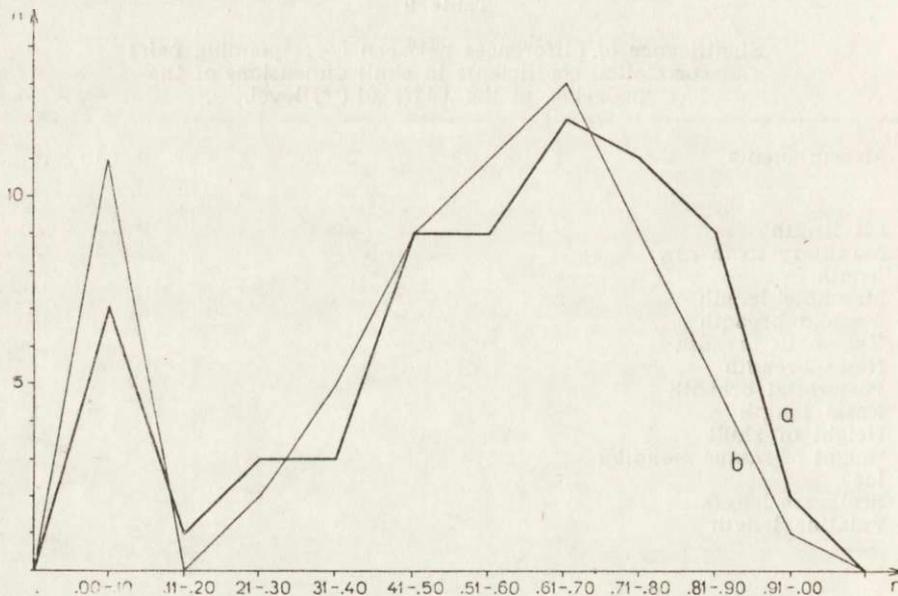


Fig. 3. Distribution of frequencies of correlation coefficients for skull dimensions in representatives of the genus *Erinaceus*.  
a — *E. europaeus*, b — *E. roumanicus*

In *E. roumanicus* the group of independent pleiads relates to the following characters: mastoidal breadth (4), zygomatic breadth (5), breadth of nasals (6) and postorbital breadth (7), and also length of nasales (8), skull height (9) and height of *ramus mandibulae* (10).

In *E. europaeus* this group has a smaller range, covering only breadth of nasals (6) and postorbital breadth (7), length of nasales (8) and height of *ramus mandibulae* (10).

