Russian J. Theriol. *24 (2)*: 92–100

Invariance of diversity parameters of the lower jaw of the common shrew (*Sorex araneus*) based on standard measurements, Procrustes coordinates and centroid size

Andrey Yu. Puzachenko* & Leonid L. Voyta

ABSTRACT. Information parameters of morphometric diversity (entropy, self-organisation index) of the lower jaw (hemimandible) of the common shrew (*Sorex araneus* Linnaeus, 1758) were estimated and compared based on (i) standard measurements or (ii) Procrustes coordinates and centroid size. In each case, two multivariate descriptive models were developed using Euclidean distances or Kendall's t_b rank correlations. In the first case, size diversity was evaluated; in the second case, diversity of shape was evaluated. For each model, entropy and self-organisation index, which were independent of sample size, were determined. It was shown that the value of the self-organisation index for models describing size diversity was independent — or invariant — of the type of source data. (invariance) of the type of initial data. In contrast, the models based on Kendall's t_b rank correlation were not equivalent. The self-organisation index for landmark Procrustes coordinates was significantly higher than the index calculated based on standard lower jaw measurements.

How to cite this article: Puzachenko A.Yu., Voyta L.L. 2025. Invariance of diversity parameters of the lower jaw of the common shrew (Sorex araneus) based on standard measurements, Procrustes coordinates and centroid size // Russian J. Theriol. Vol.24. No.2. P.92–100. doi: 10.15298/rusjtheriol.24.2.02

KEY WORDS: common shrew, morphological diversity, entropy, self-organisation index, geometric morphometrics.

Andrey Yu. Puzachenko [puzak@igras.ru], Institute of Geography, Russian Academy of Sciences, Moscow 119017, Russia; Leonid L. Voyta [leonid.voyta@zin.ru], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia.

Инвариантность параметров разнообразия нижней челюсти обыкновенной бурозубки (*Sorex araneus*) на основе стандартных измерений, прокрустовых координат и центроидного размера

А.Ю. Пузаченко*, Л.Л. Войта

РЕЗЮМЕ. Проведено сравнение информационных параметров морфометрического разнообразия (энтропия, индекс самоорганизации) нижней челюсти (гемимандибула) обыкновенной землеройки (*Sorex araneus* Linnaeus, 1758), оцениваемых на основе (i) стандартных измерений или (ii) прокрустовых координат и центроидного размера. В каждом случае построены две многомерные описательные модели с использованием евклидовых расстояний или ранговых корреляций Кендалла t_b. В первом случае оценивалось разнообразие размеров, во втором — разнообразие формы нижней челюсти. Для каждой модели были определены значения энтропии и индекса самоорганизации, которые не зависели от размера выборки. Было показано, что значение индекса самоорганизации для моделей, описывающих разнообразие размеров челюсти, не зависит (инвариантно) от типа исходных данных. В то же время модели, основанные на ранговой корреляции Кендалла t_b, были не эквивалентны. Индекс самоорганизации для прокрустовых координат ландмарок оказался значительно выше, чем индекс, рассчитанный на основе стандартных измерений нижней челюсти.

КЛЮЧЕВЫЕ СЛОВА: обыкновенная землеройка, морфологическое разнообразие, энтропия, индекс самоорганизации, геометрическая морфометрия.

---

* Corresponding author

Introduction

Over the last 50 years, the study of variation in the size and shape of organisms carried out with extensive use of multivariate statistical analysis in a framework called "morphometrics". In general, the purpose of multivariate analysis is to detect order (rules, patterns) in the variation of a set of measurements (variables) of objects and to display the relative position of objects or variables in the modelled multidimensional morphospace. Morphometric retains the traditional aims of studying variability: to identify differences between samples of organisms, to compare or classify samples, to test hypotheses about the nature of variability, and so on. Meanwhile, diversity itself, as a distinct phenomenon and subject of research, tends to escape the attention of researchers.

Morphological (morphometric) variability of organisms, as a set of different biological processes, according to Simpson's (1944) definition, is associated with the measure of difference between individuals at the population level, i.e. it acts as a statistical characteristic of a population and not of an individual. An individual (organism) is taken as the smallest unit (element) of analysis. A set of individual elements forms a system if, for any pair of elements, a rule is given according to which one element can be distinguished from another in principle. In other words, in a system, the elements have certain relationships to each other. The set of all such relations can be interpreted as the diversity of a sample, if variables characterising the elements and a specific rule defining the relations between them are given. For example, if the variables for the elements are DNA sequences and a method (metric) is specified for evaluating the differences between them, then the set of distances between all pairs of elements in the sample characterises genetic diversity. In the case of morphometric, quantitative variables, the relationships between elements reflect morphometric diversity, and in the case of phenetic, qualitative traits, phenetic diversity, and so on. In a broad scientific context, all variants of diversity are a consequence of the heterogeneity of living matter (Vernadsky, 1978: 51) and the diversity of relationships within it and with the surrounding non-living matter during the course of biological evolution on Earth.

