Morphological Diversity of Wing Structure in Rhinolophoid Bats (Chiroptera, Rhinolophoidea)

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Abstract—The results of studies on the morphological diversity of wing structure in horseshoe bats (Rhinolophoidea) are considered in relation to ecological differentiation within the superfamily. Various skeletal elements of the wing are shown to form several groups of mutually correlated characters. The main groups comprise the characters that account for the size of the wing and play a role in the formation of its outer contours. The distribution of characters shows that they describe different aspects of variation and can provide a fairly complete picture of the morphological and ecological structure of the superfamily. The results obtained by means of multidimensional scaling and clustering methods primarily reflect ecological types of bats and only then characterize their taxonomic relationships. Analysis of variation in structural features of the wing within the superfamily Rhinolophoidea shows that the same wing form in different families may be accounted for by different ratios of digit elements, primarily the lengths of distal and proximal phalanges of digits III and IV.

Keywords: rhinolophoid bats, wing form, foraging strategy, parallel and convergent evolution.

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INTRODUCTION

Bats (Chiroptera) have a wide variety of adaptations to active flight and are traditional objects of morphological and ecological studies, in which many ecological forms have been distinguished (Norberg and Rayner, 1987; Kruskop, 1998, 1999; Patriquin and Barclay, 2003; Ševčik, 2003, etc.).

Taking into account characteristic features of the physiology (Maina, 2000) and morphology of bats and their ability for active flight and echolocation (Neuweiler, 2003), it can be concluded that they represent a markedly segregated, early diverged life form of mammals (Speakmen, 2001) in which its individual representatives have evolved in parallel and acquired similar values of morphological characters, behavioral stereotypes, and generally similar ecocenotic strategies.

The structure of the wing is an important morphological parameter characterizing the ecological groups of bats. In a number of major taxa, distinct relationships have been revealed between wing form and foraging strategy, feeding preferences, biotopic association, body weight at birth, and even the risk of extinction (Hayssen and Kunz, 1996; Jones, Purvis, and Gittleman, 2003). Several indices have been introduced to characterize specific features of form, size, and, therefore, aerodynamic parameters of the wing: aspect ratio index (ARI), wing tip index (WTI), area index (AI), wing loading index, etc. (Findley, Studier, and Wilson, 1972).

In traditional taxonomy, the superfamily Rhinolophoidea includes four families: horseshoe bats (Rhinolophidae Bell, 1836); leaf-nosed bats (Hipposideridae Miller, 1907), false vampire bats (Megadermatidae Gill, 1872); and slit-faced bats (Nycteridae Dobson, 1875). The results of studies in molecular systematics (Teeling et al., 2002), place the family Nycteridae beyond the limits of this group.[1] However, since a number of morphological and ecological parameters relevant to our study are similar in all four families, the superfamily Rhinolophoidea is considered here in a broad sense. If the phylogenetic system based on the molecular genetic data is correct, then these similarities (including the specific method of echolocation) should be regarded as manifestations of parallelism or convergence.

The family Rhinolophidae consists of one genus with 69 species; Hipposideridae, of nine genera with 63 species; Megadermatidae, of four genera with five species; and Nycteridae, of one genus with 13 species (Pavlinov, 2006).

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[1] The families Megadermatidae and Rhinolophidea (with two subfamilies Rhinolophinae and Hipposiderinae) are included in the suborder Yinpterochiroptera, and the family Nycteridae, in the suborder Yangochiroptera.

Bats of the superfamily Rhinolophoidea inhabit only the Old World. They are most widespread in northeastern and central Africa, northwestern Australia, and throughout southeastern Asia, which is the center of their diversity. The majority of rhinolophoid bats are insectivores, although almost all species of false vampire bats are known to resort to predation, and predators also occur among slit-faced bats. Rhinolophoids occupy a wide range of biotopes, from open, low-noise areas (in terms of factors affecting echolocation), such as the space above the forest canopy, clearings, or roads, to areas where maneuvering flight is difficult, such as fern thickets.

With respect to wing form, representatives of the superfamily Rhinolophoidea are divided into three groups: wide-winged with a large chiropatagium, wide-winged with a small chiropatagium, and narrow-winged with a small chiropatagium.

Several groups with different foraging strategies ("morphoecological groups") have been described within the superfamily Rhinolophoidea, including aerial foragers of open or cluttered spaces, gleaners, and perch hunters. However, these large categories do not cover the entire diversity of rhinolophoid bats. As follows from our previous data, the morphoecological diversity of these bats has a much more complex structure (Panyutina, 2002, 2008). Therefore, the main purpose of this study was to further analyze variation in the wing structure of Rhinolophoidea using the methods of multivariate analysis. Dimensional characteristics of species were also analyzed, unlike in previous studies. In this course, an attempt was made to reveal the basic patterns of wing variation and to estimate the probable roles of parallel and convergent evolution within the superfamily.

MATERIALS AND METHODS

The study was performed with ethanol-preserved material from collections of the Zoological Museum of the Moscow State University and Zoological Institute of the Russian Academy of Sciences.

Variation in morphometric characters was analyzed using 229 specimens of 52 species from the following families and genera (the number of specimens studied is indicated in parentheses):

Family Rhinolophidae: 25 species of the genus *Rhinolophus*, namely, *R. affinis* (6), *R. blasii* (3), *R. bocharicus* (11), *R. coelophyllus* (1), *R. clivosus* (3), *R.* cf. *clivosus* (1), *R. cornutus* (2), *R. euryale* (4), *R. ferrumequinum* (7), *R. fumigatus* (2), *R. hildebrandti* (1), *R. hipposideros* (10), *R. landeri* (1), *R. lepidus* (6), *R. luctus* (2), *R. malayanus* (1), *R. mehelyi* (6), *R. paradoxolophus* (1), *R. pearsoni* (5), *R. pusillus* (12), *R.* cf. *pusillus* (12), *R.* cf. *rouxi* (2), *R. shameli* (1), *R.* cf. *sinicus* (9), and *R. thomasi* (1). Family Hipposideridae: *Asellia tridens* (8), *Aselliscus tricuspidatus* (4), *Coelops*

frithii (1); 16 species of the genus *Hipposideros*, namely, *H. abae* (5), *H. armiger* (8), *H.* cf. *ater* (1), *H. bicolor* (8), *H. caffer* (6), *H. cervinus* (7), *H. cineraceus* (4), *H. commersoni* (5), *H. diadema* (2), *H. galeritus* (5), *H. jonesi* (6), *H. larvatus* (9), *H. lylei* (6), *H. pomona* (6), *H. ruber* (6), *H. turpis* (3); and *Triaenops persicus* (4). Family Megadermatidae: *Cardioderma cor* (3), *Megaderma spasma* (7), and *Lavia frons* (2). Family Nycteridae: four species of the genus *Nycteris*, namely, *N. gambiensis* (1), *N. hispida* (6), *N. javanica* (2), and *N. thebaica* (6). On the whole, one-third of the total species diversity and two-thirds of generic diversity were studied within the superfamily. Only adult, sexually mature individuals were included in the analysis, which allowed us to exclude the effect of age variation in the characters of interest. In each specimen, twelve measurements of skeletal elements included in the wing membrane (the lengths of the forearm and digit elements) were made with an accuracy of 0.1 mm (Fig. 1).

On the basis of these values, conventional wing indices were calculated: the wing tip index, WTI = D3/R; the aspect ratio index, ARI = (R + D3)/D5; and the area index, AI = (WTI + R) × (D5 × 2)/ 1000000 m^2, where D3 = (MC3 + PH31 + PH32-33), D5 = (MC5 + PH51 + PH52). In addition, we analyzed the ratios between the distal and proximal phalanges of digits IV−V (IPH4 and IPH5) and between the proximal (PH31) and two distal (PH32-33) phalanges of digit III (IPH3). Sexual dimorphism was not taken into account in this study, and the samples of most species included both males and females.[2]

Since the distribution patterns of all wing measurements were bi- or polymodal and significantly differed from normal, we used a nonparametric variant of multivariate analysis, namely, nonmetric multidimensional scaling (Shepard, 1962; James and McCulloch, 1990; Puzachenko, 2000; 2001).

The problem of describing variation in wing structure was solved in several stages, and tasks to be accomplished at each stage were as follows: (1) to standardize the variables and compile matrices of morphological distances between all parameters of the objects (individuals) based on the Euclidean distance and Kendall's rank correlation[3]; (2) to estimate the minimum dimensionality (Kupriyanova et al., 2003) for the model of nonmetric multidimensional scaling in which the initial configuration is a result of applying the algorithm of metric multidimensional scaling; (3) to calculate formal, pairwise linearly uncorrelated

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[2] It is important to note that, although sexual dimorphism occurs in Chiroptera, the level of intraspecific variation in metric characters is significantly lower than that of interspecific variation.

