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Craniometry of mountain voles of the genus *Alticola* (Rodentia: Arvicolinae): Orthogonal decomposition of multivariate variability into intra- and interspecific components

Vera Y. Kovaleva*, Vadim M. Efimov, Igor V. Moroldoev & Yuri N. Litvinov

ABSTRACT. In the analysis of quantitative traits within a genus, distinguishing between intra- and interspecific variability is crucial. This study aimed to separate and compare these two components of diversity in the skull morphology of mountain voles. Using Fisher's method, we performed an orthogonal decomposition of a craniometric data matrix from 12 species and subspecies of the genus *Alticola* (311 specimens, 15 traits). We created two statistically independent matrices: one representing interspecific variation (differences between species' weighted centroids) and another representing pooled intraspecific variation (the combined within-group variability). The total variance of the original data was partitioned entirely between these two new matrices. The interspecific component accounted for 44.32% of the total variance, while the intraspecific component accounted for the remaining 55.68%. For each matrix, we computed principal components, which were interpreted as structural-functional modules. The analysis revealed that the first principal component in all cases represented general size-age variability, while the second and third components captured shape variation in the skull and mandible. However, the overall modular structure differed significantly between the interspecific and intraspecific levels. The main finding was that the integration of traits from the facial and cerebral parts of the skull, and mandible was only observed in the interspecific matrix. This suggests that the phenotypic patterns driving divergence between species are distinct from the patterns of variation within species. We propose that this difference may be due to differing rates and mechanisms of epigenetic and genetic restructuring of the phenotype operating at these separate evolutionary levels.

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Краниометрия скальных полевок рода *Alticola* (Rodentia: Arvicolinae). Ортогональное разложение многомерной изменчивости на внутри- и межвидовую компоненты

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РЕЗЮМЕ. При статистическом анализе количественных признаков на уровне рода необходимо различать внутри- и межвидовую изменчивость. Такой подход позволяет представить общую изменчивость как сумму внутри- и межвидового разнообразия и анализировать эти типы изменчивости по отдельности. По методу Фишера, мы ортогонально разложили исходную матрицу краниометрических признаков 12 видов и подвидовых форм скальных полёвок рода *Alticola* (311 объектов × 15 признаков) на две: межвидовую и объединённую внутривидовую. Значения краниометрических признаков полученных новых матриц в совокупности не коррелируют друг с другом и отражают, соответственно, изменчивость между видами (= их взвешенными центроидами) и изменчивость, которая получится из общей, если совместить центроиды всех 12 видов/форм и объединить их внутривыборочную изменчивость. Соответственно, суммы дисперсий всех признаков общей матрицы (100%) равны суммам дисперсий двух производных матриц. На долю межвидовой матрицы пришлось 44.32%, на долю внутривидовой — 55.68%. Для каждой матрицы вычислены главные компоненты, которые рассматриваются как статистически независимые структурно-

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функциональные модули. Первая главная компонента всех трёх матриц, это размерно-возрастная изменчивость. Вторая и третья — изменчивость формы черепа и нижней челюсти. Модульная структура межвидовой и внутривидовой изменчивости различается. В частности, только для межвидовой матрицы наблюдается интеграция признаков лицевого и мозгового отделов черепа и нижней челюсти. Возможной причиной этому могут быть различия в скоростях эпигенетических и генетических перестроек фенотипа.

КЛЮЧЕВЫЕ СЛОВА: метод главных компонент, размер и форма, морфологическая интеграция и модульность, лицевой и мозговой отделы черепа, *Alticola*.

Introduction

The mammalian skull is a complex structure consisting of semi-autonomous parts (modules) that demonstrate close relationships within themselves but weaker ones with other modules. Different parts of the skull can have different macroevolutionary dynamics and various links with ecological factors, developmental factors, and lifestyle, from diet and locomotion to reproductive strategy (Porto *et al*., 2009; Goswami *et al*., 2023; Kyomen *et al*., 2023). Differences in the approaches and methods of different authors are the reason for the lack of a unified model of mammalian skull modularity. Nevertheless, it appears that there is a hierarchical organization of the skull, in which the facial and cerebral parts (or the facial part, base, and vault) can be decomposed into smaller modules (from 3 to 17 according to different authors for different datasets) (Hallgrímsson *et al*., 2007; Koyabu *et al*., 2014; Goswami *et al*., 2023). The main reasons for the modular structure of the skull are considered to be the common ontogenetic origin and function of its constituent elements (Hallgrímsson *et al*., 2007; Porto *et al*., 2009; Hall & Hanken, 2023).

Currently, the methods and technologies used for the analysis of cranial data are becoming increasingly accurate, and the volume of knowledge about the mammalian skull is growing exponentially (Fostowicz-Frelik & Tseng, 2023). Because of the advent of computed microtomography and a new conceptual approach involving framing tasks and interpreting results within the concepts of MorphoEvoDevo (evolutionary developmental morphology) (Hallgrímsson *et al*., 2007; Wanninger, 2015; Koyabu, 2023), as well as ideas about the modular organization of the skull (Goswami & Polly, 2010; Goswami *et al*., 2014; Esteve-Altava, 2017; Goswami *et al*., 2023; Sherratt & Kraatz, 2023), research in this field has reached a new scientific level. Evidence of this is the recent thematic issue of the journal Philosophical Transactions of the Royal Society published in 2023, 'The mammalian skull: development, structure and function' containing review and original articles that capture the current state of affairs in this subject area and define the main directions for future research (Fostowicz-Frelik & Tseng, 2023). For example, for the paleontological record when working with fossils (due to the unavailability of DNA analysis), the search for phylogenetic, allometric, and ecological signals from different parts of the skull is discussed as a priority task, since such finds are most common. One of the current tasks related to the topic of our research is the separation of the influence of different factors (functional, evolutionary, genetic, and ecological) on the patterns of skull modularity, in ontogenetic and historical aspects, using the broadest possible coverage of different systematic groups of organisms (Fostowicz-Frelik & Tseng, 2023).

In the statistical analysis of quantitative traits at the genus level, and in current article we will focus on the species and intraspecific forms of the little-studied genus of mountain voles *Alticola* of the subfamily Arvicolinae, it is necessary to distinguish between intra- and interspecific variability. This approach allows representing the total variability as the sum of intra- and interspecific diversity and thereby focusing attention on the similarities and differences of these different types of variability. Interspecific variability reflects the diversity of species acquired during evolutionary time and genetically fixed, due to isolation, genetic drift, and features of adaptation to species-specific ecological niches. Intraspecific diversity arises and realizes in the process of individual development in interaction with the environment of individuals from different populations of the same species.