One pleiad of five characters, reciprocally connected and highly inter-

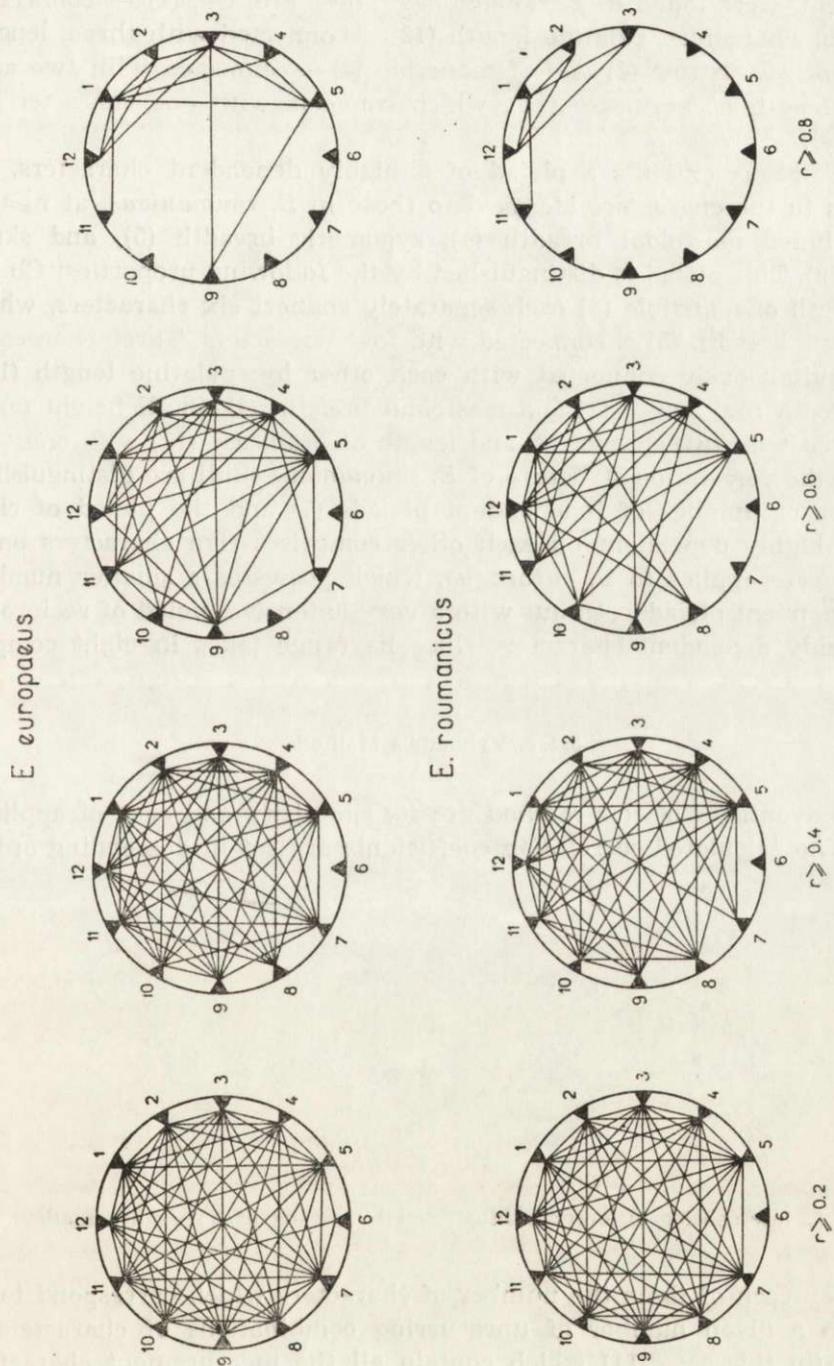


Fig. 4. Interspecies differences presented by means of Terentjev's correlation pleiad method.

dependent, were found in *E. roumanicus*. These are: Cb. (1) — connected with four characters, palatine length (12) — connected with three, length of — upper tooth row (2) and of mandible (3) — connected with two and finally length of braincase (11), which connects with one character on this level.

*E. europæus* exhibits a pleiad of 8 highly dependent characters. In addition to the characters identical to those in *E. roumanicus*, at  $r \geq .8$ , are included mastoidal breadth (4), zygomatic breadth (5), and skull height (9). This pleiad is distinguished by the following properties: Cb (1) and length of mandible (3) each separately connect six characters, while zygomatic breadth (5) is connected with four characters. Three characters are simultaneously connected with each other by: palatine length (12), upper tooth row length (2) and mastoidal breadth (4). Skull height (9) is connected with two characters, and length of braincase (11) with one.

Thus the correlation structure of *E. roumanicus* skull are distinguished by a larger number of independent pleiads (7) and the pleiad of characters highly dependent on each other comprises five characters only. The reverse applies to *E. europæus*, which possesses a smaller number of independent pleiads, (4), but with a very extensive pleiad of reciprocal and highly dependent characters since its range takes in eight components.

### 3. 1. 3. Vyhandu's Method

The advantages of this method are its simplicity and ease of application. The calculated correlation coefficients are set in descending order,

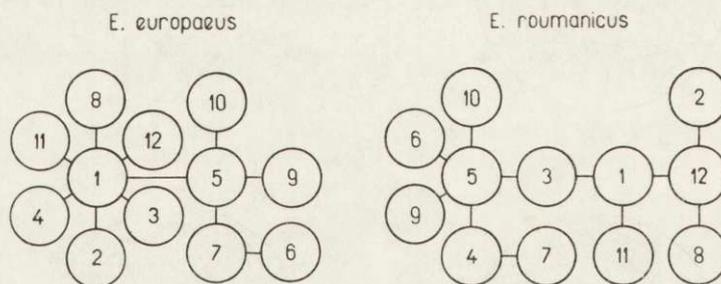


Fig. 5. Interspecies differences illustrated by means of Vyhandu's method.

giving by each of them the number of characters which correspond to it. In turn a given number of unrecurring combinations of characters is chosen (in this case, 11) which contain all the measurement characters grouped in chains used to calculate the given correlation structure.

Additionally, corresponding  $r$  values can be placed in the intervals separating the various characters, thereby forming links in the chain (V y h a n d u, 1964). In our case this value was given in the correlation coefficients matrices (Fig. 2).

The chain system formed in this way exhibits the following similarities and differences for *E. europaeus* and *E. roumanicus* (Fig. 5).