[3] Elements (r_{ij}) of the correlation matrix were transformed into distances by the formula $D_{ij} = \sqrt{1 - r_{ij}}$.
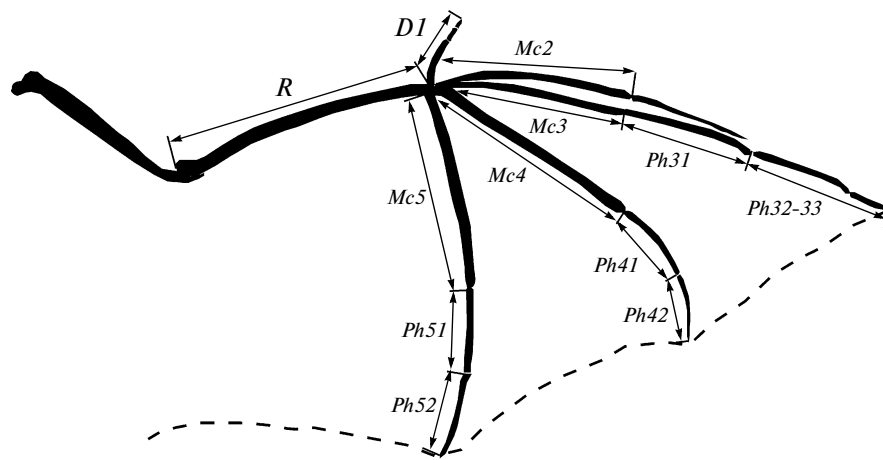
Fig. 1. Scheme of bat wing: *R,* forearm length; *D1*, digit I length; *MC2−MC5*, lengths of metacarpals II−V; *PH31−PH51* lengths of the proximal phalanges of digits III−V; *PH32-33−PH52*, lengths of the distal phalanges of digits III−V.

variables (parameters) providing basic information on variation in test characters (multidimensional scaling axes)[4]; (4) to biologically interpret new variables by means of correlation analysis with Spearman's rank correlation coefficient r_s; and (5) to make hierarchical classification of species (the UPGMA method) using formal variables obtained at stage 2, including testing of the "stochastic variation hypothesis" (Oldenderfer and Blashfield, 1989; Puzachenko, 2001). The median values of corresponding multidimensional scaling axes were used as parameters (variables) for this classification.

No general solution exists for substantiating the choice of the number of hierarchical levels (and, therefore, of clusters) in the classification. However, a formal scheme can be proposed to reduce uncertainty in choosing the cut-off distance for the dendrogram. Our approach to this problem is based on comparing parameters of the empirical tree with the model constructed using a stochastic sample with known data distribution (Puzachenko, 2001). The main characteristic of the dendrogram is the sequence of linkage, which reflects the process of dendrogram construction following the UPGMA agglomerative algorithm. If the researcher has a prototype of such a sequence for a stochastic sample with a nonhierarchical structure, then it is possible to reveal and evaluate deviations between the empirical and model classifications. The model is constructed taking into account the number of variables (characters), actual sample size, and the chosen method of classification and metrics. We used random sampling from a normally distributed data set (mean 0, variance 1), since the observed distributions are often close to the normal (canonical) pattern or

can be reduced to it through known transformation procedures. A total of 100 samples, 52 "observations" each, were generated, with the number of variables being equal to the real number of multidimensional scaling axis in the model describing bat wing variation. A sequence of linkage distances was obtained for each sample. Their values averaged over all 100 samples were taken for the "prototype" classification. Note that the distribution of linkage distance values in the prototype dendrogram was strictly lognormal, which is a characteristic feature of the UPGMA algorithm. The next step was to select the regression model most completely reproducing the empirical sequence where the prototype series of linkage distances was an independent variable (*x*). In our case, the regression model had the following form: $y = e^{(A + Bx + C\log(x))}$. We do consider this model to be applicable to other data sets, all other conditions being equal. The criterion for its selection was the strength of correlation between *y* values and "residuals" irreproducible by the model (its errors). Ideally, such a correlation should be absent. A plot of standardized residuals was used to estimate the number and "statistical" significance of hierarchical levels of classification. The maximum residual values were regarded as possible indicators of hierarchy, since they reflected a significant excess (e.g., more than two standard deviations) of the observed distances between the classification objects over their model values. The values of linkage distances corresponding to the peaks of standardized residues were used as markers of the cut-off levels of the empirical dendrogram[5].

The stability of the clustering pattern obtained by the above method was estimated by comparison with the result of classification by other agglomerative algorithms (with the Euclidean metric), such as the Single

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[4] Multidimensional scaling axes reflecting variation in wing dimensions are designated in the text by letter E, while those related to variation in wing proportions are designated by letter K.

[5] The cut-off level of the classification dendrogram determines the number of clusters included in consideration.
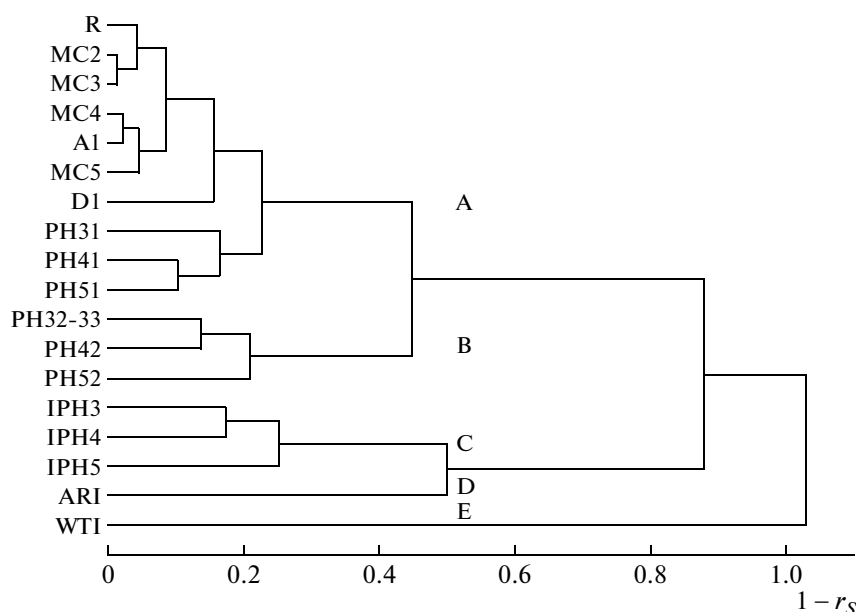
Fig. 2. Classification (UPGMA) of wing metric characters and indices of Rhinolophoidea bats based on a matrix of absolute values of Spearman's rank correlation coefficients.

linkage, complete linkage weighted pair-group centroid (median), and unweighted group average algorithms. Thereafter, the so-called additive tree was constructed (Sattath and Tversky, 1977), which reflected relative positions of the species in the Euclidean space in accordance with the geometric rule of a triangle.

At the final stage, non-parametric methods such as the Kruskal–Wallis test and median comparison test (Sokal and Rohlf, 1981) were used to estimate contributions to variation in wing characters within Rhinolophoidea from the groups distinguished as described above and to compare the resultant morphological classification with an independent ecocenotic classification.

RESULTS AND DISCUSSION

Identification of the groups of wing characters with similar variation patterns

The dendrogram in Fig. 2 reflects the degree of concordance in variation of individual wing dimensions (metric characters) and wing indices in Rhinolophoidea bats, with Spearman's rank correlation coefficient being used as a metric. Cluster A is formed by metric characters whose variation accounts for general wing dimensions, including area. The variation of distal phalanges is relatively independent of the above characters (cluster B). The indices of relative phalange length form a separate cluster (C), to which the ARI index is the closest. Variation in the WTI index shows almost no correlation with that in other wing parameters.

Basic parameters of wing variation (multidimensional scaling axes)

Variation in the sizes and proportions of wing elements is adequately reproduced by three multidimensional scaling axes (Table 1). The first axis (E1) provides the greater part of information on variation in the size of individual bones and in the integrated index of wing size (AI). The E2 axis describes part of variation in the size of the phalanges of digits III and IV as well as in indices ARI and WTI. The third axis (E3) demonstrates a weak correlation with the PH42 measurement and indices of the phalanges of digits III and IV. Thus, variation in the lengths of the radius and metacarpals is strongly correlated and described by the sole parameter E1. In contrast, the variation of phalanges has a complex pattern and is regulated by two or three linearly independent factors.

