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MORPHOMETRIC VARIATION BETWEEN KARYOLOGICAL CATEGORIES OF THE COMMON SHREW (*SOREX ARANEUS*) IN THE LEGUCKI MLYN/POPIELNO HYBRID ZONE

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ABSTRACT

Morphometric variation of the common shrew *Sorex araneus* Linnaeus, 1758 was studied in the Łęgucki Młyn/Popielno hybrid zone in north-eastern Poland. The shrews of both races and their hybrids were measured. Seventeen cranial and external measurements in 105 young shrews were analysed. Based on the results of canonical analysis and multidimensional scaling we propose a hypothesis on morphometric differences between hybrids and non-hybrids. They may involve three skull parameters: length of the upper and lower dental series, and the length of the upper row of molariform teeth.

Key words: *Sorex araneus*, morphometrics, chromosomal races, hybrids.

INTRODUCTION

The common shrew *Sorex araneus* Linnaeus, 1758 is characterised by a large chromosomal variability. In this species the number of diploid autosomes ranges from 18 to 30, while the number of autosomal arms is always 36. Chromosomal variability of *S. araneus* makes it possible to divide its range into about 70 chromosomal races, of which at least 11 occur in Poland. In many cases the neighbouring races form hybrid zones and several of them have already been described [1, 2, 5, 6, 11, 12, 13, 14, 16, 22, 23, 25, 26, 38, 42].
All chromosomal races of *S. araneus* have been classified into three karyotypic groups: the West European (WEKG), the East European (EEKG) and the Siberian (SKG) [37].

For years scientists have been interested in the analysis of correlation between the chromosome and morphological variation of *S. araneus*. So far, morphometrical analyses of this species have shown that geographic location of the site, i.e. latitude and longitude, altitude, as well as climatic differences, appear to be more important in determining the morphology than the karyotype [36, 41, 44]. However, in some case, a correlation between the chromosome and morphological variation has been observed.

Studies on the morphometric variation in *S. araneus* have dealt with variation between chromosomal races representing different or the same karyotypic groups [3, 4, 7, 15, 16, 24, 28, 36, 44].

There are at least two cases of clear morphological divergence between races of different karyotypic groups. Chętnicki et al. [7], during their studies on morphometric variation among individuals from three Polish hybrid zones (Drnholec/Łęgucki Młyn, Drużno/Łęgucki Młyn, Drnholec/Białowieża) found significant differences in body and tail length and body mass between hybrids and individuals of the two races in the Drnholec/Łęgucki Młyn hybrid zone. In this case the Drnholec race represented WEKG, and Łęgucki Młyn EEKG. Similarly, Polyakov et al. [28] found statistically significant differences in morphometric parameters of shrew skulls in the Novosybirsk/Tomsk hybrid zone. Individuals of the Tomsk race significantly differed from those of the Novosybirsk race with regard to nine features, and from hybrids with regard to three. In this case each race represented a different karyotypic group: Novosybirsk – EEKG, and Tomsk – SKG.

In case of races representing the same karyotypic group, morphological differentiation is ambiguous. Most authors failed to show any dependence between membership in a chromosomal race and morphometric parameters. For example, Meyer and Searle [24] found no metric variation between populations of different karyotypes in Britain. Comparison of mandibular parameters of specimens from three different karyotypic races (Aberdeen, Oxford and Hermitage) in Britain revealed no clear morphological difference between them [36]. However, there were small mensural differences between hybrids and non-hybrids in Oxford/Hermitage hybrid zone. The analysis suggests that there may be non-additive genetic differences between the races. Banaszek et al. [3] found morphometric variation in the submaxilla of juvenile shrews from the Guzowy Młyn/Łęgucki Młyn hybrid zone, according to where the animals were caught (juvenile shrews found in the centre of the zone were smaller than those which came from the edges or outside the zone). No such significant size variation was found among adults. However, shrews of the Łęgucki Młyn race showed significant differences in the form of submaxilla, compared to individuals of the Guzowy Młyn race and the hybrids.