1. Four skull measurements: Cb. (1), length of mandible (3), length of braincase (11) and palatine length (12) are directly dependent in both species.

2. Cb. length (1) is maximally interdependent on the other characters in both species, except that in *E. roumanicus* it is connected with three characters, and in *E. europaeus* with as many as seven. In the latter species four other characters are connected with Cb., length: zygomatic breadth (5), mastoidal breadth (4), length of the upper tooth row (2), and nasals (8).

3. Zygomatic breadth (5) is the second character in this order exhibiting the maximum number of connections with the remainder. In *E. roumanicus* it is connected with 5, and in *E. europaeus* with 4 characters.

Thus among the interrelations of skull measurement—Cb. (1) and zygomatic breadth (5) are distinguished by the greatest number of connections with the remaining measurements in both species, and they may therefore be defined as indicator characters suitable for taxonomic purposes. On the other hand, the following can be considered as taxonomically important characters in both species either due to the absence of their correlation, or to their very slight direct connection with the remainder: length (8) and breadth of nasals (6), postorbital breadth (7), and height of *ramus mandibulae* (10).

### 3.2. Interpopulation Differentiation

Using the above characters which exhibited the maximum degree of reciprocal relation, plus one character among those which formed independent pleiads were selected. Thus in descriptions of different local populations the following were considered: Cb. length (1) and length of upper tooth row (2), length of mandible (3), zygomatic breadth (5) and height of *ramus mandibulae* (10), and also additionally the rostral angle and maxillary index. On this basis analysis was made of variations in different local hedgehog populations, simultaneously making comparisons between them. The material was divided into 7 *Erinaceus roumanicus* and 6 *Erinaceus europaeus* regional groups. The number of individuals in different populations and ranges of variations in their cranio-

Table 3  
 Variations in skull dimensions of hedgehogs from different populations.  
 Averages and standard deviations are given in first line and coefficients of variation in second line for each population.

Measurements	n	Condylobasal length	Maxillary tooth-row length	Mandible length	Zygomatic breadth	Height of ramus mandibulae	Maxillar index	Rostral angle
<i>Erinaceus europaeus</i>								
Great Britain	11	56.25 ± 1.07	28.35 ± 0.60	42.38 ± 1.29	33.51 ± 1.58	18.67 ± 0.49	0.65 ± 0.07	47.33 ± 1.37
		1.90	2.10	3.05	4.71	2.65	(n=6) 11.27	(n=6) 2.89
Italy	6	55.87 ± 0.96	27.85 ± 0.14	41.92 ± 1.06	34.27 ± 0.87	19.73 ± 1.22	0.70 ± 0.16	50.67 ± 1.21
		1.73	0.49	2.52	2.54	6.18	22.75	2.39
Switzerland	7	61.49 ± 3.47	30.93 ± 1.16	46.54 ± 2.46	37.69 ± 2.02	20.63 ± 1.31	0.72 ± 0.12	49.67 ± 1.51
		5.64	3.74	5.29	5.37	6.37	(n=6) 17.06	(n=6) 3.03
USSR (Kalinin & Moscow Palatinates)	10	55.59 ± 0.79	27.66 ± 0.46	41.51 ± 0.77	34.36 ± 1.17	19.31 ± 0.91	0.90 ± 0.07	51.60 ± 1.35
		1.41	1.65	1.86	3.40	4.73	7.73	2.62
Poland	10	57.35 ± 1.96	28.42 ± 0.73	42.60 ± 1.52	35.04 ± 1.76	19.29 ± 0.87	0.80 ± 0.12	53.17 ± 2.79
		3.41	2.56	3.56	5.01	4.51	15.23	(n=6) 5.24
Germany (GDR & GFR)	22	56.56 ± 2.72	28.20 ± 1.16	42.43 ± 1.73	34.76 ± 1.88	19.31 ± 1.24	0.85 ± 0.12	51.40 ± 2.70
		4.81	4.13	4.07	5.41	6.41	(n=20) 14.62	(n=20) 5.26
<i>Erinaceus roumanicus</i>								
Brest Palatinat (Mokuszyn)	32	57.68 ± 2.29	29.07 ± 0.90	42.85 ± 1.79	34.06 ± 1.49	19.00 ± 1.24	1.26 ± 0.14	46.41 ± 1.85
		3.98	3.10	4.19	4.38	6.51	11.00	3.98
Groznyj Palatinat	14	56.46 ± 1.73	28.41 ± 0.77	42.10 ± 1.38	33.84 ± 1.40	18.99 ± 0.90	1.25 ± 0.10	47.93 ± 1.38
		3.07	2.70	3.27	4.13	4.72	7.88	2.89
Caucasus Mts	14	57.96 ± 2.02	28.70 ± 0.87	43.50 ± 1.43	35.61 ± 1.53	19.63 ± 0.96	1.22 ± 0.10	48.50 ± 2.38
		3.49	3.04	3.29	4.29	4.88	8.01	4.90
Kirov Palatinat	12	56.11 ± 2.21	28.08 ± 0.96	41.68 ± 1.54	32.75 ± 1.44	18.33 ± 0.97	1.29 ± 0.11	46.17 ± 2.12
		3.94	3.43	3.69	4.41	5.27	8.76	4.60
Crimea	8	58.74 ± 1.67	29.14 ± 0.64	43.56 ± 1.22	35.38 ± 1.20	20.05 ± 0.59	1.33 ± 0.05	48.63 ± 1.92
		2.84	2.19	2.81	3.39	2.92	4.13	3.95
Białowieża Primeval Forest	22	56.61 ± 1.92	28.27 ± 1.08	42.37 ± 1.58	33.84 ± 1.24	18.76 ± 0.78	1.24 ± 0.09	47.14 ± 1.32
		3.39	3.81	3.73	3.66	4.15	7.15	2.80
Other parts of Poland	21	57.60 ± 2.12	28.86 ± 0.95	42.81 ± 1.58	34.21 ± 1.38	19.43 ± 1.07	1.22 ± 0.11	46.09 ± 1.04
		3.69	3.30	3.70	4.05	5.53	(n=20) 8.63	(n=11) 2.27