One of the strategies for the multivariate analysis of quantitative data is orthogonal decomposition. The idea of orthogonal decomposition in the case of one trait belongs to Ronald-Fisher — one-dimensional analysis of variance (ANOVA) (Fisher, 1918). The development of this idea led Ronald Fisher to multivariate discriminant analysis (Linear Discriminant Analysis, LDA) — a method for finding several orthogonal lines (discriminant axes), onto the projection of which the point clouds representing the samples are most distinct. The method was illustrated using the example of three species of irises in the space of four morphological traits (Fisher, 1936). Both the data and the method have entered all statistical textbooks, and with the advent of computers, into packages for multivariate statistical analysis.

However, over time, LDA revealed an unexpected unpleasant effect. At the preliminary stage of statistical processing, the researcher selects traits, standardizes them, and selects a suitable Euclidean distance between objects. This was done in order to most adequately (from the researcher's point of view) represent biological diversity through the mutual arrangement of objects in multidimensional space. Therefore, from a substantive point of view, it is natural to expect that both the discriminant axes and the projections of objects onto them would be computed while preserving the distances between objects. This means that the only permissible transformation is the rotation of the entire set of objects as a rigid body in multidimensional space (Ul'yanov, 2020). However, in LDA, any non-degenerate linear transformation is permissible (Wilks, 1947). Thus, when maximizing the Fisher criterion, in addition to rotation, compression or stretching of the set of distances between objects along some axes of the multidimensional space can, and usually does, occur unnoticed by the user, precisely such that the differences between samples will be emphasized certainly better, and the calculated reliability higher, than with rotation alone. However, in essence, this will be a fitting to the desired result, and the real biological meaning can be distorted, up to its complete loss. Therefore, in this work, we use only rotation in multidimensional space.

A similar problem exists in Hotelling's canonical correlation analysis (Canonical Correlation Analysis, CCA) (Hotelling, 1936). If we have two systems of traits for the same objects, then we can find two such linear combinations of traits, one for each system, that the correlation between them will be maximum. The method is impeccable from a mathematical point of view, it is also included in all statistical textbooks and packages, but practically it does not work. The result, as a rule, is very high correlation coefficients, up to unity, but at the same time very small variances of the found linear combinations. Since proportion of the variability of both systems is too small, they are simply useless for researchers. The difference with LDA is that the lack of a biologically meaningful result when applying CCA was discovered almost immediately. However, the modern analogue of CCA — 2B-PLS analysis (Wold *et al*., 1984, 2001; Rohlf & Corti, 2000) —Instead of correlation, the covariance of linear combinations of traits is maximized, which works excellently in practice.

The aim of the article is to decompose the total variability of the craniometric traits of mountain voles of the genus *Alticola* Blanford, 1881 into two independent components: intra- and interspecific, with the subsequent search for patterns of modularity in both systems.

Material and methods

The analysis of intra- and interspecific variability of mountain voles of the genus *Alticola* was carried out on 15 traits of the skull and mandible. The total sample size was 311 specimens belonging to 10 species and 2 subspecies of the genus *Alticola* (Tang *et al*., 2018; Kryštufek & Shenbrot, 2022): *Alticola* (*Alticola*) *argentatus* (Severtzov, 1879), *A.* (*Alticola*) *barakshin* Bannikov, 1947, *A.* (*Alticola*) *olchonensis* Litvinov, 1960, *A.* (*Alticola*) *semicanus* G. M. Allen, 1924, *A.* (*Alticola*) *stoliczkanus* (Blanford, 1875), *A.* (*Alticola*) *stracheyi* Hinton, 1926, *A.* (*Alticola*) *strelzovi* (Kastschenko, 1899), *A.* (*Alticola*) *tuvinicus* Ognev, 1950, *A.* (*Alticola*) *tuvinicus khubsugulensis* Litvinov, 1973, *Alticola* (*Aschizomys*) *macrotis* (Radde, 1861), *A.* (*Aschizomys*) *macrotis fetisovi* Galkina & Epifantseva, 1986, *A.* (*Aschizomys*) *lemminus* (G.S. Miller, 1898). The main part of the sample is represented by specimens of mountain voles of the age groups subadultus and adultus, stored in the collection of the Zoological Museum of ISEA SB RAS, Novosibirsk (*n* = 235). Photos of the skulls were taken in three