The K1 parameter correlates nonlinearly with E1, indicating the presence of allometry, or, in our case, correlated variation of wing form and size. Taking into account the sign of correlations of the first MS axes with metric characters (Table 1), we can conclude (Fig. 3) that allometry is characteristic of small and medium-sized Rhinolophoidea bats, whereas the wing form in large bats shows no correlation with wing size. The K2 and K3 axes show no apparent correlation with any of the studied variables or derivative indices. In terms of multivariate linear regression, however, they play a certain role in describing the variation of AI, ARI, IPH3, IPH4, PH51, MC5, MC3, and R.

The estimates given in Table 1 show that this set of multidimensional scaling axes is sufficient for an adequate description of variation either in individual wing

Table 1. Spearman's rank correlation coefficients for multidimensional scaling axes (E1–E3, K1–K3) and wing parameters of Rhinolophoidea bats

Parameter	Variation in size			Variation in proportions			r^2
	E1	E2	E3	K1	K2	K3	
Metric characters							
R	0.93	0.10	0.15	−0.65	−0.11	−0.02	0.98
D1	0.92	−0.02	−0.07	−0.68	−0.02	0.02	0.86
MC2	0.91	0.18	0.09	−0.59	−0.08	−0.02	0.97
MC3	0.91	0.18	0.14	−0.61	−0.10	0.00	0.98
MC4	0.97	0.01	0.12	−0.68	−0.06	−0.01	0.99
MC5	0.97	−0.19	0.11	−0.75	−0.03	0.06	0.98
PH31	0.83	0.17	-0.22	−0.47	0.01	−0.07	0.90
PH32_33	0.82	−0.51	0.23	−0.74	−0.03	0.18	0.92
PH41	0.72	0.44	−0.24	−0.31	−0.03	−0.04	0.95
PH42	0.63	−0.69	0.43	−0.67	−0.05	0.15	0.95
PH51	0.79	0.39	−0.06	−0.43	−0.08	−0.08	0.95
PH52	0.76	−0.43	0.19	−0.67	−0.02	0.08	0.80
Indices							
WTI	0.17	−0.75	−0.01	−0.25	0.15	0.15	0.53
ARI	0.35	0.56	0.10	−0.14	−0.18	−0.06	0.42
AI	0.99	−0.09	0.12	−0.74	−0.06	0.02	0.99
IPH3	−0.12	0.82	−0,40.	0.38	0.00	−0.24	0.76
IPH4	0.07	0.88	−0 40	0.21	−0.02	−0.11	0.90
IPH5	0.13	0.85	−0.17	0.14	−0.12	−0.14	0.74

Note: r^2 is the determination coefficient of multivariate regression model.

Table 2. Effects of Rhinolophoidea taxonomy on variation of multidimensional scaling axes (E1–E3, K1–K3)

Axis	Generic level, $N = 52$		Species level, $N = 229$	
	Kruskal–Wallis test, H	Median comparison test, χ^2	Kruskal–Wallis test, H	Median comparison test, χ^2
E1	10.8	8.29	223.4*	217.3*
E2	40.2*	32.0*	218.6*	213.6*
E3	23.2*	12.9	200.1*	167.9*
K1	12.2	7.6	180.0*	189.6*
K2	7.28	11.23	82.3	77.0
K3	11.0	15.2	131.2*	107.1*

* $p < 0.001$.

elements (the quality of the description is, on average, 94%) or generalized wing indices (72%).

The main, axis describing the variation of metric characters (E1) is relatively weakly connected with the accepted system of bat genera (Table 2). The same concerns the parameters characterizing the proportions of wing elements (K1–K3). Parameter E2 is most informative in terms of taxonomy at the generic level. Accordingly, morphological characters of the wing that can potentially characterize individual genera are as follows (in the descending order of significance): IPH4, IPH5, WTI, PH42, ARI, and PH32–33 (Table 1). In general, it appears that the results of

classification based on morphological wing characters and, therefore, multidimensional scaling axes will not reflect the details of taxonomy of the superfamily, since morphological features of the wing show strong interspecific variation.

Classification

Figure 4a shows the model and empirical plots of linkage distances, and Fig. 4b shows the standardized values of errors from the corresponding regression model. The maxima of these errors, which supposedly indicate hierarchical levels, and their minima corre-
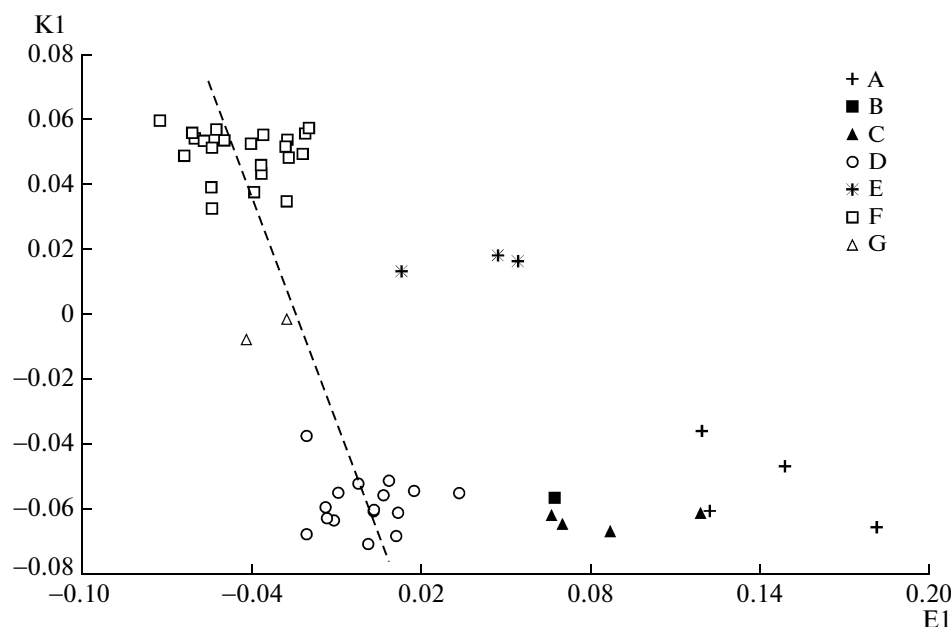
Fig. 3. Positions of seven morphological groups of Rhinolophoidea (A−G) in the space of the first multidimensional scaling axes E1 and K1. The broken line shows regression for representatives of groups D, F, and G ($r = -0.81$).

sponding to low values of linkage distances are clearly visible in the latter figure. In accordance with our hypothesis, the most significant of them are the three levels corresponding to the cut-off values of 0.11, 0.095, and 0.071 (L1–L3) in the dendrogram (Fig. 5).

Checking the composition of clusters for stability showed that 3.8–7.7% of species at the L1 and L2 levels and 5.8–26.9% of species at the L3 level were classified erroneously when other hierarchical algorithms were used. The group of inconsistently classified species includes *R. luctus, R. thomasi, R. blasii, H. abae, H. turpis, H. lylei, H. diadema*, and *Trienops persicus* at levels L1 and L2, and *R. paradoxolophus, R. coelophyllus, Coelops frithii, H. galeritus*, and *H. larvatus* at level L3. All these species occupy marginal positions in their referent clusters, which is clearly seen in the additive tree (Fig. 6). Clusters I, II, and IV at the first level proved to be the least compact; hence, we decided to limit further analysis to two hierarchical levels, L2 and L3.

Characteristic of morphological groups

At the L2 level, the sample separates into seven clusters (A−G). Cluster A is formed by four large species of the genus *Hipposideros* (Hipposideridae): *H. commersoni, H. armiger, H. lylei*, and *H. diadema*. The species of this cluster are characterized by the following values of the main wing indices: aspect ratio index ARI = 2.07−2.18 and the wing tip index WTI = 1.45−1.49. The high ARI indicates that the wing is relatively narrow, i.e., its length noticeably exceeds its width, while the WTI value indicates the absence of increase in the chiropatagium length. Moreover, the

distal phalanges of digits IV and I are significantly shorter than the proximal phalanges (IP4 = 1.3–1.6, IP5 = 1.2–1.7), which is especially noticeable in *H. commersoni*. However, this species is characterized by elongated distal phalanges of digit III: IPH3 = 0.81, while this index in other species of cluster A is higher than 0.9. These data suggest that the main flight load on the wing in large species of *Hipposideros* falls on the proximal phalanges and forearm, because when the wing has such a form, concentration of the flight load in its more distal part would be extremely energy-inefficient. The shortening of distal phalanges may be due to the necessity of reinforcing the wing structure and preventing resonance effects. *Hipposideros commersoni* is segregated from other species of the cluster and forms an independent cluster at the L3 level (1). Among all species studied, this leaf-nosed bat has the greatest wing size and area index (AI - 0.04–0.06).