metric dimensions were set out in table 3. In *E. roumanicus* the local populations distinguished were from relatively limited and uniform areas (Table 3), but in the case of *E. europaeus* the term »population« meant natural groups of animals coming from territories of different countries. These local populations were thus taken as »centres« from which material was obtained on the scale of the palaeoarctic distribution of *E. europaeus*. Representatives of *E. europaeus* from the USSR were obtained from the Kalinin and Moscow palatinates, *i.e.*, from a relatively small area fully comparable in size with other territories. It is of course obvious that divisions of this type are artificial.

### 3.2.1. *E. roumanicus*

In order to obtain the most uniform groups of populations possible within the given species (bearing in mind positive correlation of the characters examined) the following procedure was adopted: (a) average values of each character from different populations were ranked; (b) the total of such ranks was calculated in each population and these totals used as a basis for accepting two possible variants of uniform groups; (c) analyses of variances were made separately for each variant.

The first variant was distinguished by the exclusion of the population from the Crimea, while the second would exclude the populations from the Crimea, the Caucasus and the Kirov regions.

Reciprocal comparison of average skull dimensions and maxillary index simultaneously in 7 populations showed statistically significant differences in all characters except for the index. Cb. length and mandible length were different ( $.01 < P < .05$ ) and the means for the remaining three dimensions differed in a highly significant way ( $P < .01$ ) — Table 3.

The first comparison shows that the hedgehog population from the Crimea differs most from the remainder. In the second comparison this population was omitted and the remaining 6 populations compared with each other. No statistically significant differences were found between average values for: Cb. length, mandible length and maxillary index. Statistically significant differences were found among of the three remaining characters ( $P < .01$ ) as in the height of *ramus mandibulae* ( $.01 < P < .05$ ).

Thus populations from the Caucasus (large dimensions) and the Kirov palatinate (small dimensions) were excluded as differing to the greatest extent.

In the third comparison only the four other populations were considered and then statistically significant differences were found only

between mean upper tooth row length ( $.01 < P < .05$ ) and the rostral angle ( $P < .01$ ).

It would thus appear that populations from the Brest region (Mokuszyn), Groznyj region, Białowieża Primeval Forest and other Polish territory from a uniform group. Individuals from the remaining populations are significantly larger (Crimea and Caucasus) or smaller (Kirov region)