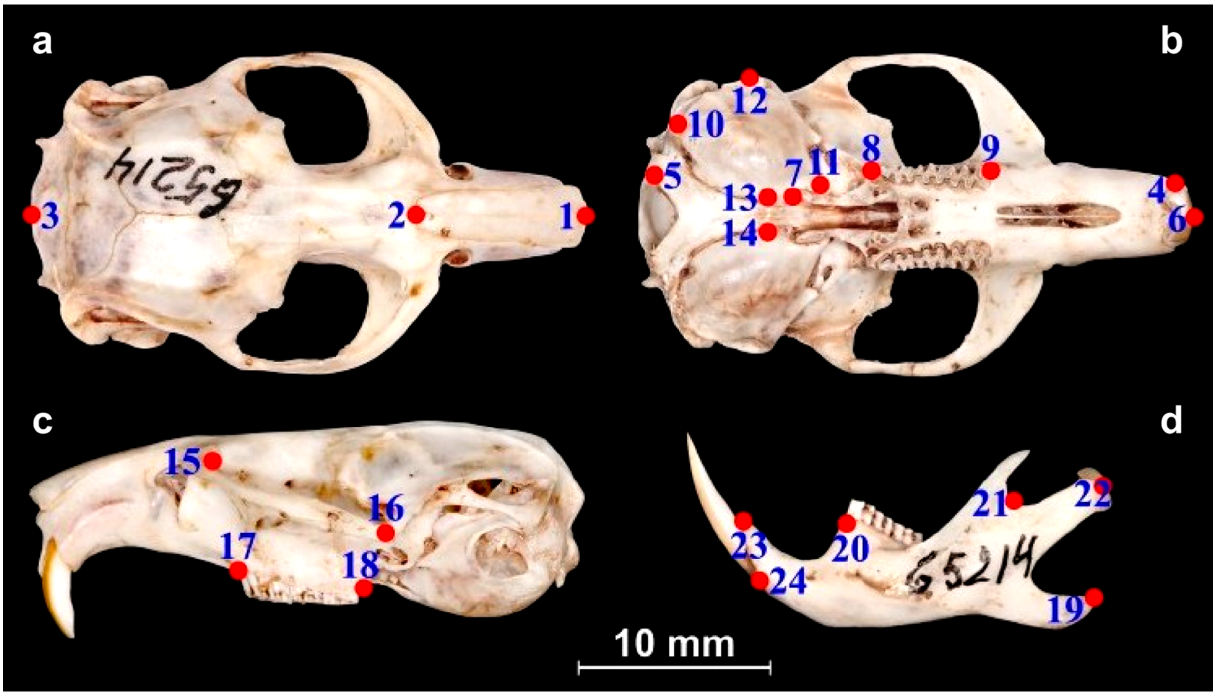

Fig. 1. Placement of reference points for the dorsal (a), ventral (b), and lateral (c) projections of the skull and the mandible (d). Specimen *A. tuvinicus*, collection of the Zoological Museum of ISEA SB RAS, Novosibirsk.

projections (dorsal, ventral, and lateral) and of the mandible — in lateral projection (Canon EOS 1100 D camera with Tamron SP 60 mm F/2 macro 1:1 lens) with a ruler, graduated in millimeters at a fixed distance of 38 centimeters. Fifteen measurements of each specimen were obtained from the photographs (Fig. 1) using the tpsDig ver. 2.22 environment (Rohlf, 2015). Abbreviations for these measurements (Tang *et al*., 2018) are as follows: skull greatest length (SGL), skull basilar length (SBL), zygomatic breadth (ZB), median palatal length (MPL), nasal length (NL), length of maxillary toothrow (LMxT), length of upper molar row (LUMR), length of maxillary diastema (LMxD), length of tympanic bulla (LTB), width of tympanic bulla (WTB), distance between tympanic bullas (DTB), length of mandible (LM), oral height of the vertical ramus (OHVR), length from the condyle (LC), and length of the mandible diastema (LMD). Then, the resulting matrix of craniometric traits was supplemented with measurements of mountain vole specimens from China (n = 76 specimens), which were taken from the table published in the Appendix to the article by Tang *et al*. (2018: 44).

In this study, we deliberately used the craniometric measurement scheme of our Chinese colleagues in order to subsequently combine both samples. Before combining the samples, we assessed the measurement error. It turned out that the centroids of the species *A. argentatus* and *A. semicanus* (and these species are most fully represented in both samples), computed separately for the samples from Russia and China, are closer to each other than to neighboring species, and the single specimen of *A. strelzovi* from China is included within the sample from Russia. This gives us every reason to combine both samples (Table 1).

One of the main directions of morphological variability in voles, both intra- and interspecific, is the nonlinear variability of size associated with the growth of organisms — allometry, usually expressed by the formula $y = ax^b$. After logarithmization, the relationship becomes linear: $\log(y) = \log(a) + b \times \log(x)$. In this regard, before statistical processing, all traits were logarithmized.

As a variable reflecting the entire size component of the total variability of traits, either the mean of all logarithmized values of all traits of a given individual is used (Mosimann, 1970; Darroch & Mosimann, 1985), or the first principal component (PC1) arising from the analysis of quantitative traits by the principal component analysis (PCA) method of all logarithmized traits of all individuals (Klingenberg, 1996).

These same methods are also used in modern geometric morphometrics (Mitteroecker & Schaefer, 2022). In practice, both methods give similar results. For example, in the work (Kovaleva *et al*., 2014) the correlation coefficient between the mean size by Mosimann's method and PC1 by Klingenberg's method was 0.991. In the present work, the mean size of each specimen was computed using James Mosimann's method and decomposed into intra- and interspecific components.

Table 1. Characteristics of the mountain vole samples.

Species/Subspecies	*n*	Region
A. (*Alticola*) *argentatus*	36	Kyrgyzstan (Central Tien Shan, Naryn-Too Range, Terskey Ala-Too Range), Tajikistan (Gissar Range), China (Xinjiang Uygur Autonomous Region)
A. (*Alticola*) *barakshin*	12	Russia (Tuva, Mongun-Taiga District)
A. (*Alticola*) *olchonensis*	29	Russia (Irkutsk Region: Baikal, Olkhon, Ogoy, Zamogoy, Khubyn Islands)
A. (*Alticola*) *semicanus*	56	Russia (Tuva, Erzin District), Mongolia (Arkhangai Aimag, Khangai Range; Khövsgöl Aimag, Khuvsgul Lake), China (Inner Mongolia)
A. (*Alticola*) *stoliczkanus*	13	China (Gansu Province, Qinghai Province, Tibet Autonomous Region)
A. (*Alticola*) *stracheyi*	10	China (Qinghai Province, Tibet Autonomous Region)
A. (*Alticola*) *strelzovi*	31	Russia (Altai: Chemal District, Onguday District, Ulagan District, Kosh-Agach District), China (Aletai region, Xinjiang)
A. (*Alticola*) *tuvinicus tuvinicus*	36	Russia (Tuva: Tes-Khem District, Barun-Khemchik District, Bay-Tayginsky District, Ulug-Khem District; Khakassia: Bograd District, Ordzhonikidzevsky District, Shirinsky District; Krasnoyarsk Territory, Uzhur District)
A. (*Alticola*) *t. khubsugulensis*	23	Mongolia (Khövsgöl Aimag, Khuvsgul Lake)
A. (*Aschizomys*) *macrotis macrotis*	30	Russia (Buryatia: Severo-Baikalsky District, Kabansky District, Barguzinsky District; Altai, Ulagan District; Kemerovo Region, Novokuznetsk District; Khakassia, Tashtypsky District)
A. (*Aschizomys*) *m. fetisovi*	30	Russia (Zabaykalsky Krai, Sokhondinsky Nature Reserve)
A. (*Aschizomys*) *lemminus*	5	Russia (Zabaykalsky Krai, Kalarsky District)

Note: Within the framework of this work, the subspecies *A.* (*Alticola*) *tuvinicus khubsugulensis* and *A. (Aschizomys) macrotis fetisovi* are considered on a par with species (without claiming to change the systematics) solely for the purpose of a more detailed characterization of the craniometric variability of the genus *Alticola*.