The second cluster (B) consists only of *H. turpis*. This species also has large wings and is close to the species of cluster A in the values of basic wing indices (WTI = 1.44, ARI = 2.05). However, it differs from them in having a smaller wing area index (AI = 0.03) and even shorter distal phalanges, especially in digit IV (IPH3 = 1.04, IPH4 = 1.73, IPH5 = 1.43).

The morphological cluster C comprises all studied species of the family Megadermatidae (*Cardioderma cor, Megaderma spasma*, and *Lavia frons*) and, in addition, *R. luctus*. The main wing indices in this group are as follows: ARI = 1.82−2.08, TWI = 1.73−1.91. The chiropatagium is noticeably elongated and broadened, and the length of the wing exceeds its width almost twofold. Accordingly, distal phalanges are longer than proximal, especially in digit III (IPH3 = 0.51−0.56,
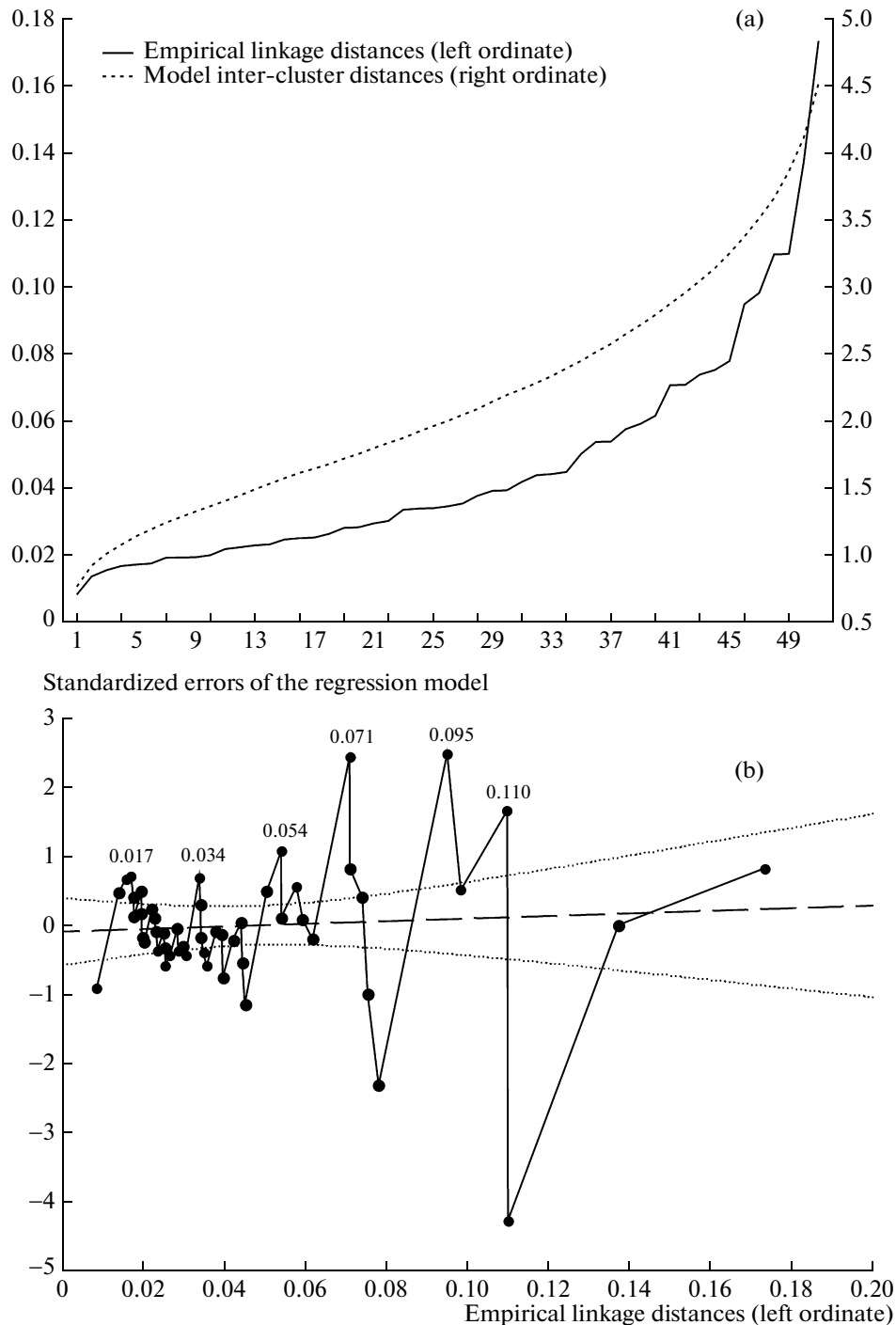
Fig. 4. Substantiation of the number of levels in the hierarchical classification (UPGMA) of 52 Rhinolophoidea species: (a) empirical and model linkage distances, (b) standardized errors of the nonlinear regression model $y = e^{(-4.63 + 0.37x + 0.81\log(x))}$, where y is the empirical linkage distance and x is the model distance.

IPH4 = 0.67−0.99, IPH5 = 0.72−0.96). In addition, the species of this cluster have a well-developed third phalange of digit III, which can reach 5 mm in length. The woolly horseshoe bat *R. luctus* occupies a *marginal* position in this cluster and forms a separate cluster (5) at the L3 level (Fig. 6). It has the lowest ARI and WTI indices but the highest wing area index (AI = 0.04 vs.

0.02−0.03 in other species). All distal phalanges are noticeably longer that proximal phalanges. In this cluster, not only the enlargement of the chiropatagium but the widening of the entire wing takes place.

The next cluster D includes 12 species of the genus *Rhinolophus* (*R. pearsoni, R. mehelyi*, . *landeri, R. fer-rumequinum, R. fumigatus, R. clivosus, R.* cf. *clivosus,*
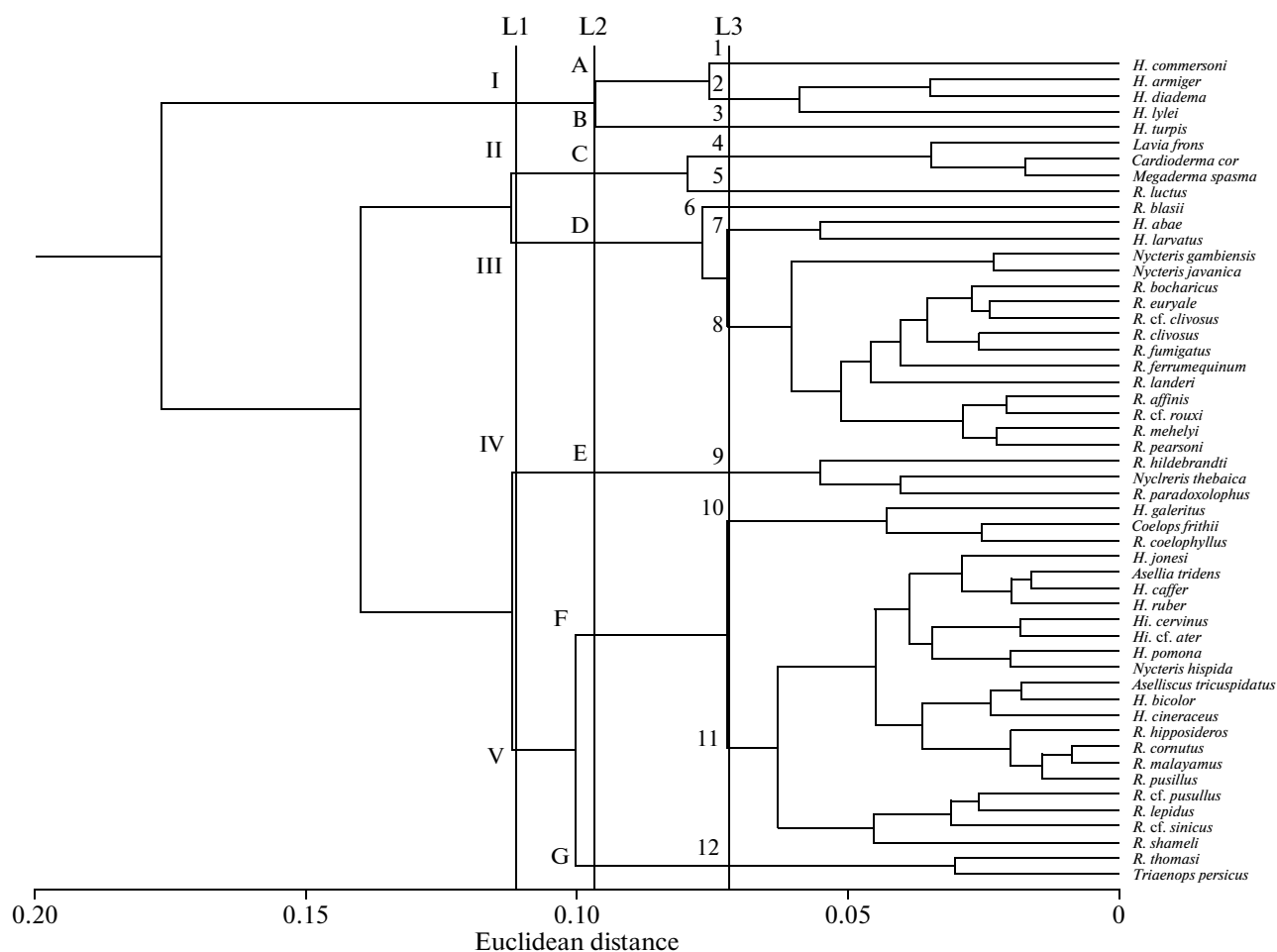
Fig. 5. Classification (UPGMA) of 52 Rhinolophoidea species based on group median values of multidimensional scaling axes E1–E3, K1–K3; L1–L3 are cut-off levels of the dendrogram; I–V, A–G, and 1–12 are morphological groups (here and in Fig. 6).