As a general approach to the semantics of "diversity" as a term, in our opinion, it is reasonable to consider the generalisation proposed by Stirling (1998, 2007). According to this approach, "diversity" is composed of three specific components or "subordinate properties": "variety", "disparity" and "balance". Variety refers to the number of categories into which the quantity under consideration can be divided. The balance or equitability refers to the pattern of distribution of this quantity among the relevant categories. The more evenly balanced these fractions are, the greater the diversity. Disparity refers to the nature and degree to which the categories are different from each other. That is semantic close to interpretation of this term, for example, in palaeontology (Foote, 1997). In general, diversity is positively correlated with all three components. Disparity and, to a lesser extent, variety are subjective and context-dependent aspects of diversity. They depend on the particular system of measures and the given objectives of the study. It is important to note that the interpretation of diversity presented above is not the only and universal interpretation. A certain advantage of considering diversity as a more general concept in relation to its three composed components is that such a view is consistent with the content of quantitative information parameters (indices), such as entropy, used in the natural sciences to evaluate the diversity within "systems". In particular, maximum physical entropy is proportional to the number of elements that differ from each other in a system. Furthermore, it is evident that informational entropy is proportional to the number of elements and of classes of elements, regardless of how these elements or classes were distinguished within a specific system.

All methods of multivariate analysis aim to reduce the dimensionality of a descriptive model of a system by reducing the number of the original variables, which entails the models of lower dimensionality, usually with a small number of orthogonal coordinates. In these model hyperspaces, the relative position of elements is not determined by the original metric, but by individual sets of coordinates. The distances between the position of elements in the model hyperspace are proportional to the distances between the elements in the system calculated using the original metric. Such methods include principal component analysis, variants of factor analysis, non-metric multidimensional scaling and some others. Thus, the specific descriptive models obtained as a result of applying multivariate analysis encompasses the patterns of similarity/dissimilarity relations between the elements of the studied system and, therefore, they contain information about the diversity within the system.

It should be emphasised that, firstly, models reproduce "stable" or "basic" relationships between elements. These relationships are usually linear or close to it. Strong nonlinearities, such as discontinuities, are ignored and filled with dummy values because the model hyperspace is principally continuous. Stochastic components ("noise") usually make a small quantitative contribution to the total variance and are not taken into account either at the level of the algorithm or by the researcher according to a certain rule. Therefore, the diversity estimate of the model will always be somewhat lower than the diversity of the system being modelled.

The methodology we develop for measuring diversity is based on the use of multivariate methods to reduce dimensionality, and on the use of information theory tools, including the theory of signal transmission and models developed in cybernetics (Shannon, 1949; Ashby, 1958; Conant & Ashby, 1970; Haken, 2006; Puzachenko, 2016, 2020, 2023). To quantitatively characterise the structure of a descriptive model, information variables (entropy, self-organisation index or "redundancy", etc.) are used, which have the meaning of macro-parameters in relation to the model. In particular, using a large data set on the variability of cranial and postcranial elements of the mammalian skeleton in representatives of the orders Artiodactyla, Carnivora, Perissodactyla and Rodentia, it was shown that the variation of entropy normalised by the number of model coordinates and the self-organisation index are, on the one hand, essentially limited and, on the other hand, invariant with respect to the set of variables and their number (Puzachenko, 2016, 2023).

Methods of geometric morphometrics have become widespread in recent decades (Zelditch *et al*., 2004; Klingenberg, 2011; Vasil'ev *et al*., 2018). Geometric morphometric shares the same basic aims with common morphometric analysis, but the main object of study is the variability of "shape". In contrast to the traditional approach, geometric morphometric does not use conventional measurements, but coordinates of points (landmarks) located on the contour of the object or on the object itself. The intermediate products of the initial coordinate processing are centroid size and Procrustes coordinates. In this study, the variables were used to develop of descriptive morphometric models of common shrew, *Sorex araneus* Linnaeus, 1758 (Soricidae, Eulipotyphla), lower jaw size and shape variation, and subsequently to calculate diversity parameters. Independently, the models were developed for a part of the sample using a set of traditional (standard) craniometrics measurements. The variation of information parameters of diversity in different samples of shrew mandibles was compared with the variation in the same parameters calculated for the skulls (cranium and mandible together) of pygmy (*Sorex minutus* Linnaeus, 1766), Laxmann's (*Sorex caecutiens* Laxmann, 1785) and common shrews (Puzachenko & Kupriyanova, 2023).

We wanted to evaluate the impact of the ways, in which disparity is measured, on the values of diversity indices. More specifically, we tested the hypothesis of invariance of diversity parameters, not only with respect to the particular measurement sets (variables), but also with respect to the methods of primary data processing.

Materials and methods

Sampling

Specimens of the "Manturovo" chromosome race of common shrews were collected in 1972–1984 at the "Velsky" Research Station (Velsky District, Arkhangelsk Region, Russia) and in 1981–1988 at the "Kortkerossky" Research Station (Kortkerossky District, Komi Republic, Russia). Sample of 154 animals was analysed. A set of 7 measurements of the hemimandibula is described in Puzachenko & Kupriyanova (2023). In addition to these, the length of the condylar process was used in this study (see scheme in Puzachenko & Kupriyanova, 2023: Fig.1). Immature animals captured in August, either at peak or low abundance, were included in the analyses. Measurements were taken using an MBR 10 microscopic ocular micrometer for large and small structures at eight and sixteen times magnification respectively.