The decomposition of the total variability into intra- and interspecific is carried out as follows. From the matrix of the original craniometric traits, two new matrices of the same size are computed: interspecific and pooled intraspecific. In the interspecific matrix, each specimen for each trait is assigned the value of the centroid of its species; in the pooled intraspecific matrix — the difference between the original value and the centroid. The sum of these matrices is obviously equal to the original matrix. This method was proposed by Fisher in the ANOVA method (Fisher, 1918). The idea is that the intergroup variability is subtracted from the total variability, leaving the intragroup variability, in which the intergroup one is absent. In this case, the general matrix of traits is decomposed into interspecific and pooled intraspecific. The sum of the squared distances between two specimens for all traits of the new matrices is equal to the squared distance between them in the general matrix, and the new matrices are mutually orthogonal to each other, that is, the correlation of any trait from the interspecific matrix with any trait from the pooled intraspecific matrix is zero.

The sum of the squared distances between all specimens for all traits of the new matrices is equal to the sum of the squared distances between them in the general matrix. This relationship is preserved under any rotations of the set of all objects in the multidimensional space. However, this is a property of the aggregate, and it does not have to hold for each individual trait. Therefore, one can reconsider the task set by Fisher, but, unlike him, use only rotations: to find the subspace in the projection onto which the proportion of interspecific variability is maximum. For this, it is necessary to compute the principal components (PCs) of the interspecific matrix of traits. For the purposes of this article, we computed the PCs of the three matrices considered here.

To solve the problem of multiple comparisons when calculating the reliability of the correlation coefficients of the components with the original traits, the Bonferroni correction was used (Narkevich *et al.*, 2020). When applied, statistically significant values of the correlation coefficients for a sample size of $n = 311$, number of correlation coefficients $N_B = 154$ (9×16) and significance level $p < 0.001$ start from 0.253 (effect size 6.3%), therefore in the article we analyze only correlation coefficients exceeding this value.

Calculations were performed using Excel 2016, statistical packages Statistica12 (StatSoft Inc., Tulsa, OK, USA), PAST4 (Hammer *et al.*, 2001) and Jacobi4 (Polunin *et al.*, 2019).

Results

Using Fisher's method, we orthogonally decomposed the original (All) matrix of craniometric traits of 12 species and subspecific forms of mountain voles of the genus *Alticola* (311 objects × 15 traits) into two other matrices: interspecific (Inter) and pooled intraspecific (Intra), each also sized 311 × 15. Accordingly, the sums of the variances of all traits of the All matrix (100%) are equal to the sums of the variances of the Inter and Intra matrices. The Inter matrix accounted for 44.32%, and the Intra matrix for the remaining 55.68%.

PCs were computed separately for all matrices, in order to find the directions of maximum variability and identify the traits associated with these directions. We focused on the discussion of the first three PCs of the studied matrices, which together account for: All — 84.53%, Inter — 93.39% and Intra — 81.58% of the trait variances (Table 2).

Traditionally, in the analysis of quantitative traits, the direction with the greatest variance — PC1, represents size-age variability. This unconditionally holds for All-PC1; all 15 craniometric traits of this matrix

Table 2. Variances of the principal components (PC1–PC15) of the total (All), inter- (Inter) and intraspecific (Intra) matrices of craniometric variability of mountain voles.

PC	All-Var,%	All-Sum,%	Inter-Var,%	Inter-Sum,%	Intra-Var,%	Intra-Sum,%
PC01	70.69	70.69	74.87	74.87	68.83	68.83
PC02	7.85	78.54	10.17	85.04	7.32	76.15
PC03	5.99	84.53	8.35	93.39	5.42	81.58
PC04	4.10	88.63	3.23	96.63	4.25	85.83
PC05	2.78	91.41	1.49	98.11	3.09	88.92
PC06	2.34	93.76	0.86	98.97	2.70	91.63
PC07	1.96	95.72	0.56	99.53	2.37	93.99
PC08	1.07	96.79	0.26	99.79	1.58	95.57
PC09	0.96	97.75	0.15	99.94	1.31	96.88
PC10	0.68	98.44	0.03	99.98	1.00	97.88
PC11	0.57	99.01	0.02	100.00	0.75	98.63
PC12	0.40	99.40	0.00	100.00	0.56	99.19
PC13	0.34	99.75	0.00	100.00	0.46	99.65
PC14	0.15	99.90	0.00	100.00	0.21	99.85
PC15	0.10	100.00	0.00	100.00	0.15	100.00
Σ Λ, %	100.00		44.32		55.68	

Note: Σ Λ, % — total variance of the PCs of the three matrices of craniometric variability in percent.

contributed highly significant positive loadings to the component (Table 3).

However, for the orthogonal matrices Inter and Intra, this does not seem so obvious. Since a variable reflects the size component of variability, we computed the mean size of each specimen using James Mosimann's method and decomposed it into intra- and interspecific components (Table 3, trait M). The table shows that the correlation coefficients of M with the corresponding PC1 of all matrices (All, Inter and Intra) were close to unity, and with other PCs — were not significant (Table 3). This indicates that the size of individuals in the orthogonal matrices (Inter and Intra) is also almost entirely concentrated in PC1. Here, for the Inter-matrix, these are interspecific differences, and for the Intra-matrix, these are within-sample differences in the size of the skull and mandible.

It is noteworthy that the trait DTB is the only one that has no size variability in the Inter-matrix, and almost entirely enters the next component — PC2. PC2 and PC3 are responsible for the variability of proportions and are free from the size influence. Inter-PC2 (λ= 10.17%) is formed by the contributions of traits related to different parts of the skull and mandible. The main contribution to the component is made by DTB; it partially determines the width of the skull in its cerebral part, and, together with SBL, characterizes the ratio of the length and width of the skull. LUMR and LMxD contribute approximately equal in value but opposite in sign contributions to the component, which is also a characteristic feature of intramodular interactions in the facial part of the skull in different species. In addition, traits OHVR and LC, have significant contributions to this component, belonging to another bone structure — the mandible.

The direction of interspecific variability Inter-PC3 (λ=8.35%) is formed by the traits LTB and WTB. These are the proportions of the auditory capsule. NL, LMxD and LMD make negative contributions to the component. These traits are located quite far from each other, but from a structural-functional standpoint, their coordinated variability looks quite logical. The length of the nasal bones on the dorsal side of the skull is related to the length of the upper diastema on the ventral side, such that they fuse to form the rostrum, which in turn corresponds to the diastema of the lower jaw. Species are grouped in the Inter-PC1–Inter-PC2 and Inter-PC2–Inter-PC3 spaces as follows (Figs 2 and 3).