R. euryale, R. bocharicus, R. cf. *rouxi, R. affinis*, and *R. blasii*), two *Nycteris* species (*N. javanica* and *N. gambiensis*), and two *Hipposideros* species (*H. larvatus* and *H. abae*). All these species are of the medium or small size classes (R = 41–65 mm). The values of the main wing indices are broadly scattered over almost the entire range of their variation within the superfamily (AI = 0.015–0.024, ARI = 1.9–2.15, WTI = 1.44–2.07).

Hipposideros abae and *H. larvatus* are segregated from all other species of cluster D (Fig. 6). On the additive tree, the former is closer to the group of species from clusters A–C, whereas the latter is closer to a couple of *Nycteris* species. In the hierarchical classification, both form cluster 7 at the L3 level. *Hipposideros abae* is the largest bat in cluster D (R = 65, AI = 0.025). It also differs from other species of this group (except for *Nycteris*) in having relatively long proximal phalanges of digits IV–V and, accordingly, high indices IPH4 (1.25) and IPH5 (1.3). The values of WTI and ARI in *H. abae* are similar to those in *H. commer-*

soni. Two species: *N. javanica* and *N. gambiensis*, are characterized by a long digit I (about 16.5 mm) and the highest (for the cluster) WTI values (1.89 and 2.07, respectively) at a relatively high ARI (2.0). The distal phalanges of digits IV–V are much shorter than the proximal ones. *Hipposideros larvatus* is relatively close to species of the genus *Nycteris* but differs from them in significantly larger body size, short digit I, low TWI (1.44), and significantly shortened distal phalanges of digits IV–V (IPH4 = 1.45, IPH5 = 1.42).

Eleven similar species of the genus *Rhinolophus* in cluster D are characterized by a relatively high aspect ratio index (ARI = 1.9–2.05) and medium wing tip index (WTI = 1.6–1.7), with the wing area index (AI) being approximately the same in all these species (on average, about 0.02). The distal phalanges of digits III–V in these species are longer than the proximal ones.

Segregation of *R. blasii* from cluster D into cluster 6 at the L3 level is most probably accounted for by the
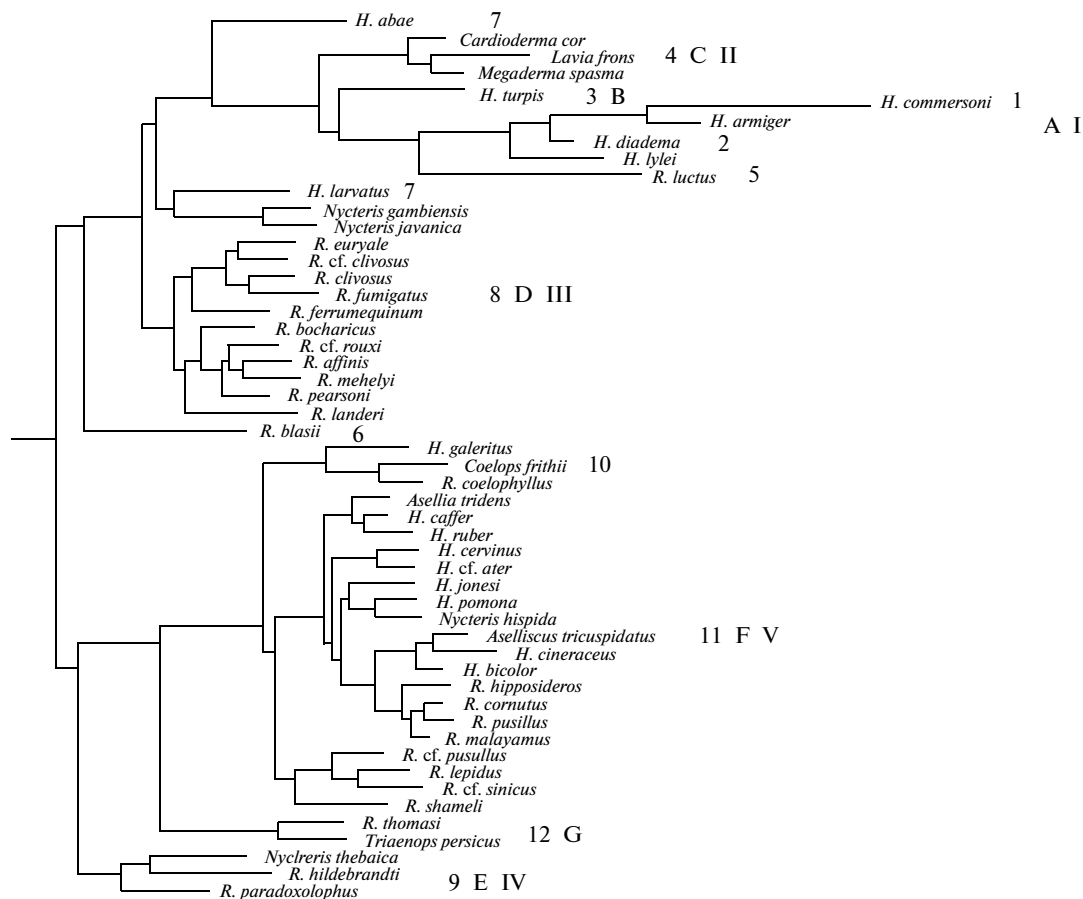
Fig. 6. Additive tree reflecting morphological distances between 52 Rhinolophoidea species.

very small (minimum for the group) sizes of metacarpals III and IV (32.5 and 35.5 mm, respectively).

Cluster E includes two species of the genus *Rhinolophus* (*R. paradoxolophus* and *R. hildebrandti*) and *N. thebaica*. They occupy a medium position with respect to the main wing indices (ARI = 1.93–2.04, WTI = 1.55–1.95, AI = 0.02–0.028) but belong to the large size class. In *R. hildebrandti*, all distal phalanges of digits III–IV are longer than proximal ones; in the two other species, the phalanges of digits IV–V are of approximately equal length.

The large cluster F includes the majority of *Rhinolophus* species (*R. coelophyllus, R. cornutus, R. hipposideros, R. lepidus, R. malayanus, R. pusillus, R.* cf. *pusillus, R. shameli, R.* cf. *sinicus,* and *R. thomasi*), representatives of *Hipposideros* (*H.* cf. *ater, H. bicolor, H. caffer, H. cervinus, H. cineraceus, H. galeritus, H. jonesi, H. pomona*, and *H. ruber*), one *Nycteris* species (*N. hispida*), and the genera *Asellia, Aselliscus,* and *Coelops.* All these species are the smallest among Rhinolophoidea (R = 53–63, AI = 0.02–0.028). They are also characterized by a wide range of variation in wing proportions (WTI = 1.54–1.93, ARI = 1.93–2.05) and relative size of the distal phalanges of digits III–V, which may be longer, equal, or shorter than the proximal phalanges (IPH3 = 0.35–1.16, IPH4 = 0.73–1.46, IPH5 = 0.73–1.45).