The sample for geometric morphometrics included 634 hemimandibles belonging to four karyotypic races: "Serov" (Yaksha, Garevka, Zhani, "Bolshaya Kokshaga", Komi Republic, Mari El Republic, Russia), "Manturovo: (Ramenye, Dan, Komi Republic, Arkhangelsk Oblast, Russia), "Pechora" (Ulashevo, Dan, Komi Republic, Arkhangelsk Oblast, Russia), "Sok" (Verkhnyaya Puzla, Storogevsk, Malaya Sluda, Komi Republic, Russia. The chromosomal race was determined in a previous morphometric study by Shchipanov *et al*. (2014), and was later confirmed by Shchipanov & Pavlova (2017).

All animals were captured during summer and early autumn (June–September), except for the sample from Bolshaya Kokshaga ("Sok" race), which was collected in October 2009. The collection of skulls and mandibles of shrews is kept in the museum of the Pechora-Ilychsky State Nature Reserve (Komi Republic, Troitsko-Pechorsky District, Yaksha settlement). This sample also included 154 hemimandibles of the "Manturovo" race for which standard measurements were available.

The lateral side of the mandible was digitised using an Epson Perfection V300 flatbed scanner at high resolution (2400 dpi). We used 17 landmarks for which coordinates were determined in two-dimensional projection with Cartesian coordinate system.

Statistics

Centroid size and Procrustes coordinates (Bookstein, 1991; Zelditch *et al*., 2004) were calculated in the MorphoJ (Klingenberg, 2011). Object equalisation was based on consensus configuration using Generalized Procrustes Analysis (Rohlf & Slice, 1990).

Descriptive morphometric models were elaborated using the same method regardless of the initial data. To remove the influence of scale, the variables were pre-ranked. For this, the smallest data value of each variable was subtracted from each value and divides by its range. Thus, the new scale starts at 0 and ends at 1. Then, Euclidean distances and Kendall t_b rank correlation (Kendall, 1975) were calculated between all pairs of sample elements (for more details on the method, see (Puzachenko, 2016, 2023). In the first case, the model mainly characterized the diversity in sizes.

For any pair of sample individuals, the standardised variable values (Vn) can be ranked in the order, for example, V1≥V2 ... ≥Vn (we do not consider unlikely cases when the ranks of all variables are equal to 1 or 0). If these two sequences are close, it means that the shape of the individuals are similar. In other words, Kendall's t_b estimates the probability ($|k|$) that a randomly selected pair of individuals will have the same order of variables versus the probability that they will have the opposite order.

In the case of Procrustes coordinates (with centroid size), the Euclidean metric estimates the variation of “shifts” of elements relative to each other (analogous to size variation) in two-dimensional space. We include a centroid size in the calculation, because it is the measure of size used almost in geometric morphometrics (Klingenberg, 2016). The Kendall’s t_b reflects of the consistency of “shifts” of landmarks relative to each other in the same space. The latter, most probably, cannot be interpreted as variation in the proportions of elements.

The matrices obtained were then processed by nonmetric multidimensional scaling with the number of coordinates ranging from 1 to 8 (standard mandibular measurements) or from 1 to 15 (centroid size and Procrustes coordinates). A set of values characterising the quality of the descriptive models (called “stress”) was compared with the model sets of similar values obtained for the random data sets with normal or uniform distributions. The results of this comparison were used to estimate the optimal number of coordinates (*d*) for each of the four descriptive models. Descriptive models of size diversity were referred to by the abbreviation SZM and their coordinates were E1, E2, etc. Models of shape diversity or coherence of landmark shifts were denoted by the abbreviation SHM, and their coordinates were K1, K2, etc.

The coordinates of the descriptive models were used as input variables in the calculations of the diversity parameters. A necessary condition for this was the orthogonality of the coordinates, which ensured their independence with regard to the information contained in them. The values of the diversity parameters should depend on the shape of the distribution of the images of the system elements in the space of the descriptive model. A natural parameter that fulfils this requirement is the information entropy (H). In order to measure the entropy, the range of values of each coordinate of the SZM and SHM models was divided into *k* intervals, as follows: $k = 1 + \log_2 N$, where N is the number of elements in the system (sample size) (Sturges, 1926). For each interval, the relative frequency of element projections was calculated: $p_i = n_i/N$. The entropy was then calculated using the formula $H = -\sum_{j=1}^{d}\left(\sum_{i=1}^{k} p_i \log_2 p_i\right)$, where d — number of coordinates of the descriptive model. The key parameter of diversity, namely, the self-organisation index, was calculated from the entropy values: $R = H_{\max} - H/H_{\max} = 1 - H/d\log_2 k$, where $H_{\max}$ was the theoretical value of the entropy under the condition of uniform distribution of the elements throughout the volume of the descriptive model. *R* ranges from 0 (maximum “disorder”) to 1 (perfect “order”). Since the number of coordinates varied from model to model, it was natural to introduce an entropy norm relative to one conditional coordinate (average or relative entropy) calculated as $H_d = H/d$.