In the projection onto the size axis, Inter-PC1, three groups of species are recognized: with small-sized (*A.m. fetisovi, A. lemminus*), medium-sized (*A. stracheyi, A. stoliczkanus, A. argentatus, A.t. khubsugulensis, A. macrotis, A. strelzovi*) and large-sized skulls (*A. barakshin, A. olchonensis, A. semicanus, A. tuvinicus*). In the projection onto the axes Inter-PC2 and Inter-PC3, characterizing the proportions of the skull and mandible, the species lie more densely, but groups can be distinguished. For Inter-PC2 — three groups are recognized: *A. argentatus, A. stoliczkanus, A. barakshin, A. stracheyi*; *A. macrotis, A.m. fetisovi, A. tuvinicus, A.t. khubsugulensis, A. semicanus, A. olchonensis*; *A. lemminus* and *A. strelzovi*; and for Inter-PC3 — two groups are recognized: *A. argentatus, A. barakshin, A. semicanus, A.m. fetisovi* and

Table 3. Correlation coefficients (×1000) of the first three principal components (PC1–PC3) of the total (All), inter- (Inter) and intraspecific (Intra) matrices of craniometric variability of mountain voles with the original (logarithmized) traits.

Traits	All-PC1	All-PC2	All-PC3	Inter-PC1	Inter-PC2	Inter-PC3	Intra-PC1	Intra-PC2	Intra-PC3
SGL	**962**	69	114	**976**	202	0	**948**	–32	–26
SBL	**942**	128	128	**909**	**331**	–54	**963**	–75	–57
ZB	**925**	58	213	**953**	210	136	**900**	24	–124
MPL	**957**	96	–8	**986**	86	–67	**946**	25	39
NL	**883**	84	–186	**892**	–83	**–353**	**873**	43	75
LMxT	**969**	32	–117	**972**	–103	–158	**970**	37	–37
LUMR	**793**	–239	–178	**880**	**–381**	–16	**724**	15	**–372**
LMxD	**875**	202	–2	**821**	**313**	**–346**	**909**	–116	39
LTB	**786**	–245	**476**	**811**	143	**556**	**763**	**–365**	–105
WTB	**718**	**–409**	**475**	**788**	–8	**602**	**652**	**–487**	–147
DTB	**257**	**878**	238	–1	**942**	–125	**452**	**831**	–44
LM	**866**	–38	–200	**951**	–147	–124	**801**	89	114
OHVR	**742**	–154	**–268**	**730**	**–422**	–12	**769**	40	–193
LC	**936**	–82	–215	**932**	**–319**	–87	**947**	69	51
LMD	**727**	83	**–278**	**829**	–50	**–282**	**676**	–54	**675**
M	**999**	37	16	**998**	60	–13	**999**	15	–3
λ, %	70.69	7.85	5.99	74.87	10.17	8.35	68.83	7.32	5.42
Σ Λ, %	100			44.32			55.68		

Note: Correlations of traits with PCs significant by the Bonferroni criterion at p <0.001 are highlighted in bold font. Row M — correlation of the mean size of an individual, computed by James Mosimann's method, with the PCs of the three matrices of craniometric variability of mountain voles. Σ Λ, % — total variance of the PCs of the three matrices in percent.

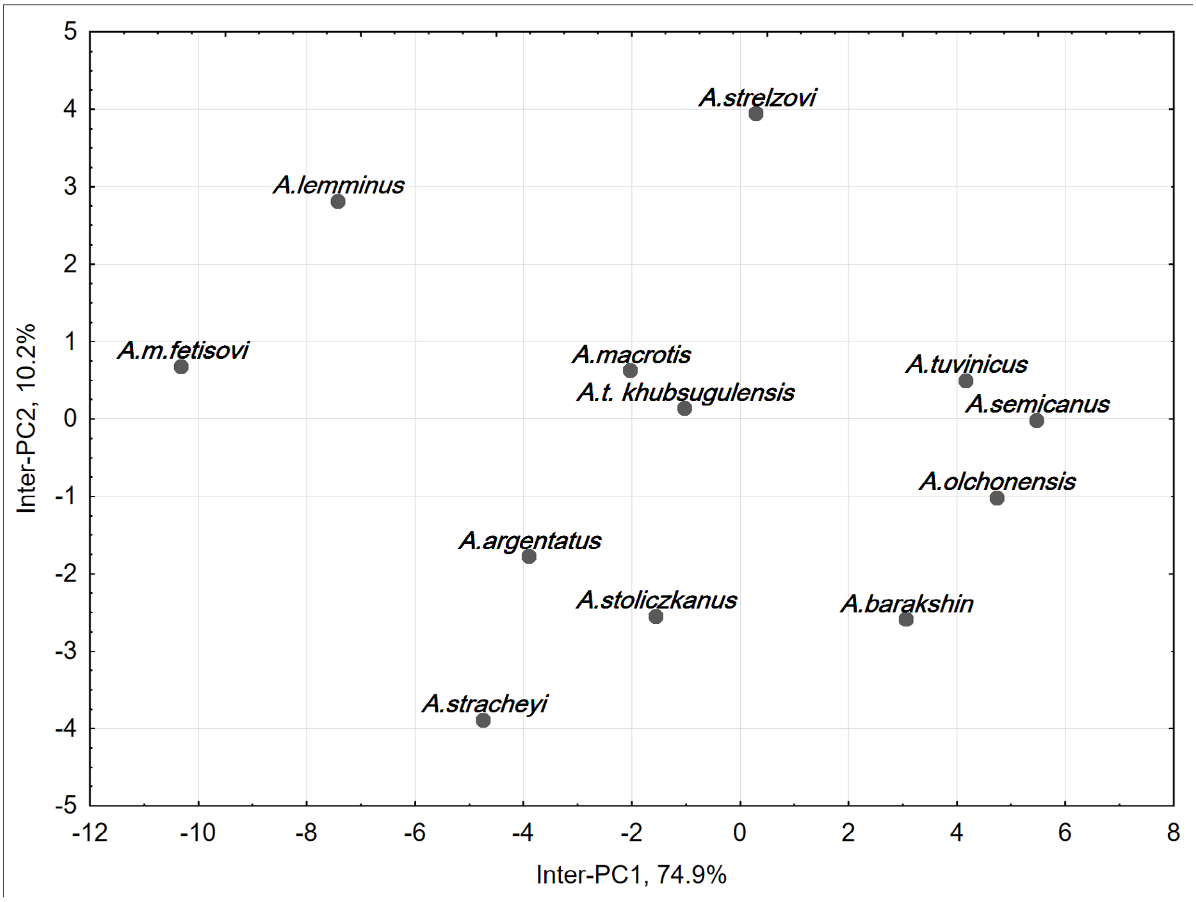

Fig. 2. The configuration of species centroids of mountain voles of the genus *Alticola* on the Inter-PC1–Inter-PC2 plane of craniometric variation (n = 12).