Three species are segregated within cluster F. These are *Coelops frithii, R. coelophyllus,* and adjoining *H. galeritus*, which form cluster 10 at the third level. They differ from other members of cluster F in low IPH3 (0.35 in *C. frithii,* 0.65 in *R. coelophyllus,* and 0.81 in *H. galeritus*) combined with relatively high IPH4 and IPH5: respectively, 1.0 and 0.89 in *C. frithii,* 0.75 and 0.82 in *R. coelophyllus,* and 1.24 and 1.45 in *H. galeritus.*

The second group segregated within this cluster consists of four *Rhinolophus* species: . *R. lepidus, R.* sf. *sinicus, R. shameli,* and *R.* cf. *pusillus.* They are characterized by low indices of the phalanges of digits III–IV (IPH3 = 0.59–0.61, IPH4 = 0.74–0.88).

The last cluster (G) consists of two species of different genera: *Rhinolophus thomasi* and *Trienops persicus.* Both belong to the medium size class but are characterized by a small area of the strongly narrowed wing (respectively, AI = 0.012, 0.015; ARI = 2.04, 2.21), with the chiropatagium not being increased (WTI = 1.43, 1.52). The distal phalanges of digit III are longer than the proximal ones (IPH3 = 0.73, 0.83). The distal phalange of digit IV is longer than proximal in *R. tho-*
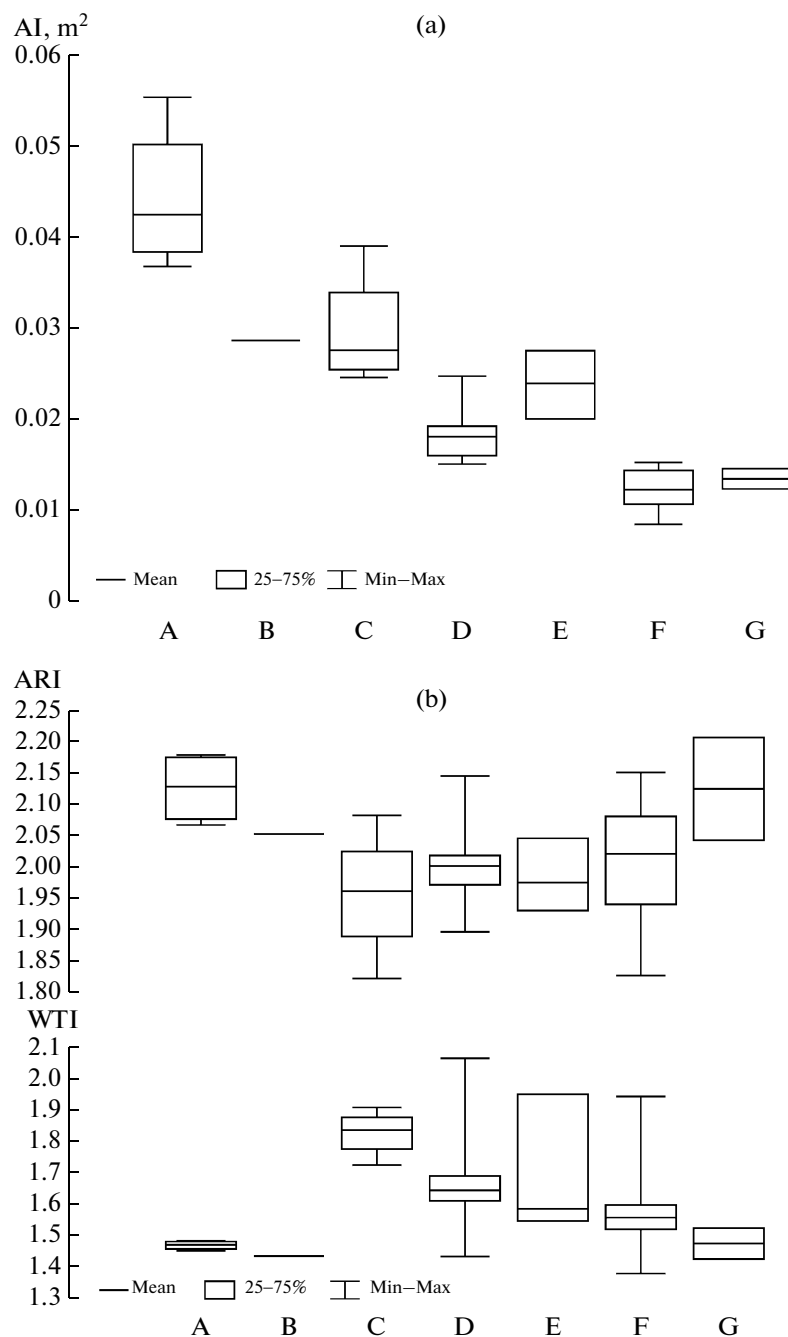
Fig. 7. Variation in (a) the wing area index AI and (b) aspect ratio index ARI and wing tip index WTI in Rhinolophoidea bats from different morphological groups (A–G).

masi (IPH4 = 0.81) but shorter in *T. persicus* (IPH4 = 1.36). In both species, the distal elements of digit V are shorter than the proximal ones (IPH5 = 1.13, 1.34).

The main morphological trends

Morphological clusters A–G are most distinctly ordered by the wing area index AI (Fig. 7a), since it integrates information on variation in almost all wing components but primarily characterizes variation in wing size.

Clusters A and B are segregated by the values of the indices characterizing the form of the wing (ARI and WTI) (Fig. 7a). In general, there appears to be a negative correlation between WTI and ARI ($r_s = -0.36$, $p < 0.01$), but this does not apply to some species from clusters C, D, E, and F (all *Nycteris* species, *Megaderma spasma*, *Cardioderma cor*, and *Lavia frons*),
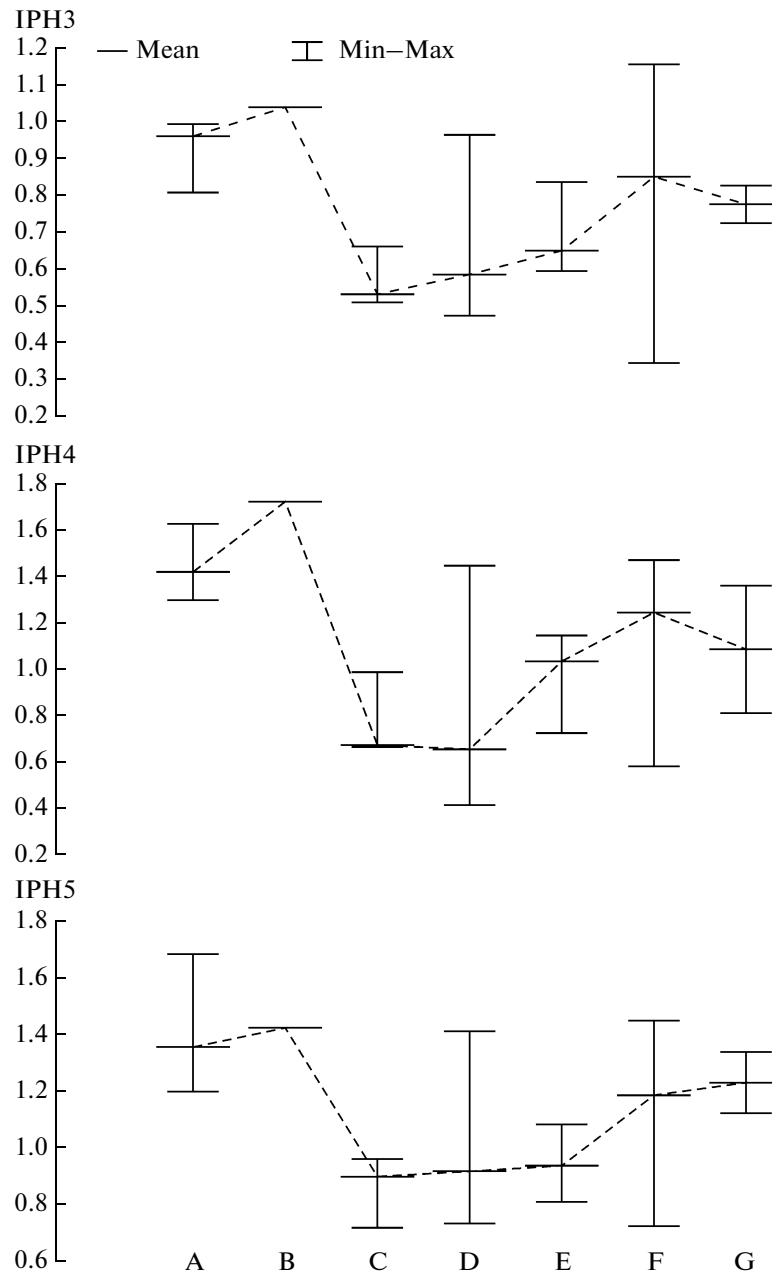
Fig. 8. Variation in the length ratio of proximal and distal phalanges of forelimb digits III–V (IPH3–IPH5) in Rhinolophoidea bats from different morphological groups (A–G).

which are characterized by the maximum WTI at relatively high ARI values.