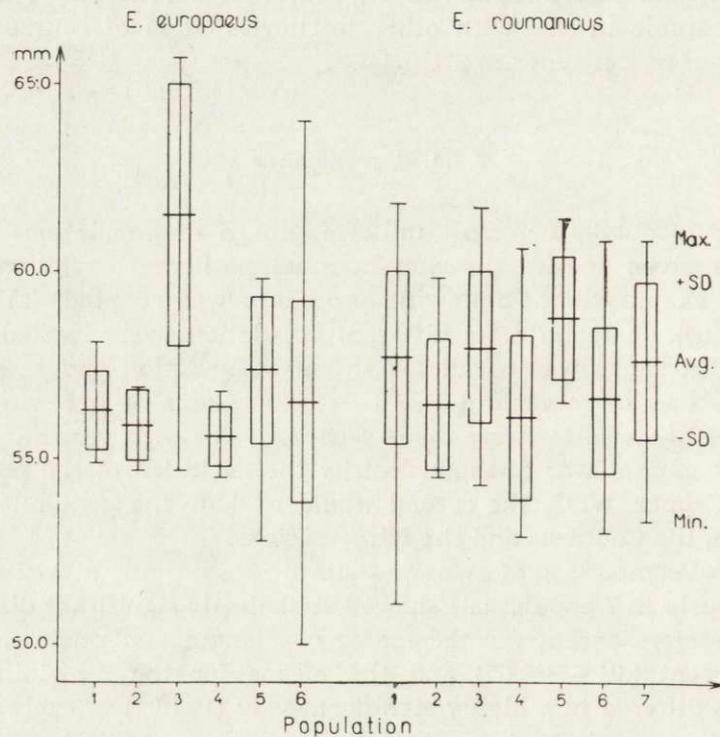


Fig. 6. Condylobasal length (Cb.) variations in both species of hedgehog from different populations.

*E. europaeus* 1—Great Britain, 2—Italy, 3—Switzerland, 4—USSR (Kalinin & Moscow Palatinates), 5—Poland 6—Germany, *E. roumanicus* 1—Brest Palatinate (Mokuszyn), 2—Groznyj Palatinate, 3—Caucasus Mts, 4—Kirov Palatinate, 5—Crimea, 6—Białowieża Primeval Forest, 7—Other parts of Poland.

than this group. Among the seven *E. roumanicus* populations those originating from mountainous areas (Caucasus, Crimea) were distinguished by the maximum skull dimensions, and this was accompanied by greater breadth of *pars rostralis* (Table 3 and Fig. 6).

3.2.2. *E. europaeus*

The rank system for average values was used also for *E. europaeus*, the totals of which indicated three variants of possible comparisons. The first of them did not consider Swiss, Polish and German populations, and in the second excluded the British, Italian and Russian populations. The third variant omitted the latter three and German populations from comparisons.

The first comparison of six populations of *E. europaeus* showed that there are statistically significant differences between them. Differences between average values for all skull measurements and for the index were highly significant ( $P < .01$ ), except for height of *ramus mandibulae* ( $.01 < P < .05$  — Table 3).

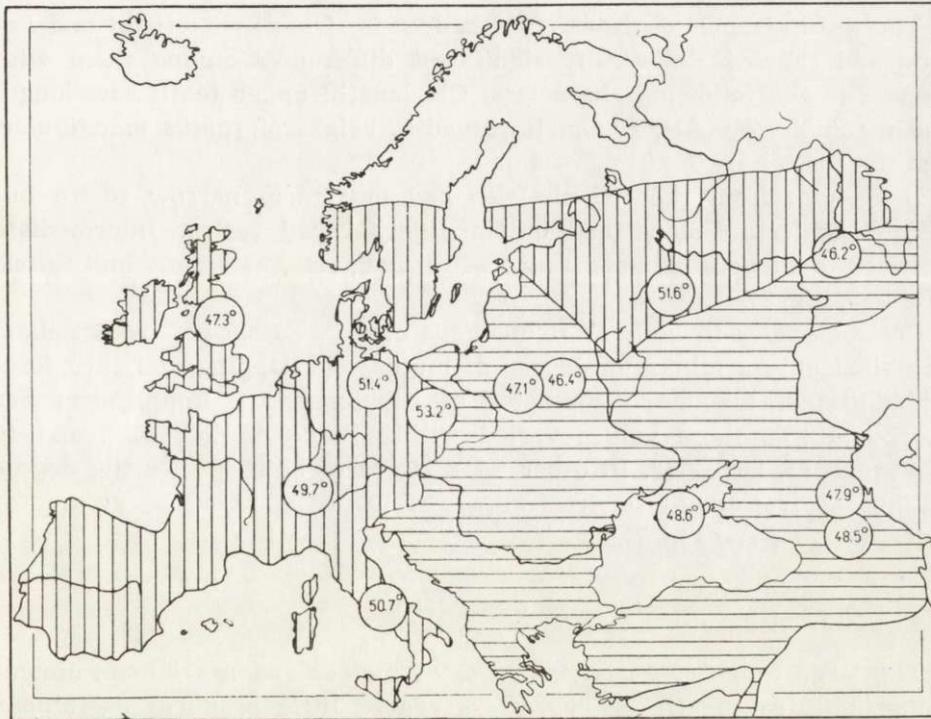


Fig. 7. Variations in rostrum breadth in both species of hedgehog from different populations (Geographical ranges after Wettstein, 1942).