A. stracheyi, A. stoliczkanus, A. olchonensis, A.t. khubsugulensis, A. tuvinicus, A. macrotis, A. lemminus, A. strelzovi.

Now transitioning to the PCs of the Intra- matrix. Intra-PC2 (λ=7.32%) in terms of the contributions of traits of the cerebral part: LTB, WTB and DTB and in terms of the variance value is similar to All-PC2 (λ=7.85%), which is not surprising, since the general matrix is a mixture of inter- and intraspecific variability and the variance of the Intra-matrix predominates in it. The statistical relationship between the traits looks quite logical: the smaller the sizes of the auditory capsules, the greater the distance between them, assuming there is a certain "limit" on the intraspecific width of the skull. The traits LUMR and LMD make a significant contribution to the component Intra-PC3. The following intramodular interactions is observed: a decrease in LUMR is accompanied by an increase in LMD.

In the pooled intraspecific Intra-space, due to the large number of specimens, we considered the samples separately by species (Fig. 4). Intra-PC1–Intra-PC2 plane of craniometric variability (n = 311). Sample centroids are aligned with the zero coordinates of PC.

It can be seen, that the intraspecific samples are heterogeneous in size in the projection onto the Intra-PC1 axis. At the same time, large and small individuals (projection onto the Intra-PC2 component) can have the same proportions. This is especially clearly manifested in the subspecies *A.m. fetisovi* and *A.t. khubsugulensis*.

Discussion

The structural elements of the skull form subsets of traits that tend to change together during ontogeny and evolution, as opposed to others that are less connected. Traits included in such subsets are called 'integrated' (Olson & Miller, 1958). Division into subsets can be done formally by correlations between traits (r-groups) and substantively — by the principle of joint functioning of traits (F-groups). Ideally, both divisions should correspond to each other. The division of traits into r and F groups corresponds well to what was later called statistical and functional modules (Klingenberg, 2014). Everett Olson and Robert Miller believed that the description of such associations, as well as the study of the causes and consequences of integration, would lead

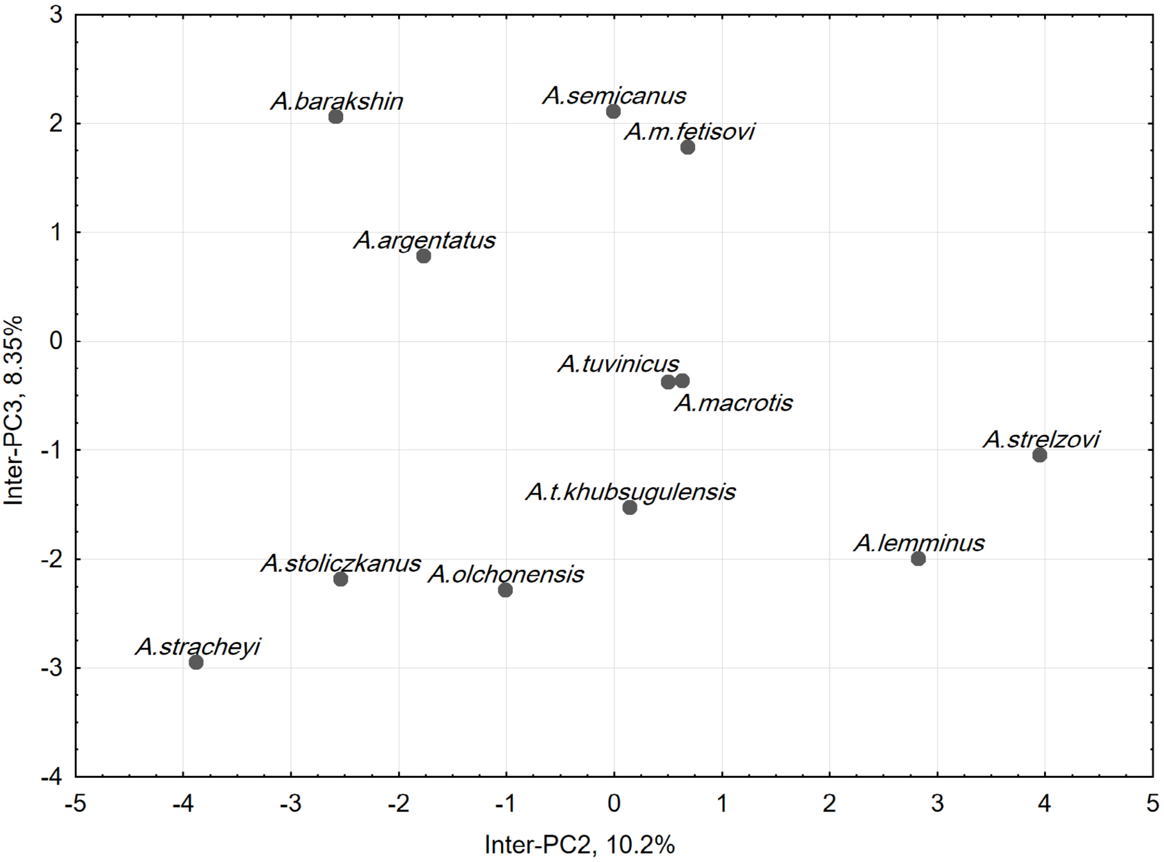

Fig. 3. The configuration of species centroids of mountain voles of the genus *Alticola* on the Inter-PC2–Inter-PC3 plane of craniometric variation (*n* = 12).

to more interesting and profound ideas about the nature of phenotypic evolution (Magwene, 2006).

In this article, using Fisher's method, we orthogonally decomposed the total variability (All) of the craniometric traits of mountain voles of the genus *Alticola* into two independent components: inter- (Inter) and pooled intraspecific variability (Intra). The application of PCA separately for these matrices made it possible to identify craniometric modules — PCs, characteristic of each of these systems/subsystems, which, by the method of identification, although they are statistical, however, in our opinion, are also united by the commonality of origin and function.