The results obtained by Searle and Thorpe [36] and Banaszek et al. [3] do not solve the problem of correlation between karyotypic and morphological variation within karyotypic groups of *S. araneus*. This encourages further studies in this direction.

The purpose of this study was to characterise morphometric variation of *S. araneus* in the Łęgucki Młyn/Popielno hybrid zone, and to check if there were any relationships between morphometric parameters and karyological categories.

MATERIAL AND METHODS

A total of 105 young shrews (year-born) were trapped, from June to September and karyotyped during the 1996-1999 field studies in Łęgucki Młyn/Popielno hybrid zone in north-eastern Poland [25].

Mitotic preparations were made from the spleen after colchicine treatment *in vivo* [10], and subjected to differential staining for G-bands using trypsin and Giemsa stain [35].

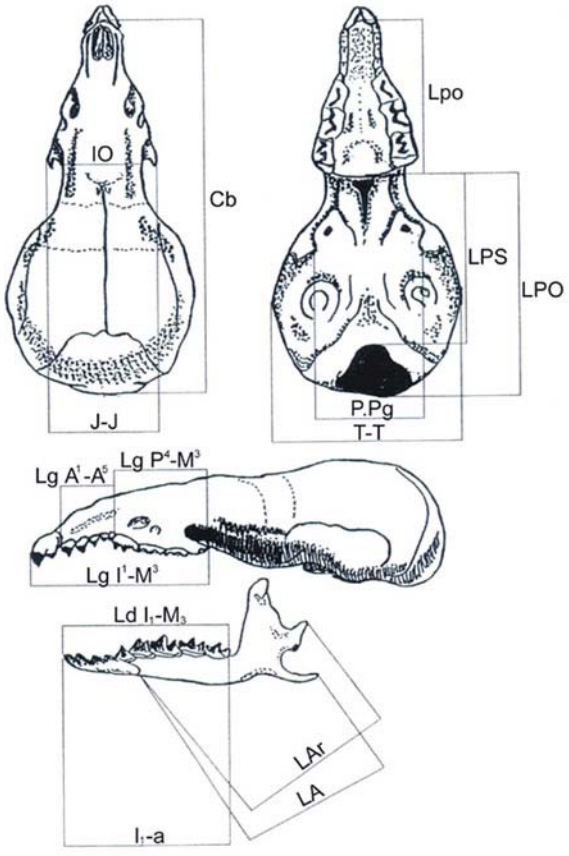
The specimens were divided in five karyological categories. The karyological category was defined by the complement of diagnostic metacentrics: *hk*, *io* for the Łęgucki Młyn race (category 1) and *hq*, *ik* for the Popielno race (category 2). Inter-racial hybrids were heterozygous for those diagnostic chromosomes. They were additionally subdivided in three categories, depending on the potentially forming meiotic complexes: *i/ik/kh/h* (category 3), *k/ki/io/o* (category 4), *i/ik/kh/hq/q* (category 5).

The analysis of cranial and external features was carried out on 105 individuals. Seventeen features (two external and fifteen cranial) were measured with electronic calliper.

External measurements (with 0.1 mm accuracy) have been taken according to Pucek [31] and referred to tail length (C) and foot length (P).

Cranial measurements (with 0.01 mm accuracy) have been taken partly according to López-Fuster et al. [20], as follows (Fig. 1): maximal length of the skull (Cb), maximal breadth of the skull (T-T), interorbital width (IO), postglenoid width (p.Pg), rostral length (Lpo), zygomatic width (J-J), staphylion-basion length (LPS), skull case length (LPO), length of the upper dental series (Lg I^1– M^3), length of the unicuspid tooth row (Lg A^1– A^5), maximum length of the molariform tooth row (Lg P^4-M^3), length of the lower dental series (Ld I_1 – M_3), articular length (LAr), angular length (LA), incisor-angle length (I_1-a).