In general, *H* and other information parameters depend on the sample size (*n*) (Foerster, 1960). In order to obtain comparable values, it is necessary to calibrate the parameters so that all values are adjusted to a standard sample size. A sample of 50 elements was taken as a standard. The number 50 was chosen because, according to calculations for a random normally distributed variable, the increase in entropy was only ~3.5% when *n* increased from 40 to 100. Furthermore, the number 50 was close to the modal value of *n* in the museum collections we studied (Puzachenko, 2013, 2023), with more than 45% of the samples falling in the interval 30–40 and 70% in the interval 30–80 specimens. First, the value of *d* corresponding to the optimal dimensionality of the descriptive model was determined and fixed. Then, *n* samples of different sizes (min $n = 25$) were selected from the initial sample of volume *n* using the Monte Carlo method. For each *n*, a descriptive model was obtained using the method described above and parameters of diversity were calculated. In practice, it is usually sufficient to have 7–10 such samples and their corresponding descriptive models. The statistical significance of the dependence of *H* or any other macroparameter (*MP*) on the sample size (*n*) was evaluated using the linear regression equation: $MP = A + B\lg n$. The value of the calibrated MP_{50} is calculated in accordance with the expression: $MP_{50} = [MP_n - (A + B\lg n)] + (A + B\lg 50)$.

The calculation was made using STATISTICA ver. 8.0 (StatSoft, Tulsa, Oklahoma), NCSS ver. 12 (ncss.com/software/ncss) и PAST (Hammer & Harper, 2005).

Results

Estimation of optimal dimensionality of descriptive models

For standard mandibular measurements, the optimal dimensionality of the SZM and SHM models was 6 and 2, respectively. The dimensionality of SZM was 4 and SHM was 3 coordinates for the combination of centroid size and Procrustes distances. Fig. 1 shows an example of the estimation of the dimensionality of the SZM model (centroid size, Procrustes coordinates) based on the minimum value of the standard residual of a linear regression of the observed stress and its model values.

Calibration of diversity parameters

For all descriptive models, a statistically significant positive correlation was observed between the logarithm of sample size (lg*N*) and *H* (H_d) (Fig. 2: A, C). In the SHM (standardised measures) model, R did not correlate with sample size, but this correlation was present in the other three models. Calibration removes the dependence of the parameters on sample size (Fig. 2: B, D). The calibrated values are then used as samples to estimate the statistics of the parameters. Table 1 summarises the calibrated values of the diversity parameters for the four descriptive models.

Table 1. Diversity parameter statistics of SZM and SHM descriptive models of two samples of common shrew mandibles.

Model type	H_{d50} ± m	Min–Max	R_{50} ± m	Min–Max
	Procrustes coordinates and centroid size, n = 17			
SZM	2.20 ± 0.027	1.99–2.39	0.187 ± 0.008	0.135–0.259
SHM	2.15 ± 0.033	1.91–2.39	0.205 ± 0.010	0.129–0.286
	Standard variables, n=13			
SZM	2.10 ± 0.024	1.96–2.24	0.227 ± 0.008	0.180–0.287
SHM	2.30 ± 0.023	2.13–2.42	0.144 ± 0.009	0.099–0.239

Comparison of samples by parameters of diversity

For the SZM models, the interval H_{d50} and R_{50} values were quite close; the mean H_{d50} values were slightly lower and the R_{50} values correspondingly higher for the sample with standard measurements. The mean H_{d50} and R_{50} differed statistically significantly (t = 2.67, p = 0.01 и t = 3.77, p = 0.001). This result was consistent with the characteristics of the samples compared. The sample of mandibles measured by standard variables was composed of specimens collected in contrasting phases of population dynamics. Puzachenko & Kupriyanova (2023) have found that the size and diversity of shrew skulls differed significantly in peaks and depressions, and the presence of two contrasting groups in one sample resulted in greater internal order (lower entropy, higher "organisation") than in another sample in which no special filtering of animals was performed. For the sample with variables of geometric morphometrics, H_{d50} and R_{50} were lower and higher for SHM, respectively. There were also statistically significant differences between the parameters (t = 3.44, p = 0.002 и t = 4.22, p = 0.0002). The interpretation of these differences is not obvious, as the semantics of the SHM models are not the same for different samples in this case.

We compared the extent of variation of H_{d50} and R_{50} for SZM models with variations of these parameters, calculated for the skulls and mandibles of the Laxmann's and pygmy shrews, as well as the common shrew (Fig. 3A). It turned out that H_{d50} and R_{50} obtained on the basis of intermediate results of geometric mor-