First of all, PC1 of all three matrices demonstrates that the skull and mandible are well-integrated structures. We can judge their coordinated ontogenetic growth by the uniform contributions of traits to the component. High correlations of trait M (mean size of the specimen, computed by Mosimann's method) reinforce the conclusion that for the Inter and Intra matrices, PC1, as well as for the All-matrix, is the direction of variability of general sizes. We can only guess that for Inter-PC1 these are interspecific genetic differences, and for Intra-PC1 — combined intraspecific ontogenetic and possibly epigenetic differences.

In the direction of Inter-PC1, three groups of species/intraspecific forms of voles that are well differentiated by size stand out (Fig. 2). The smallest form is the subspecies *A. m. fetisovi*. Judging by the figure, it differs noticeably from the nominative *A.m. macrotis* in the general size of the skull and mandible, but not in proportions (see the projection of the subspecies onto the Inter-PC2 axis). The same picture is observed in relation to the other two subspecies: *A.t. tuvinicus* and *A.t. khubsugulensis* (Fig. 2.). The subspecies differ only in size.

Intra-PC1 demonstrates high intraspecific heterogeneity of the samples, namely the presence for most species/forms of at least two size-age groups.

For PC2 and PC3 of all three matrices, correlations with size are not significant, so these components characterize certain features of the shape of the skull and mandible. Interspecific differences are mainly manifested in the trait DTB; almost all of its variability is invested in Inter-PC2 (effect size 88.7%). In the direction of the component, this trait increases, reaching maximum values in *A. strelzovi*. Integrated with DTB, the lengths SBL, LMxD increase and LUMR decreases. The mandible, at the same time, becomes lower and shorter.

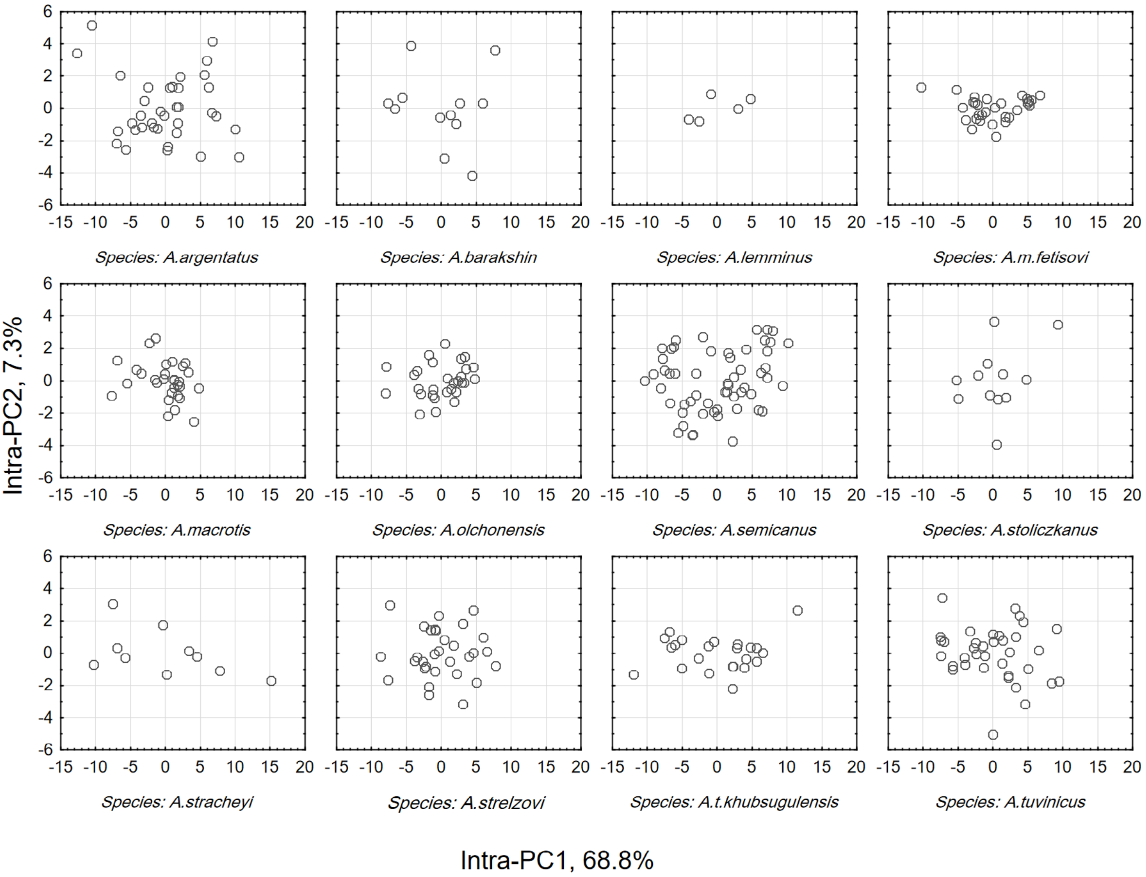

Fig. 4. Configuration of mountain vole specimens of the genus *Alticola*, separated by species and subspecies, on the Intra-PC1–Intra-PC2 plane of craniometric variability ($n = 311$). Sample centroids are aligned with the zero coordinates of PC.

In the projection onto the Inter-PC2 axis, the first group of species, located in the lower part of the graph (*A. argentatus, A. stoliczkanus, A. barakshin, A. stracheyi*) (Fig. 2) coincides with the so-called 'southern group' of species, inhabiting lower latitudes and higher altitudes, which we previously identified based on data on the variability of *cytb* amino acid sequences (Kovaleva *et al*., 2024). In the species of the 'southern group', an increase in the frequency of Leu → Val, Phe substitutions was found compared to the groups of 'northern species'. These amino acids with nonpolar (hydrophobic) radicals are similar in physicochemical properties, so the substitutions should not lead to significant changes in the structure of the protein molecule; nevertheless, an ecological conditionality of these substitutions has been discovered. The factors that have the greatest influence are soil frosts (especially in transitional seasons) and indicators of evapotranspiration or total evaporation from the soil surface and vegetation, which in all regions of the world correlate with the bioproductivity of ecosystems. Thus, based on the results of these two studies, the conclusion suggests itself about the influence of habitat factors on the phenotypic evolution of mountain voles at different levels of biological organization, molecular and organismal (the level of organ systems).