An analysis of variation in structural features of the wing in the superfamily Rhinolophoidea showed that it is accounted for primarily by variation in the length ratio of the distal and proximal phalanges of digits III–V. In large *Hipposideros* bats, distal phalanges are, as a rule, longer than proximal (clusters A and B, Fig. 8). However, a tendency toward an increase in the IPH3 and IPH4 indices is also observed among small and medium-sized bats, in which distal phalanges are longer than proximal. The minimum values of these

indices are characteristic of clusters C (Megadermatidae) and D (mainly *Rhinolophus*).

The first (probably original) variant of wing variation, based on the length ratio of distal and proximal phalanges that is closest to that typical of other mammals, is observed in most Hipposideridae. The second variant, accounted for by hypertrophy of distal phalanges (first of all, in digit III) is characteristic of the families Rhinolophidae and, to a lesser extent Megadermatidae and Nycteridae. In turn, these differences in the morphological bases of wing variation deter-
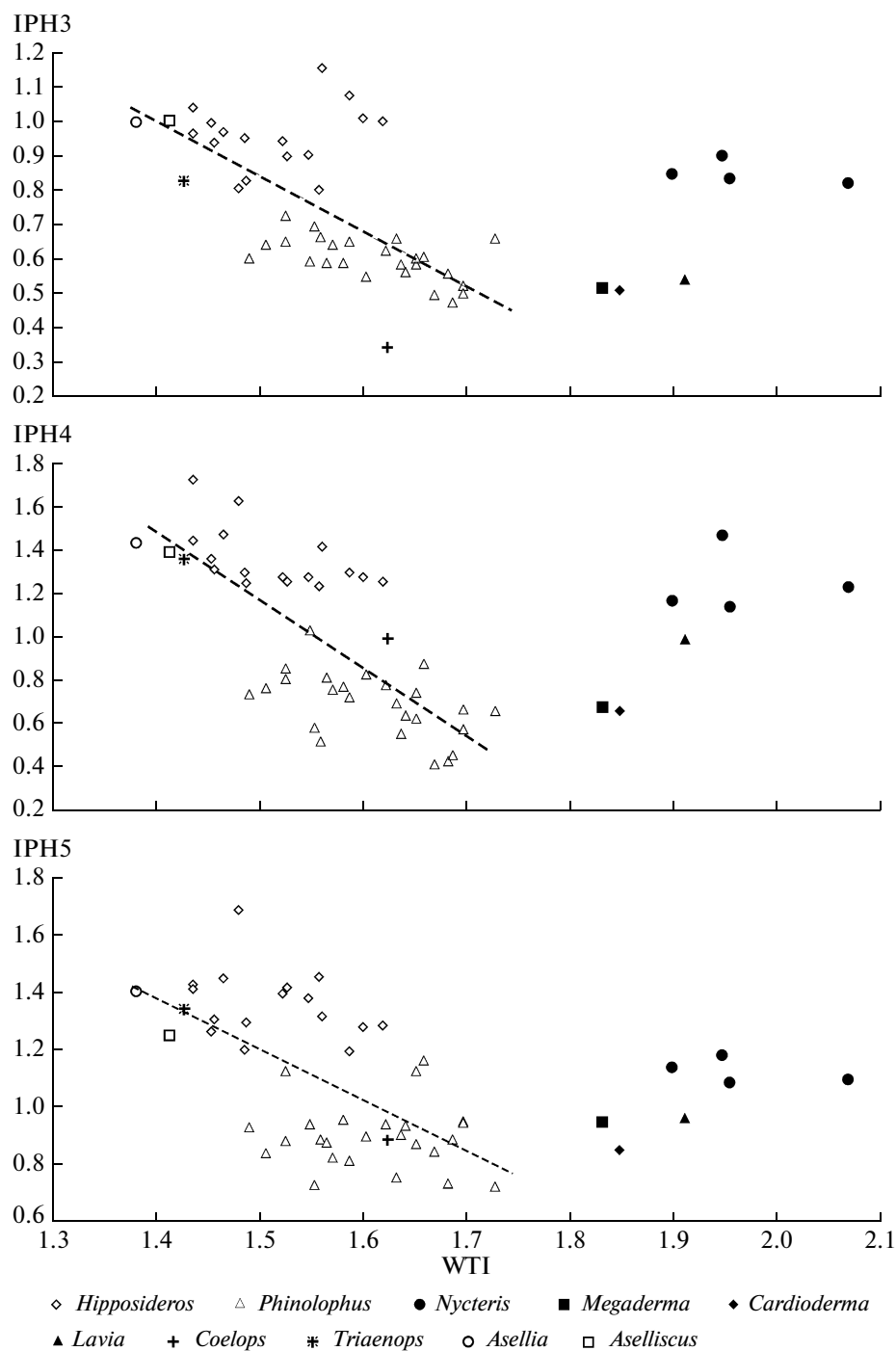
Fig. 9. Ratios of phalange indices (IPH3–IPH5) and the wing tip index (WTI) in different genera of Rhinolophoidea.

mine the potential for choosing a certain ecological strategy.

Figure 9 shows that the same value of WTI can be acquired at different ratios of digit elements. In several genera (*Hipposideros*, *Rhinolophus, Coelops*, etc.), WTI is negatively correlated with indices IPH3–IPH5; in the families Megadermatidae and Nycteridae, conversely, this correlation is positive.

Figure 10 illustrates typical variants of variation in the proximal and distal phalanges of digit III in cluster D. In *Hipposideros*, proximal phalanges are approximately equal to or slightly longer than distal; in *Nycteris*, proximal phalanges are slightly shorter, and in *Rhinolophus*, significantly shorter than distal phalanges.

Close WTI values can be accounted for by variation in different phalanges of digits III–V. Thus, in some
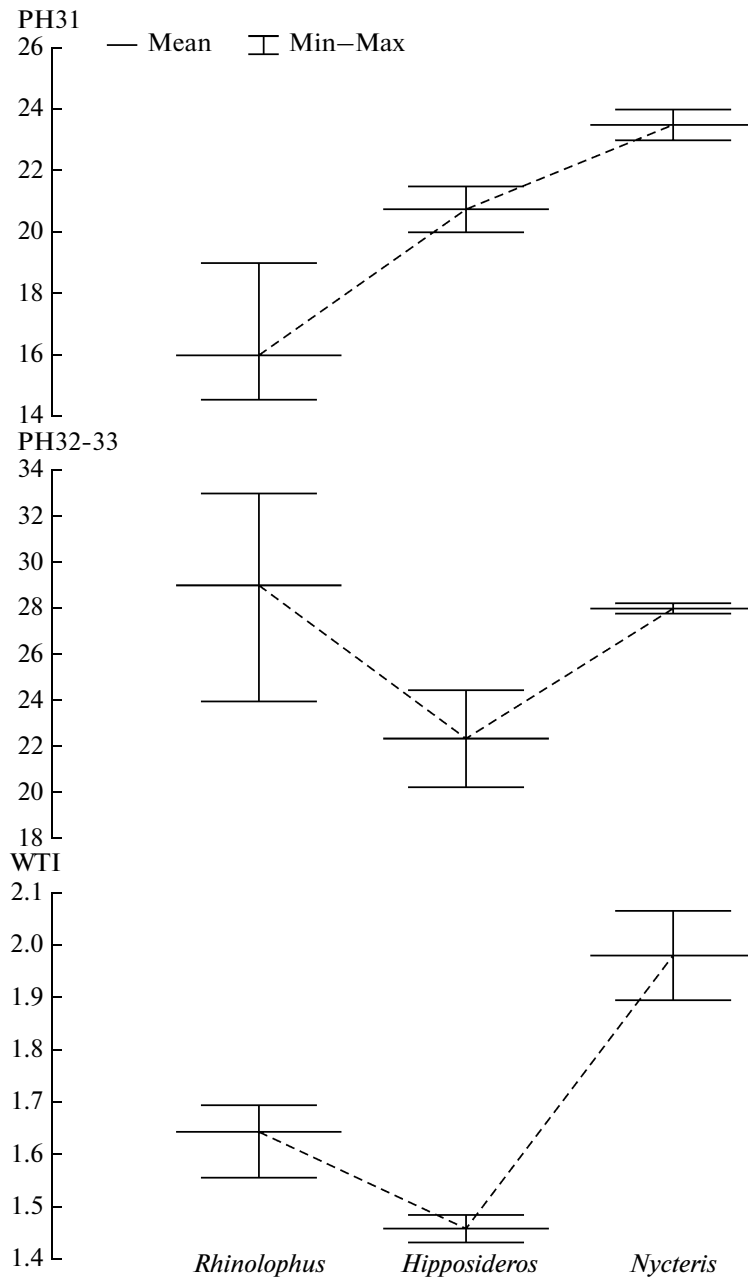
Fig. 10. Variation in the length of digit III phalanges (PH31, PH32−33) and the wing tip index (WTI) in Rhinolophoidea bats from morphological group D.