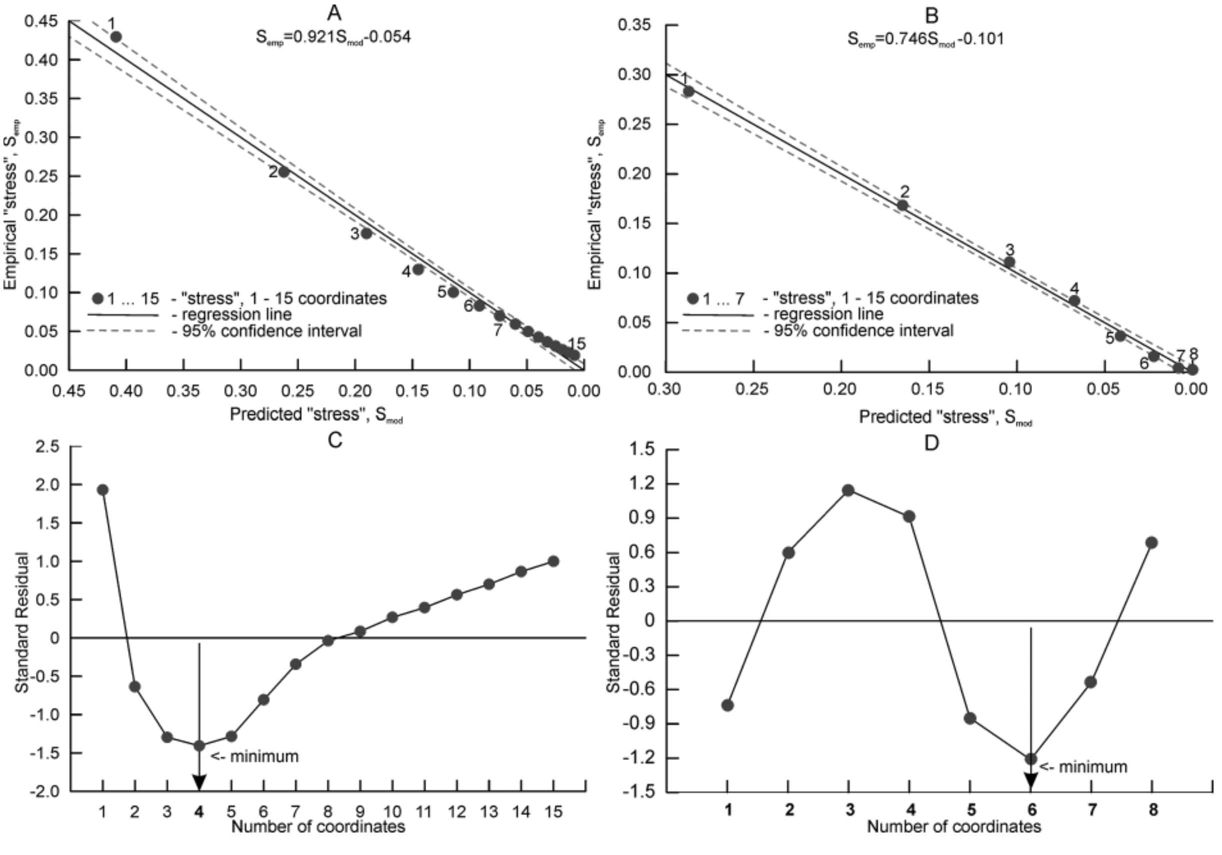

Fig. 1. Estimation of the optimal dimensionality (number of coordinates) of the SZM descriptive model. A, C — sample of 634 lower jaws of common shrew with the centroid size and Procrustes coordinates of landmarks as the variables. B, D — sample of 154 lower jaws of common shrew with 8 standard variables. A, B — linear regression of empirical and predicted stress, C, D — standardised residuals from the regression models.