The question arises, why exactly does DTB occupy a central place among the other traits forming Inter-PC2? First of all, this trait apparently has the least age-related variability, since it is anatomically located at the base of the skull, and this structure reaches adult size and shape slightly earlier than the vault and facial part (Hallgrímsson *et al*., 2007). Secondly, the process of bone tissue formation at the base of the skull (endochondral ossification) differs from the process of ossification of the vault and facial part (intramembranous ossification). This difference is significant because endochondral ossification may be less susceptible to epigenetic interactions with neighboring tissues and organs than intramembranous ossification (Hallgrímsson *et al*., 2007). If this is the case, the component Inter-PC2, (with the trait DTB included in it to the maximum degree), can be considered as interspecific variability in the duration (rate) of ontogeny. Furthermore, a number of works have shown that the shape of the skull base (basicranium) has a significant phylogenetic signal (Cardini & Elton, 2008; Arnaudo *et al*., 2019).

In the facial part of the skull, there are also traits with early stabilization in ontogeny, for example, interorbital width. In craniometric studies, this trait almost always forms PC2 and is a marker of growth rate in populations. In particular, voles from different phases of population dynamics, as well as spring and autumn generations of voles having different ontogenetic developmental pathways, differ in this trait (Vasil'ev *et al*., 2003).

The third direction of interspecific differences, Inter-PC3, is associated mainly with the proportions of the auditory capsules (LTB and WTB) and the length of the rostrum (NL + LMxD), which are in a negative correlative relationship with each other and are integrated with LMD. From the point of view of possible interpretation, these bone structures are a reflection of sensory functions: hearing and smell. In the projection onto the Inter-PC3 axis, two groups of species are distinguished. The species of the first group: *A. argentatus, A. barakshin, A. semicanus* and *A.m. fetisovi* have skulls that are wider in the cerebral part with a shortened rostrum (animals with brachycephalic proportions of the facial part) than the others, forming the second group.

Intra-PC2–Intra-PC3 characterize the proportions of skulls associated with intraspecific variability. In Intra-PC2, the main contribution is made by the trait DTB already known to us, which is negatively dependent on the proportions of the auditory capsules (traits LTB and WTB); together they form a characteristic intramodular connection at the base of the skull. Intra-PC3 demonstrates the integration of the mandible and facial skull.

Over the past few years, a number of studies have been published in which the commonality of ontogenetic origin is considered as a possible cause of cranial integration and modularity (Goswami *et al*., 2023; Hall & Hanken, 2023). Two embryonic cell populations give rise to the cranial neural crest (CNC) and the paraxial mesoderm (PM). The CNC is derived from the embryonic ectoderm and forms the facial part of the skull, including the structures of the middle ear, zygomatic arch and palate, pterygoid bones, and the mandible. The PM is derived from the embryonic mesoderm and forms the cerebral part of the skull: the base, the posterior vault, and the occipital part. The boundary regions, approximately corresponding to the coronal (fronto-parietal) suture on the dorsal side of the skull and the spheno-occipital synchondrosis on the ventral side, may experience competitive pressure and have contributions from two cell populations. Structures derived from the CNC have a greater capacity for change, including under natural and sexual selection, domestication, and breed production (e.g., dogs and cats), although this phenotype also occurs in nature (Kyomen *et al*., 2023). Data on experimental domestication of foxes (Trut, 2008), minks, and sables (Trapezov, 2007) and selection of rats under stress conditions (Markel', 2008) show that all domesticated species exhibited an increase in the rate and amplitude of modification variability. Along with characteristic exterior features (Belyaev & Trut, 1989), such as changes in body size and proportions, floppy ears, changes in the length and position of the tail, specific piebaldness (white spotting), etc., shortening of the facial part of the skull (brachycephaly) was also observed. These observations together led to the 'neural crest/domestication syndrome' hypothesis (Wilkins *et al*., 2014), which linked the phenotypic traits of domestication with the biology of the CNC. The hypothesis sparked a heated debate between its supporters and opponents (Johnsson *et al*., 2021; Wilkins *et al*., 2021). However, the fact remains that the time of cranial suture closure is an important source of variability in the shape of the skull in its facial part.

Conclusion

In this study, we orthogonally decomposed the total craniometric variability of mountain voles of the genus *Alticola* into two independent parts: interspecific (44.32%) and pooled intraspecific (55.68%). This approach, based on Fisher's method, enabled a separate analysis of variability patterns resulting mainly from different biological processes — evolutionary divergence of species and ontogenetic and epigenetic variability within species.

PC1s in all three matrices (All, Inter, and Intra) reliably reflects the overall size of the skull and mandible. This is confirmed by a near-unit correlation correlation with the mean size calculated using Mosimann's method. The structure of craniometric modules (identified as PCs free from size influence) differs between the inter- and intraspecific levels. Interspecific variability (Inter-PC2, Inter-PC3) is characterized by the integration of traits of the facial and cerebral parts of the skull with the mandible. The distance between the tympanic bullae (DTB) plays a key role here, likely reflecting interspecific differences in rate of ontogenesis and carrying a phylogenetic signal. Modules associated with the proportions of the auditory capsules and rostrum were also identified.

Intraspecific variability (Intra-PC2, Intra-PC3) demonstrates modularity within the same functional parts: integration of traits of the skull base (DTB, LTB, WTB) and coordinated variability of the tooth row and diastema (an increase in the LMD trait with stable LM leads to a decrease in LUMR). The observed difference in modularity patterns may be linked to different rates and nature of variability. Intraspecific variability is likely due to rapid ontogenetic and epigenetic rearrangements, whereas interspecific variability is due to the slow accumulation of genetic differences over the course of evolution. The integration of skull parts at the interspecific level might be explained by common embryonic origin (neural crest cells, CNC, and paraxial mesoderm, PM).

As a perspective for further research, it is worth noting the search for relationships between the identified interspecific craniometric modules and molecular genetic data (evolutionary distances), as well as with key ecological factors (such as climatic parameters and habitat characteristics). This will help identify the driving forces of morphological evolution in the genus *Alticola*. Expanding the study to include data obtained through geometric morphometric methods and the examination of ontogenetic series will provide a more detailed picture of cranial integration and modularity.

Thus, the proposed methodology of orthogonal decomposition of variability has proven effective for the separate study of intra- and interspecific phenotypic diversity and opens new avenues for investigating the factors that shape this diversity at different levels of biological organization.

The concept of phenotypic integration and modularity currently provides an opportunity for a new perspective on the quantitative analysis of traits and the study of variability at different levels of biological organization.

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