Fig. 1. Measurements used in morphometric analysis of *Sorex araneus*



The skull of the common shrew reaches essentially adult size during nestling development [29, 34, 36, 43, 44], therefore possible differences in young shrews are age-independent. The only parameter which unambiguously shows seasonal variation in shrews is the brain case depth [8, 18, 19, 29, 31, 39], and thus it was omitted from the analysis.

We assumed the absence of sexual dimorphism in the common shrew with respect to the parameters measured. Consequently, the sample was not split according to sex. Such a lack of sexual dimorphism has been found (with reference to cranial and external features) by: Homolka [17], López-Fuster et al. [21], Pankakoski [27], Ruprecht [34], Searle and Thorpe [36].

Descriptive statitics: mean and variance (Table 1) were given for raw data. In order to ascertain the degree of morphological separateness between the karyologically defined categories, and to identify characters which might affect it, we used uni-dimensional Kruskal-Wallis tests for characters departing from normal distribution [32] and ANOVA for characters with normal distribution.

We also used discriminant and canonical analyses, which are rather resistant to waiving normalcy assumptions [9, 40] and to slight departures from homogeneity [40]. Compatibility of the data with assumptions of homogeneity of variance was checked with uni-dimensional tests of Leven, as well as Hartley, Cochran and Bartlet. The characters that showed non-homogenous variance in both tests were rejected from the analysis. In order to approach the data distribution to the multidimensional normal distribution, most calculations (except descriptive statistics) were done on logarithmically transformed data. Unidimensional normalcy was tested for all characters following transformation, with Shapiro-Wilks W test.

No character proved to be non-homogenous in both tests. The results of the tests for normalcy of distribution showed that most of them, in spite of logarithmic transformation, had abnormal distributions and thus the multidimentional distribution was also abnormal (Table 2). We decided, however, tu use them in multidimensional analysis. The absence of data was replaced with means of values for corresponding characters in respective groups.

The data were not corrected for body size and allometry (e.g. Burnaby method – [34]) since all the examined animals were at a similar stage of ontogeny. Thus it would be hazardous to adopt the largest variability fraction explained by PC1 as a complex indicator of body size [9, 33].

In order to describe the morphological similarity between specimens representing karyological categories, the distance method and multidimensional analysis (MDS) were used. The matrix of D^2 distances (square of Mahalanobis distance) between populations was calculated and analysed with MDS.

All the calculations were carried out using the Statistica 6 package [40].

RESULTS

The division of hybdrids in three subcategories resulted from the assumption that each of the hybrid genotypes might differently affect morphology.

Kruskal-Wallis test and ANOVA showed no statistically significant differences between karyological categories for any character (Table 3).

Table 1. Means (in mm) and variance for the 17 external and cranial features of shrews representing different karyological categories. N – sample size. Łg – Łęgucki Młyn race. P – Popielno race. *i/ik/kh/h*. *k/ki/io/o*. *i/ik/kh/hq/q* – different categories of hybrids