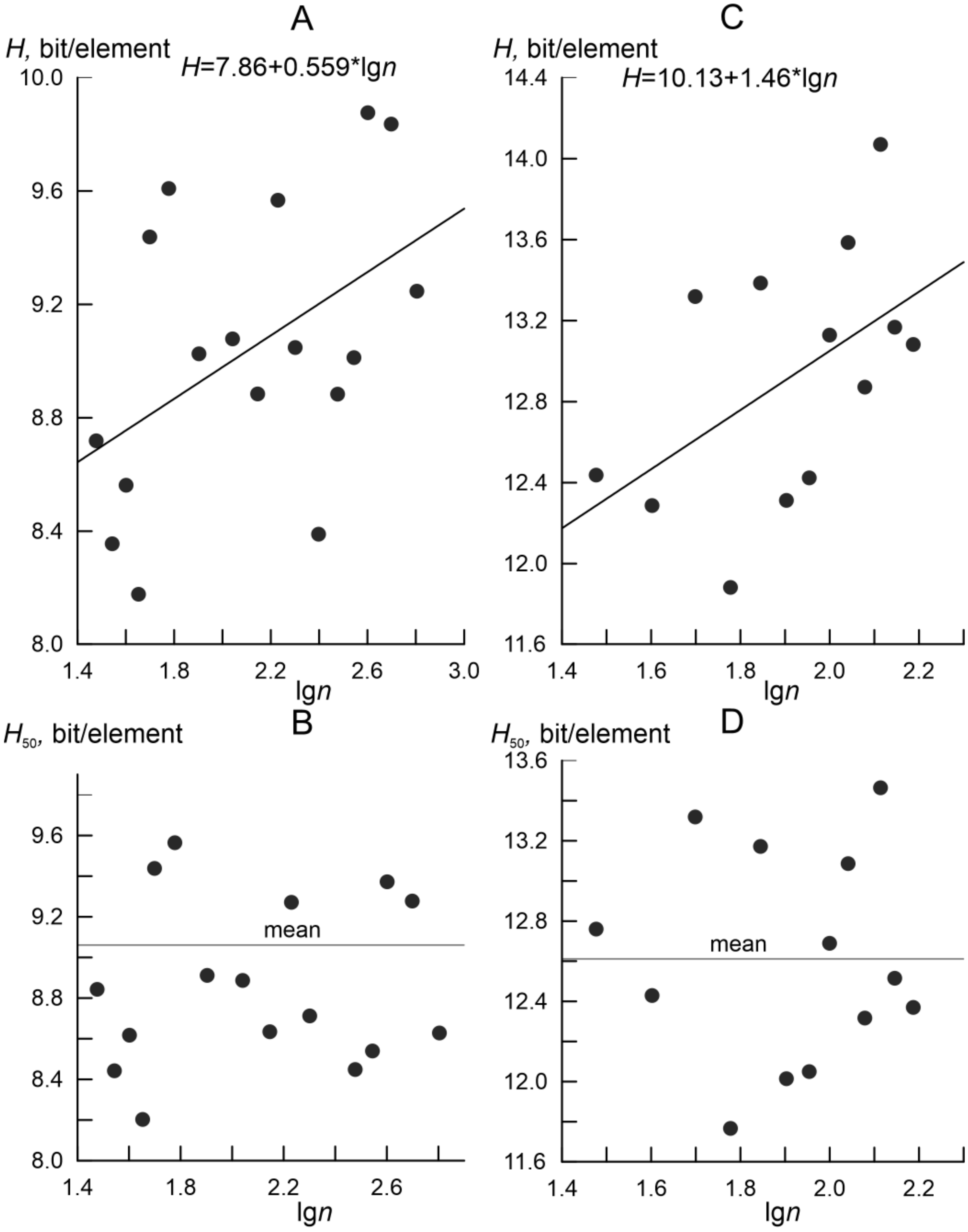

Fig. 2. Dependence of the entropy value (*H*) on the logarithm of the sample volume (lg*n*) before calibration (A, C) and its absence after calibration for H_{50} (B, D). A, B — SZM model based on centroid size and Procrustes coordinates, C, D — SZM model based on standard measurements.

phometrics, fit completely within the limits of variability of these parameters obtained on the basis of standard variables of the skull and mandible in this species. This result confirmed the hypothesis of invariance of the parameters of dimensional diversity with respect to the method of measuring the element sizes (standard variables or variables of geometric morphometrics).

Parameters H_{d50} and R_{50} did not characterise the shape variability in the SHM model based on intermediate results of geometric morphometrics (Fig. 3B). The range of variation of the parameters significantly shifted relative to the range of variation of the same parameters obtained based on standard measurements. For Procrustes coordinates, Kendall's Tau metric reflected an estimate of the probability that the landmark coordinates changed in a consistent manner, versus the probability of random variability. This interpretation differed from that for standard measurements (variables). In the latter case, the probability that the ranked variables changed in a consistent manner was assumed to be proportional to the similarity in "shape" between the two items for positive values of the metric, or to the differences between them for negative values of the metric. The results indicate that the R50 of variation of the Procrustes coordinates of different landmarks is significant larger than in the case of standard variables. Therefore, the SHM model based on primary geometric morphometrics data is not equivalent to a similar model based on standard variables.

The interpretation of SZM and SHM models based on intermediate results of geometric morphometrics is

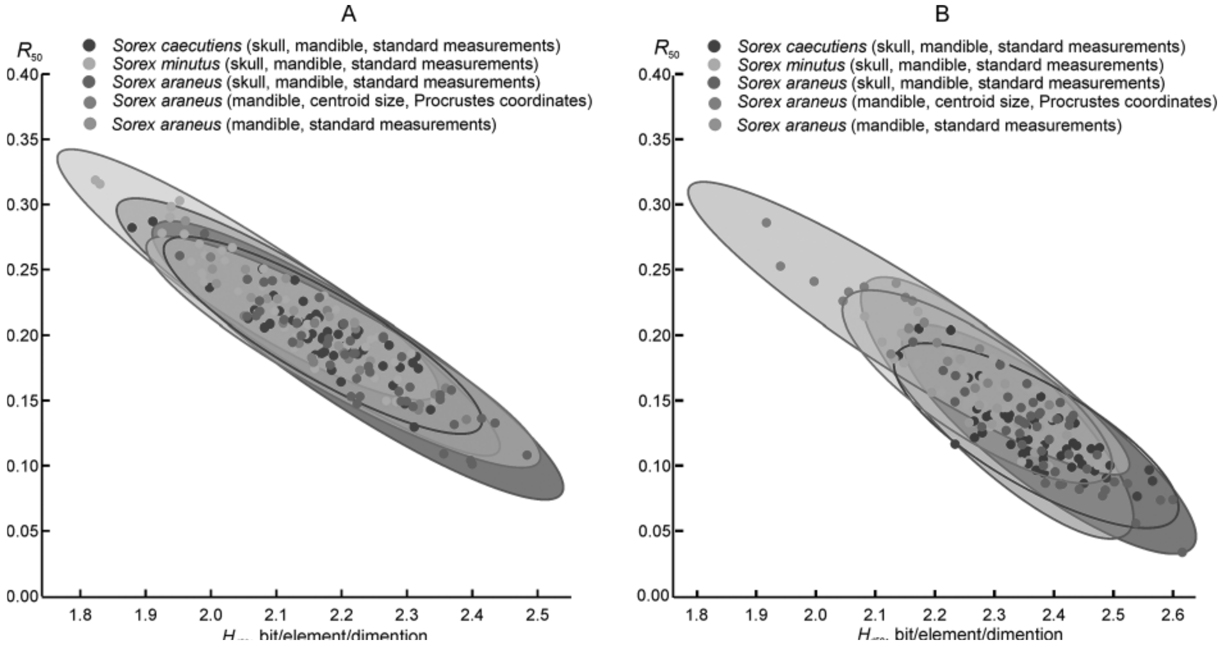

Fig. 3. Co-variation of R_{50} and H_{d50} in SZM (A) and SHM (B) descriptive models of skull and mandible diversity or only mandible diversity in three shrew species. Ellipses bound the 95% confidence interval of the mean values of parameters of diversity in different samples.