Certain differences were also found between British, Italian and Russian hedgehogs, but although they were highly significant they referred only to upper tooth row length, the rostral angle, and maxillary index ( $P < .01$ ). In this arrangement British hedgehogs differed significantly from the other two populations, having a longer upper tooth row,

narrower rostrum and low maxillary index, which to a certain extent confirmed the data given earlier by Wettstein (1942).

Statistically these three populations were differentiated to the least degree from the remainder, from the respect of hedgehog subspecies systematics, they corresponded *occidentalis*, *italicus* and *centralrossicus* forms. Nevertheless the separate character of the British *occidentalis* form would appear justified and is based on different structure of rostral skull elements (cf. Wettstein, 1942).

Swiss, Polish, and German hedgehogs differed in the following characters: Cb. length, length of upper tooth row and mandible ( $P < .01$ ), and also height of *ramus mandibulae* ( $.01 < P < .05$ ). In this arrangement the Swiss population differed significantly from the remainder (Table 3, Fig. 6).

The third comparison referred to hedgehogs from Switzerland and Poland and showed statistically significant differences among them with respect to the following characters: Cb. length, upper tooth row length and mandible ( $P < .01$ ), zygomatic breadth, height of *ramus mandibulae*, and the rostral angle ( $.01 < P < .05$ ).

Hedgehogs from the British Isles had extremely narrow rostra but hedgehogs from Poland had outstandingly broad rostra. Intermediate between them were animals from Switzerland, Italy, Germany and Russia (Table 3, Fig. 7).

Rostral angles in both *E. roumanicus* and *E. europaeus* from Poland exhibited only a minimum degree of mutual overlapping and thus form an additional taxonomic character of supplementary importance. For *E. roumanicus* these values varied within limits of  $45^\circ$ — $50^\circ$ , and in *E. europaeus*,  $50^\circ$ — $57^\circ$ . In other populations of both species the degree of mutual overlapping of rostral angle values was either greater or lesser (Table 3 and Fig. 7).

#### 4. DISCUSSION

The large range of variations in skull indices and nasal bone dimensions indicates that these characters are of little practical usefulness. Their variability, expressed in coefficients was one of the highest in the material examined, both in the series of the two species and in different populations (Table 1 and 3). On this account the skull indices used by Rödl (1966), in particular the nasal, based on the two dimensions of nasals and also the parietal index, and considering measurement of spread of *proc. parietalis ossis frontalis*, can only be important as convenient diagnostical characters under given local conditions. Despite their taxonomic value, which is not very great (both dimensions of the nasal bones

constituted independent pleiads in our case) even exhibited a certain degree of mutual overlapping in both forms from Czechoslovakia (cf. Röd l, 1966). It would seem that material originating from so small area as Czechoslovakia should be distinguished by an appropriately small scale of index variations, but this proved not to be the case, and thus simultaneously confirmed M a y r's opinion (1968) that all characters used for distinguishing between species are subject, like others, to geographical variation. This certainly also applies to the rostral skull angle which we used, but is of certain taxonomic value only in Poland. It would seem that the practical usefulness of skull indices is defined to a great extent by the degree of proximity of the forms compared. Indices from different genera of hedgehog (*Erinaceus* and *Hemiechinus*) proved more useful here (Z a i d o v a, 1961).

The cause of a certain degree of morphological similarity of cranial characters in the two European species of hedgehog is their close degree of relationship, including the possibility of their crossbreeding (H e r t e r, 1938). On the other hand analysis of chromosome formulae (K r á l, 1967) and autoradiographic studies (G r o p p & C i t o l e r, 1969) fully confirm the species status of the two forms previously proposed by H e r t e r (1938) and K r a t o c h v i l (1966), according to whom these two species should be considered sibling species.