character	Łg			P			*i/ik/kh/h*			*k/ki/io/o*			*i/ik/kh/hq/q*		
	N	mean	variance	N	mean	variance	N	mean	variance	N	mean	variance	N	mean	Variance
C	66	40.38	5.65	20	40.78	5.79	10	39.49	6.51	2	39.25	0.50	4	40.81	6.68
P	67	12.70	0.24	20	12.66	0.39	10	12.52	0.11	2	13.00	0.12	4	12.58	0.15
Cb	68	18.81	0.11	21	18.78	0.14	9	18.67	0.19	2	18.98	0.02	4	19.08	0.15
T-T	67	9.38	0.04	21	9.32	0.06	8	9.40	0.02	2	9.35	0.02	4	9.30	0.05
IO	68	3.54	0.01	21	3.53	0.02	10	3.47	0.02	2	3.59	0.01	4	3.57	0.00
p.Pg	67	5.36	0.02	21	5.34	0.02	10	5.29	0.03	2	5.23	0.02	4	5.20	0.01
Lpo	67	8.33	0.06	21	8.37	0.03	10	8.26	0.07	2	8.28	0.00	4	8.42	0.03
LPS	67	8.54	0.10	21	8.55	0.06	10	8.60	0.03	2	8.72	0.00	4	8.66	0.06
LPO	66	11.16	0.03	19	11.19	0.04	9	11.20	0.11	2	11.02	0.00	4	11.24	0.02
J-J	52	5.33	0.01	17	5.29	0.02	10	5.29	0.02	2	5.20	0.00	2	5.25	0.12
LgI1-M3	65	8.56	0.03	20	8.62	0.03	8	8.53	0.03	1	8.30		4	8.57	0.00
LgA1-A5	66	2.89	0.00	20	2.90	0.00	8	2.91	0.00	1	2.80		4	2.82	0.00
LgP4-M3	67	4.67	0.01	20	4.66	0.02	10	4.60	0.02	2	4.70	0.02	4	4.65	0.01
LdI1-M3	65	7.92	0.04	20	7.95	0.04	9	7.94	0.03	2	7.65	0.00	4	7.92	0.00
I1-a	59	12.27	0.06	20	12.32	0.03	8	12.19	0.08	2	12.33	0.01	3	12.37	0.11
LA	57	9.89	0.07	20	9.91	0.05	8	9.87	0.09	2	9.98	0.02	3	10.12	0.01
LAr	65	9.62	0.04	21	9.56	0.04	9	9.56	0.02	1	9.50		4	9.70	0.00

Table 2. Results of tests for variance homogeneity and normalcy of distribution of characters; p – significance level, Łg – Łęgucki Młyn race

Cecha	Cochran C. Hartley. Bartlett p	Levene p	Shapiro-Wilk p for all groups collectively	Shapiro-Wilk p for the most numerous group Łg
C	0.18			p=0.16641
P	0.68	0.366264		
Cb	0.95	0.732975	p=0.94249	p=0.78696
T-T		0.157661		p=0.22832
IO	0.16	0.117027	p=0.45561	p=0.31512
p.Pg	0.99	0.807175	p=0.40605	p=0.13275
Lpo	0.83	0.184093	p=0.25702	p=0.36851
LPS	0.53	0.382313		
LPO	0.89	0.651760	p=0.35380	p=0.15559
J-J	0.22	0.105816		
LgI1-M3	1.00	0.260229		
LgA1-A5	0.89	0.735919		
Lg P4-M3	0.79	0.601953		
Ld I1-M3	0.70	0.749549		
I1-a		0.798236		
LA		0.521712		
LAr	0.48	0.237492	p=0.94621	p=.068447

Table 3. Results of ANOVA or Kruskal-Wallis test for individual characters

Character	Kruskal-Wallis p
C	0.62
P	0.60
Cb*	0.84
T-T	0.91
IO*	0.73
p.Pg*	0.63
Lpo*	0.85
LPS	0.70
LPO*	0.48
J-J	0.43
LgI1-M3	0.25
Lg A1-A5	0.37
Lg P4-M3	0.54
Ld I1-M3	0.36
I1-a	0.77
LA	0.45
LAr*	0.66

* ANOVA

Likewise, discriminant and canonical analysis did not reveal any significant differences between the karyological categories. Significance level p for Wilks's Lambda multidimensional test was < 0.23.