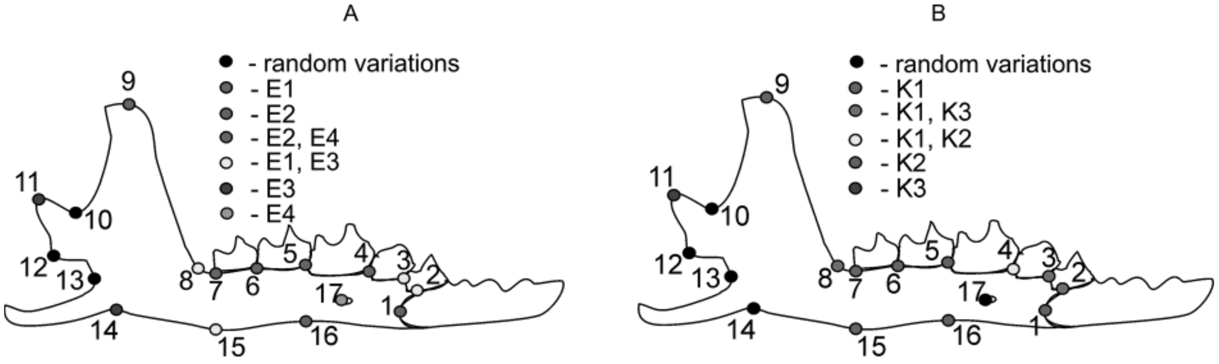

Fig. 4. Landmarks whose Procrustes coordinates correlate with different coordinates of the SZM (A) and SHM (B) descriptive models.

not included in the list of tasks of this study. Only the following should be noted. The coordinates of models E1, E2 and K1, K2 were statistically significantly correlated with the logarithm of the centroid size. This usually implied the presence of allometric variability. This diversity had two independent components in our case. Landmarks whose position variability was described by only one coordinate form an orthogonal variability basis (Fig. 4). In the SZM model, this base consists of landmarks correlated only with coordinate E1 (landmarks 6, 7 and 9), coordinate E2 (1 and 16), coordinate E3 (11 and 14) and coordinate E4 (17). In the SHM model, variation of landmarks 6, 7, 9 and 15 were correlated with coordinate K1. The landmarks 1, 5 and 15 correlated with coordinate K2, 16 and landmark 11correlated with coordinate K3. The position of landmarks 10, 12, and 13 varied randomly in both models.

Finally, we did not find any clusters in the SZM and SHM morphospaces that could be linked to the chromosomal races of shrews.

Discussion and conclusion

Here, we probably for the first time talk about the problem of information parameters of diversity invariance from the methods of getting initial data (measurements). Earlier, one of the authors (AP) showed on different objects that parameters like entropy, self-organization index and some others (Puzachenko, 2013, 2016) do not depend on the number of skull measurements (starting from about 10) or differences in the sets of standard measurements used for different groups of mammals. The lack of sensitivity of information parameters to the primary skull measurement system is due to the fact that they are general characteristics (*macro*parameters) of the skull, and comparable information about diversity is contained in almost any standard set of measurements used by morphologists. This invariance of the parameters may be due to the fact that the measured diversity is the result of the same morphogenetic developmental mechanism for the skull in mammals. It can be well correlated with the concept of a "generalised regulator", as defined by Ashby (1956, 1962) and Conant & Ashby (1970). The totality of these mechanisms at the level of morphological structures in mammals (skull, postcranial elements) does not provide a "hard" control of size or shape diversity. Under the natural limitation that single morphosystem or several systems, weakly differentiated within the morphological space, are analysed, the norm for the value of R_{50} of the mammalian skeleton is less than ≈ 0.301 and greater than ≈ 0.01 (Puzachenko, 2023). The range of R_{50} variation within this interval has a theoretical basis that is supported by a large array of empirical data (Puzachenko, 2016, 2023). We especially emphasize that information variables (macroparameters) obtained on the basis of entropies (not only Shannon entropy) by definition (Shannon, 1949) are applicable to objects of different nature, as well as to their mathematical models (see, for example, O'Keefe *et al*., 2022).

In this study, we tested the hypothesis that diversity parameters are invariance of a specific set of variables used in geometric morphometrics. We used the centroid size and Procrustes coordinates together to make our calculations. Here, centroid size acted as variable of size a relatively independent from shape. We did not specifically study the problem of allometry, but the dimensionality of SZM (4) itself indirectly indicates the presence of allometric variability.

In our case study, the hypothesis of invariance of diversity parameters regardless of the set of measurements (variables) and the method of primary data processing was confirmed for the SZM models describing size diversity. This model was based on a matrix of Euclidean distances. Therefore, we believe that centroid size and Procrustes landmark coordinates can be used to calculate size diversity parameters. This means that SZM models based on geometric morphometrics data and standard measurements are equivalent. This expands the range of research objects that can be involved in the study of the phenomenon of morphological diversity when linear measurements are lacking. The combined use of the centroid size and the Procrustes coordinates of landmarks seems to be permissible without restrictions for calculation of diversity parameters by SZM descriptive model. At the same time, SHM models were not equivalent. Another variant of analysis in Procrustes form space while maintaining centroid sizes (Klingenberg, 2016) is also possible. In the future, it would be advisable to conduct a series of tests for various models of geometric morphospaces.