Although the correlation structures presented here cannot be directly applied as key characters for distinguishing between the two forms, a knowledge of correlation relations of skull measurements can be successfully used in studies of fossil remains. For instance, on the basis of mandible length conclusions can be reached as to the remaining skull dimensions, depending on the degree of their reciprocal correlation. Similar methods of drawing conclusions as to the animal's size from the inner length of skull have been devised by W y r o s t & K u c h a r c z y k (1967) as the result of correlation analysis of skull measurements and height at the rump of different breeds of dogs. The value of the results obtained also consists of the fact that although the two species of hedgehog could not be reciprocally distinguished on the basis of absolute values of the 12 dimensions used, the analysis of correlation structure of measurements of their skulls proved here to be a method of exceptional advantage since it simultaneously indicates the similarities and differences between them.

Simultaneous use of the three ways of illustrating differences in correlation structures of hedgehog skulls in diagram form made exact comparative analysis possible. The starting point was the correlation matrix, which when arranged on a C z e k a n o w s k i diagram (1913) became a basis for the other two methods—T e r e n t j e v's (1943 and 1960)

and Vyhandu's (1964), introducing new and reciprocally supplementing details. These methods are distinguished by simplicity and by sensitivity and considerable suggestiveness in emphasising differences and similarities in the correlation structures of the skull. The degree of reciprocal correlation of skull measurements proved to be higher in the »western« hedgehog (Fig. 2 and 3). This was confirmed by a certain number of statistically significant differences resulting from comparison of corresponding pairs of correlation coefficients (Table 2). The majority of these differences applied to the *neurocranium*, i.e., degree of correlation of the skull's height and breadth with its other dimensions.

Terentjev's (1943), method of correlation pleiads, provides a full description of the skull of a given species by selective limitation of the number of its measurements which can form a basis for taxonomy. Rossolimo (1962) found taxonomically important characters of *Clethrionomys glareolus* (Schreber, 1780) are zygomatic breadth, interorbital breadth and braincase breadth. Depending on the nature of the objects examined with this method, their differences are also emphasised. The example of its application to correlation structures for the skull of *Lepus europaeus* Pallas, 1778 shows that they are subject to age dependent differentiation. The greatest interdependence of skull measurements occurred in young hares, and decrease significantly in adults. Thus correlation structures considerably differed qualitatively, reflecting phases in formation of the hare's skull during postnatal development (Caboń-Raczyńska, 1964). The differentiating influence of age classes on the correlation structures of the skull in *C. glareolus* has also been shown by Gerasimov (1969). Kanep (1967), on the other hand, by comparing correlation structures of the skull measurements of six species of voles of the genus *Microtus*, found that there were considerable differences between them. In *Erinaceus* it was possible to define the degrees of differentiation in correlation structures of the skull in the two species and to show that they are qualitatively different. This is shown by the presence or absence of given pleiads, in their differing scope and order in which characters fall out from the pleiad when the level of interdependence of characters is increased, and also in the different character of curves for correlation connections (Fig. 3 and 4).

Differences between the two species of hedgehog were analogically revealed in the diagram of results using Vyhandu's method (1964), pointing to the existence of indicator-characters which, in hedgehogs, are condylobasal length and zygomatic breadth. These characters exhibit a different degree of connection with the other skull measurements for the two forms, expressing their structural differences (Fig. 5).

The reciprocal degree of differentiation in skull measurements corre-

lation structures for the two forms of hedgehog examined would thus appear to be one more argument confirming the correctness of Herter's hypothesis (1938 and 1952), according to which hedgehogs of the genus *Erinaceus* occurring in Europe belong to two species.

Estimation of the degree of variation in hedgehog skull material from different populations allows several general observations. The »western« hedgehog is statistically more differentiated in the skull dimensions than the »eastern« form (Fig. 6, Table 3). In addition hedgehogs from mountainous and hilly regions had maximum skull measurements, in »western« (Swiss population) and »eastern« hedgehog species (populations from the Caucasus and Crimea). Lowland population skull measurements were usually similar to each other (Fig. 6). It would appear that the variations found in hedgehog skull measurements are chiefly due to the fact that the material originated from differing localities often at great distances from each other and thus might reflect differences between populations expressed in the appropriate skull forms.