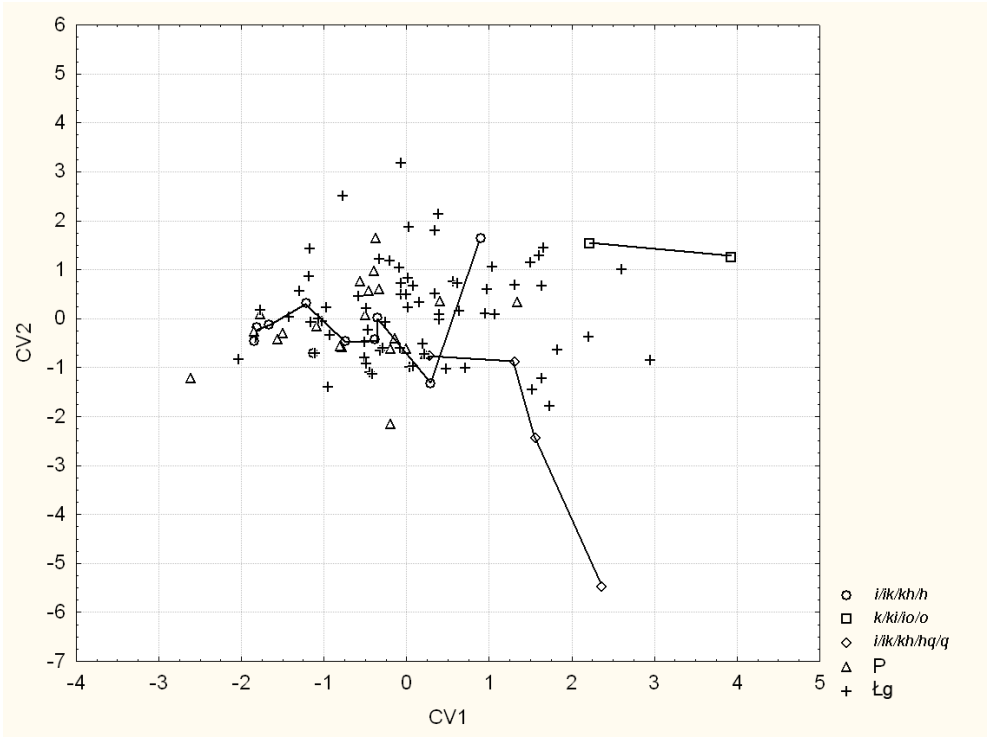
However, the relatively low p value, at the very low numbers within each hybrid category in the total sample, as well as large differences in the effect of individual characters on canonical variables (Table 4), make it possible to single out some characters which, when a larger sample of hybrids is analysed, might prove to be associated with the karyotype to a different degree. These characters are dentition-related: length of the upper dental series (Lg $I^1 – M^3$), length of the lower dental series (Ld $I_1 – M_3$) and maximum length of the molariform tooth row (Lg P^4-M^3).

Table 4. Standardized coefficients for the first and second canonical variable. Characters with the greatest effect on the variable underlined

Cecha	CV1	CV2
C	0.05	-0.13
P	0.54	0.49
Cb	0.48	-0.30
T-T	-0.18	-0.08
IO	0.30	-0.35
p.Pg	-0.47	0.48
Lpo	-0.01	0.09
LPS	0.20	0.20
LPO	-0.47	-0.34
J-J	-0.20	0.13
LgI1-M3	-0.72	-0.80
Lg A1-A5	-0.08	0.51
Lg P4-M3	0.73	0.70
Ld I1-M3	-0.60	-0.18
I1-a	0.33	-1.02
LA	-0.22	1.00
LAr	0.56	-0.53
Proper values	0.42	0.29
Cumulated percent	0.42	0.72