ACKNOWLEDGEMENTS**.** We are very grateful to three anonymous reviewers for their pertinent and very substantial comments and suggestions, which were taken into account or reflected directly in the revised manuscript. The research was conducted as part of the State Assignment of the Institute of Geography RAS Project No. FMWS-2024-0007 (conceptualization, data processing, draft preparation) and was completed within the framework of the Federal themes of the Zoological Institute RAS project No.125012800908-0 (data collection, data processing).

References

Ashby W.R. 1956. An introduction to cybernetics. London: Chapman & Hall. 306 p.

Ashby W.R. 1958. Requisite variety and its implications for the control of complex systems // Cybernetica. Vol.1. No.2. P.83–99.

Ashby W.R. 1962. Principles of the self-organizing system // Foerster H. von G. & Zopf W., Jr. (eds.). Principles of Self-Organization: Transactions of the University of Illinois Symposium. London: Pergamon Press. P.255–278

Bookstein F.L. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge: Cambridge University Press. 435 p.

Conant R.C. & Ashby R.W. 1970. Every good regulator of a system must be a model of that system // International Journal of Systems Science. Vol.1. No.2. P.89–97.

Foerster H. von. 1960. On self-organizing systems and their environments // Yovits M.C. & Cameron S. (eds.). Self-Organizing Systems. London: Pergamon Press. P.31–50.

Foote M. 1997. The evolution of morphological diversity // Annual Review of Ecology and Systematics. Vol.28. P.129–152.

Haken H. 2006. Information and Self-Organization. A Macroscopic Approach to Complex Systems. Berlin, Heidelberg: Springer-Verlag. 258 p.

Hammer Ø. & Harper D.A.T. 2005. Paleontological Data Analysis. Malden: Wiley. 351 p.

Kendall M.G. 1975. Rank Correlation Methods. London: Charles Griffin and Co., Ltd. 202 p.

Klingenberg C.P. 2011.MorphoJ: An integrated software package for geometric morphometrics // Molecular Ecology Resources. Vol.2. No.11. P.353–357.

Klingenberg C.P. 2016. Size, shape, and form: concepts of allometry in geometric morphometrics // Development Genes and Evolution. Vol.226. No.3. P.113–137.

O'Keefe F.R., Meachen J.A. & Polly P.D. 2022. On information rank deficiency in phenotypic covariance matrices // Systematic Biology. Vol.71. No.4. P.810–822.

Puzachenko A.Yu. 2013. [Invariants and dynamics of morphological diversity (a case study of mammalian skull)]. Doctoral (Biol.) Thesis. Moscow: IPEE RAN. 494 p. [in Russian].

Puzachenko A.Yu. 2016. [The quantitative patterns of morphological disparity of mammalian skull] // Archives of Zoological Museum of Lomonosov Moscow State University. Vol.54. P.229–268 [in Russian].

Puzachenko A.Yu. 2020. [Shannon-Hartley law and the limit of internal ordering of biological systems] // Principles of Ecology. Vol.3. P.28–44 [in Russian].

Puzachenko A.Yu. 2023. Basic limitations of self-organization by the example of high and low-integrated very complex systems (mammalian skeleton elements and mammalian fossil assemblages): from empirical evidence to theory // Biology Bulletin. Vol.50. Suppl.1. P.34–47.

Puzachenko A.Yu. & Kupriyanova I.F. 2023. Morphological diversity of the skull and lower jaw of three shrew species (Eulipotyphla, *Sorex*) during depressions and abundance peaks // Biology Bulletin. Vol.50. Suppl.2. P.52–68.

Rohlf F. J. & Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks // Systematic Zoology. Vol.1. No.39. P.40–59.

Shannon C.E. 1949. Communication in the presence of noise // Proceedings of the Institute of Radio Engineers. Vol.37. No.1. P.10–21.

Shchipanov N.A. & Pavlova S.V. 2017. Density-dependent processes determine the distribution of chromosomal races of the common shrew *Sorex araneus* (Lipotyphla, Mammalia) // Mammal Research. Vol.62. P.267–282.

Shchipanov N.A., Voyta L.L., Bobretsov A.V. & Kuprianoba I.F. 2014. Intra-species structuring in the common shrew *Sorex araneus* (Lipotyphla: Soricidae) in European Russia: morphometric variability could give evidence of limitation of interpopulation migration // Russian Journal of Theriology. Vol.13. P.119–140.

Simpson G.G. 1944. Tempo and Mode in Evolution. New York: Columbia University Press. 217 p.

Stirling A. 1998. On the economics and analysis of diversity // Science Policy Research Unit (SPRU), Electronic Working Papers Series. No.28. P.1–156.

Stirling A. 2007. A general framework for analysing diversity in science, technology and society // Journal of the Royal Society Interface. Vol.4. No.15. P.707–719.

Sturges H. 1926.The choice of a class-interval // Journal of the American Statistical Association. Vol.21. P.65–66.

Vasil'ev A.G., Vasil'eva I.A., Shkurikhin A.O. 2018. [Geometric Morphometrics: from Theory to Practice]. Moscow: KMK Scientific Press. 471 p. [in Russian]

Vernadsky V.I. 1978. [Living Substance]. Moscow: Nauka. 358 p. [in Russian].

Zelditch M.L., Swiderski D.L., Sheets H.D. & Fink W.L. 2004. Geometric Morphometrics for Biologists: a Primer. London: Elsevier Academic Press. 437 p.