Irrespective of the above, certain differences in the dimensions of hedgehog skulls from Switzerland, the Caucasus and Great Britain may also point to the effect of geographical isolation. Mountain ranges and islands can present sufficient isolating barriers to the hedgehog to bring about formation of population of a decidedly local character. It is likely that this is the explanation of the form occurring in the Caucasus being given the rank of a subspecies, *Erinaceus europaeus transcaucasicus* S a t u n i n, 1905. Although hedgehogs from the Caucasus are distinguished by a broad rostrum, similar to some extent to that of *E. europaeus*, they most certainly belong to the species *E. roumanicus* which is indicated, in addition to other morphological characters of the skull, by their maxillary index (Table 3). The absence of a land bridge connecting the British Isles with the Continent may have similarly contributed to the formation of a local population of hedgehogs there, the systematic appurtenance of which has been connected with the form *Erinaceus europaeus occidentalis* B a r r e t t - H a m i l t o n, 1900. In the light of results of the analysis of variance made in the population of the two species of hedgehog it is possible to confirm the different character of the British population of the western hedgehog and the Caucasus eastern type of hedgehog, postulated earlier by Wettstein (1942) and Herter (1952).

On the other hand Italian and Russian hedgehogs proved to be most similar in respect of dimensions. Among the six populations of the western hedgehog examined, these two corresponded to the forms *italicus* and *centralrossicus* proposed by Wettstein (1942) and Herter (1952).

The finding of significant differentiation in skull measurements between different hedgehog populations does not always form a criterion provi-

ding the existence of separate forms in the subspecific sense. Most often these differences apply to skull dimensions, less often to the proportions between their dimensions, as was the case only with the maxillary index in British hedgehogs. In both the first and the second species it is possible to distinguish populations with small, medium and large skull dimensions (Fig. 7). It is difficult to discern any distinct trends in the differences found, apart from those clearly differentiating populations from montane and insular areas, which have been subject to the influence of geographic isolation and the ecological factors proper to these regions in a lesser or greater degree. Thus the differences found in various populations of the two species of hedgehog are without doubt primarily interpopulation differentiation.

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STRUKTURA KORELACYJNA WYMIARÓW CZASZKI PRZEDSTAWICIELI  
RODZAJU *ERINACEUS LINNAEUS*, 1758

Streszczenie

Zbadano zmienność i wzajemne zależności między 12 wymiarami linearnymi czaszki dwóch gatunków jeży z rodzaju *Erinaceus*, pochodzącymi z obszaru Europy północnej, południowej, zachodniej, środkowej i wschodniej. Na części materiału dodatkowo mierzono kąt rostralny (Ryc. 1) i obliczono wskaźnik maxillarny. Ogółem dysponowano 133 czaszkami dorosłych i starych okazów *E. roumanicus* i 74 — *E. europaeus*. Samce i samice traktowano łącznie z uwagi na brak statystycznie istotnych różnic między nimi w badanych wymiarach czaszki (Tabela 1).

W oparciu o 12 cech pomiarowych czaszki obu gatunków obliczono macierze korelacji, które uporządkowano i zestawiono na diagramach Czekanowskiego (Ryc. 2). Dokonano wzajemnych porównań między odpowiadającymi sobie parami współczynników korelacji wymiarów czaszki obu form, stwierdzając istnienie szeregu statystycznie istotnych różnic między nimi (Tabela 2). Diagramy posłużyły do wykreśle-

nia krzywych rozkładu frekwencji współczynników korelacji wymiarów czaszki (Ryc. 3).

Diagramy wykorzystano następnie do graficznego zilustrowania podobieństw i różnicowań między strukturami korelacyjnymi czaszki obu form. Różnice międzygatunkowe, wypukłone przy pomocy metody Terentjeva przejawiały się w obecności lub braku określonych plejad, w różnej ich objętości oraz kolejności wypadania cech z plejady przy podwyższaniu poziomu ich współzależności (Ryc. 4). Wyniki oparte o metodę Vyhandu, wskazują, że zarówno długość kondylobazalna czaszki jak i szerokość jarzmowa są dla obu jeży cechami-indykatorami, powiązanymi z pozostałymi wymiarami czaszki w różny sposób u obu form (Ryc. 5).

Wyniki porównań między populacjami w obrębie każdego gatunku (Tabela 3), wskazują, że największymi rozmiarami czaszki odznaczały się zarówno u jeża zachodniego jak i wschodniego, zwierzęta pochodzące z populacji bytujących w rejonach górskich i podgórszych w odróżnieniu od populacji nizinnych (Ryc. 6). Kąt rostralny czaszki wykazywał również zmienność, zależną od miejsca pochodzenia materiału (Rys. 7). Stwierdzone różnice międzypopulacyjne w wymiarach czaszki obu gatunków jeży, autor tłumaczy różnicami ekologicznymi środowisk, zamieszkiwanych przez te ssaki.