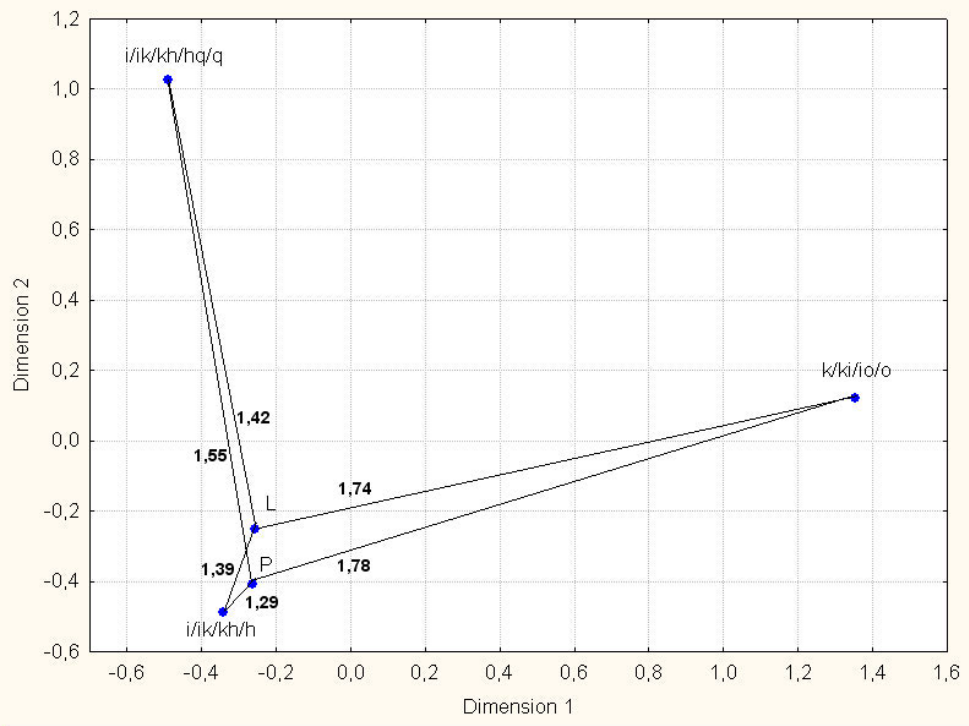
Dependences between karyological categories presented within the space of the first two canonical variables (CV1 and CV2) (Fig. 2) show that the only karyological categories that may differ morphometrically from some of or all the remaining ones are two hybrid categories: *i/ik/kh/hq/q* and *k/ki/io/o*.

Fig. 2. All karyological categories within the space of the first two variability axes CV1 and CV2. Łg – Łęgucki Młyn race, P – Popielno race



A similar message is conveyed by the scatterplot resulting from MDS (Fig. 3). Though the D^2 distances are in no case statistically significant, it appears that there are reasons to suspect that non-hybrid individuals i.e. those of the Łęgucki Młyn and Popielno races are the closest to each other, while the *i/ik/kh/h* and then *i/ik/kh/hq/q* hybrids are more remote from them. The *k/ki/io/o* hybrids are the least similar to other categories.

Fig. 3. Karyological categories in two-dimensional space resulting from multidimensional scaling. Numbers denote distances between races Łg and P and each category of hybrids, considering all three measurements



Considering the three characters that may display differentiation, the *k/ki/io/o* hybrids seem to show lower values of Lg $I^1 - M^3$ and Ld $I_1 - M_3$, and thus both dental series shorter compared to pure individuals of the races Łęgucki Młyn and Popielno, and a higher Lg P^4-M^3 value, i.e. longer upper row of molariform teeth (Table 1).