small *Hipposideros* bats (Fig. 11, cluster F), WTI reaches the values characteristic of *Rhinolophus*, but this is due to elongation of proximal rather than distal phalanges of digit III; i.e., this is an example of convergence. In *Nycteris hispida*, as in other species of this genus, the distal phalange of digit III is slightly longer than the proximal one. In *Coelops*, hypertrophy of digit III occurs exclusively due to elongation of the distal phalange, which appears to be accompanied by reduction of the proximal phalange (WTI is at the level characteristic of *Rhinolophus−Hipposideros*). In the genera *Asellia* and *Aselliscus*, both phalanges change proportionately, resulting in almost the same (relatively low) WTI values.

Index ARI positively correlates with the length ratio of the phalanges of digits III−V: $r_s = 0.31$ for IPH3, 0.52 for IPH4, and 0.70 for IPH5 (Fig. 12). Large species from morphological clusters A and B and small forms from cluster G (Fig. 7b) are characterized by the highest ARI. Species from clusters C−F have similar values of this index.
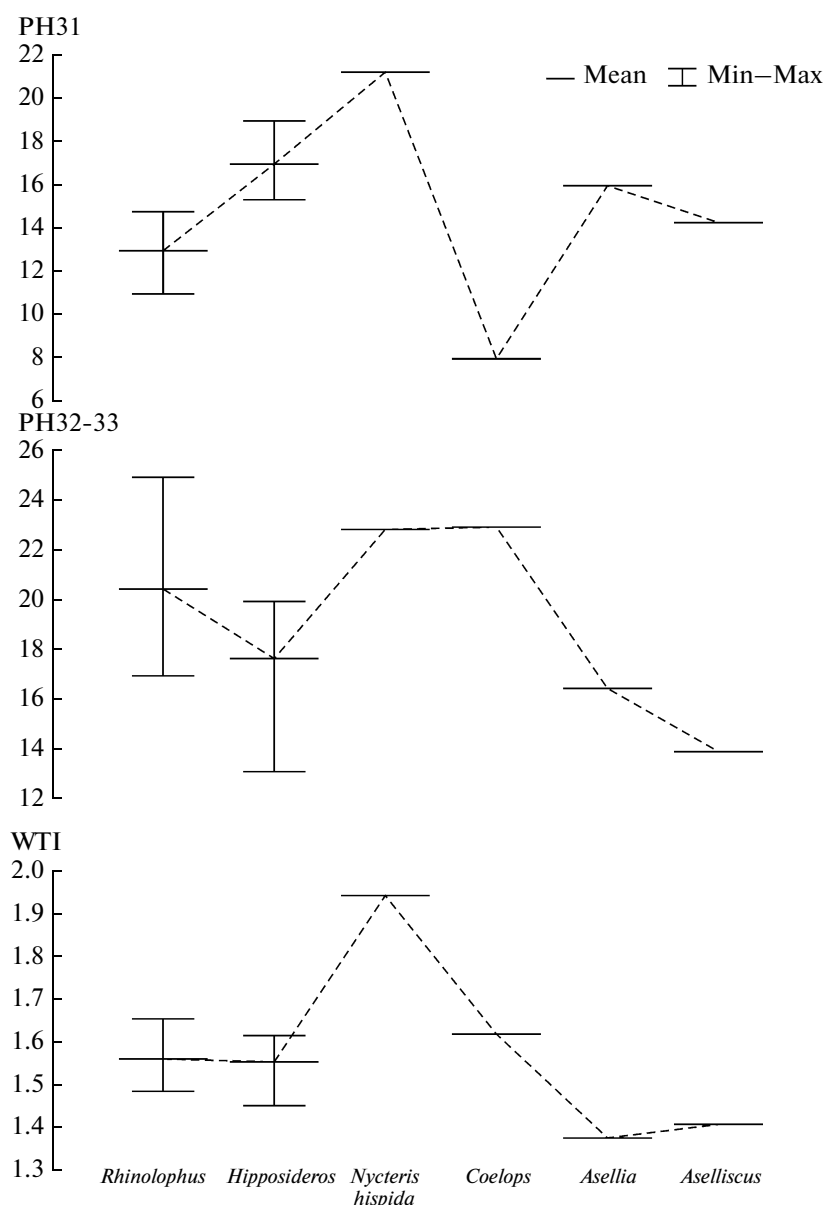
Fig. 11. Variation in the length of digit III phalanges (PH31, PH32−33) and the wing tip index (WTI) in Rhinolophoidea bats from morphological cluster F.

The pattern of variation described in this study is almost discrete in many cases (Fig. 3). This is evidence that a limited set of wing structure variants (relative to their potentially possible range) has been realized in recent Rhinolophoidea. On the other hand, the genera *Hipposideros* and *Rhinolophus* show both relatively high morphological diversity of wing structures and corresponding diversity of ecological strategies.

CONCLUSIONS

(1) Wing elements form several groups of mutually correlated characters. Characters of the first group account for the size of the wing, and characters of the second group have a role in the formation of its exter-

nal contours. The indices of phalange length ratios are mutually correlated and segregated from other characters, as does the wing tip index. Such a distribution of characters shows that they describe different aspects of variation and can provide an adequate idea of the structure of the group.

(2) The multidimensional scaling axes reproduce variation in both individual elements and generalized parameters of wing structure. The results obtained by this method reflect primarily the ecological types of bats and only then characterize their taxonomic relationships.

(3) Ordination by multidimensional scaling divides the diversity of Rhinolophoidea bats into seven stable clusters, with significant morphological similarities
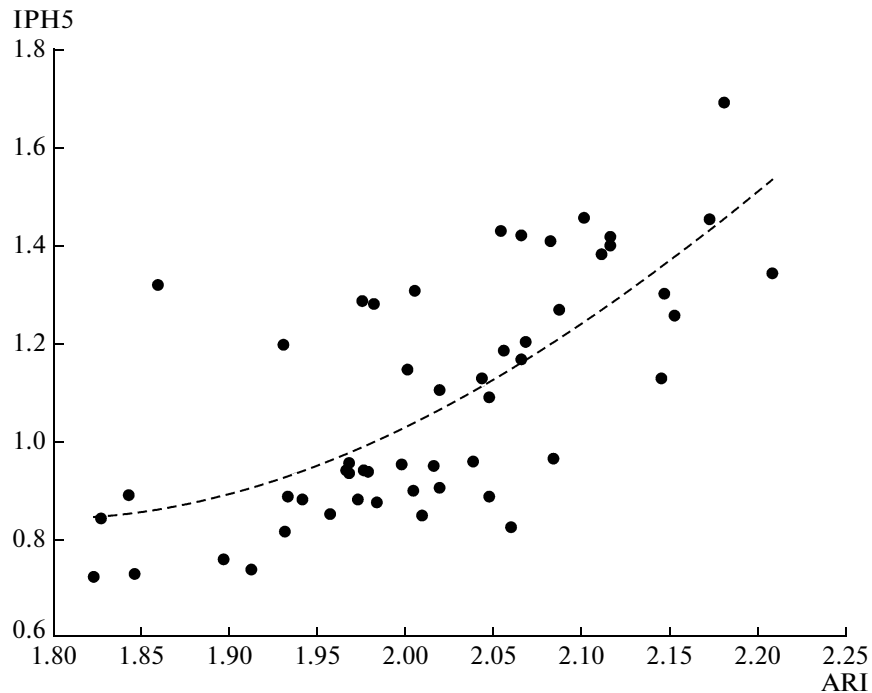
Fig. 12. Correlation of variation in the phalange index of digit V (IPH5) and the aspect ratio index (ARI) in 52 species of Rhinolophoidea bats.

being revealed between the species of each cluster. These similarities appear to be due to ecological specialization and do not reflect the taxonomic position of the species.

(4) Analysis of variation in the structural features of wing form in the superfamily Rhinolophoidea has shown that it is accounted for mainly by variability in the length ratio of the distal and proximal phalanges of digits III−V. The same wing form in different families is observed at different ratios of digit elements.

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