DISCUSSION

The results of our study, suggesting a possibility of correlation, in *S. araneus*, between the karyological category and morphometric features seem interesting. Morphometric differences between individuals – members of different karyological categories in hybrid zones were found, among others, by Chętnicki et al. [7] and Polyakov et al. [28]. Chętnicki et al. [7] studied the Drnholec/Łęgucki Młyn hybrid zone in Poland and found significant differences in body and tail length and body mass between hybrids and non-hybrids. Similarly, Polyakov et al. [28] found a morphological differentiation of shrew skulls in Novosibirsk/Tomsk hybrid zone in Russia. Individuals of the Tomsk race had significantly greater values of cranial parameters (maximal skull length, rostral length, hard palate length, maximal skull breadth, basal length of lower jaw, maximal length of the lower jaw, height of coronoid process, length of unicuspid tooth row, length of maxillary tooth row) in comparison to individuals from the Nowosybirsk race. The skulls of shrews of the Tomsk race seem also to be longer in comparison to those of hybrids. This is indicated by the significantly greater values of the following parameters: maximal skull length, length of unicuspid tooth row, length of maxillary tooth row. However, in both cases the research focused on hybrid zones where contacting races represented different karyotypic groups. This fact could be an additional factor affecting the observed differentiation. In our study the hybrid zone (Łęgucki Młyn/Popielno) involved two races of the same karyotypic group (EEKG), and thus the possible morphological differences between the karyological categories would have reasons other than group membership.

Some of our statistical analyses make it possible to conjecture that in the hybdrid zone Łęgucki Młyn/Popielno the hybrids may significantly differ in some skull parameters from non-hybrids. The fact seems interesting though not surprising. Morphological differences between categories were observed by Searle and Thorpe [36]. These authors found small differences in the mandible parameters between hybrids and non-hybrids from the Oxford/Hermitage hybrid zone in Britain. Also Banaszek et al. [3] found significant differences in the form of submaxilla between shrews of the Łęgucki Młyn race and specimens of the Guzowy Młyn race and hybrids in Łęgucki Młyn/Guzowy Młyn hybrid zone in Poland.

All the potential morphological differences, suggested by our results, are associated with dentiture and involve the length of the two dental series (upper and lower), and the length of the upper row of molariform teeth. Literature data suggest that dental morphology in *S. araneus* shows an intraspecific variation. Polyakov et al. [28] found for example that the races Novosibirsk and Tomsk differed, among others, in the length of unicuspid tooth row and maxillary tooth row. In this case the reason is sought in membership of the contacting races in different karyotypic groups. However, research in Scandinavia showed that the length of the upper row of unicuspid teeth increased from south to north, and the length of upper row of molariform teeth decreased slightly in that direction [41]. These authors suggested that significant intraspecific differences in dental morphology of various chromosomal races of *S. araneus* in Scandinavia depended on environment. A wide intraspecific variation in e.g. length of the upper dental row in *S. araneus* from Poland was also mentioned by Bogdanowicz and Pucek [4]. Based on multidimensional analysis, the authors found that skulls of shrews from western Poland were smaller than in the eastern part of the country. An intrapopulation variation in mandible parameters was observed by Wójcik et al. [43] in a population of shrews from Białowieża (Białowieża race).

The examples show that skull parameters, and especially dental morphology, vary much in *S. araneus* under the effect of a variety of non-karyotypic factors. Our observations, suggesting significant differences in dental morphology between hybrids and non-hybrids in the zone Łęgucki Młyn/Popielno, seem interesting because in our studies most of the factors listed above could not affect the variation. The two contacting races represented the same karyotypic group (EEKG). The zone, located in north-western Poland, is rather narrow, its width not exceeding 10 km [26], and thus the distance between the population was small, and so was probably the effect of geoclimatic factors. All our shrews were trapped in very similar habitats – wet uncultivated meadows, which excludes the effect of habitat heterogeneity on metric differences [43].

Canonical analysis and multidimensional scaling indicate that the *i/ik/kh/h* hybrids are the closest to non-hybrids, they are followed by *i/ik/kh/hq/q*, while *k/ki/io/o* are the least similar to non-hybrids. It can be conjectured that the genotype of the last group has the strongest effect on morphology. At present this is only a hypothesis which can be tested only based on a morphometric analysis of larger samples of hybrids.

CONCLUSIONS

Based on our results we propose a hypothesis on morphometric differences between hybrids and non-hybrids of *Sorex araneus* in Łęgucki Młyn/Popielno hybrid zone. They may involve three skull parameters: length of the upper and lower dental series, and the length of the upper row of molariform teeth.

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