CORRELARTIONS BETWEEN HARDNESS OF FOOD AND CRANIODENTAL TRAITS IN NINE *MYOTIS* SPECIES (CHIROPTERA, VESPERTILIONIDAE)

M. Ghazali, I. Dzeverin

Schmalhausen Institute of Zoology, NAS of Ukraine,
vul. B. Khmelnytskogo, 15, Kyiv, 01601 Ukraine
E-mail: ghazali.maria@gmail.com, igordzeverin@gmail.com

Correlations Between Hardness of Food and Craniodental Traits in Nine *Myotis* Species (Chiroptera, Vespertilionidae). Ghazali M., Dzeverin I. — We studied 8 skull and 42 dental characters in nine *Myotis* species (*M. myotis, M. blythii, M. bechsteinii, M. dasycneme, M. emarginatus, M. nattereri, M. daubentonii, M. brandtii, M. mystacinus*) to analyze correlations between hardness of food and skull and dental traits. Contrary to the common bat pattern, *Myotis* that are specialized on hard-shelled dietary items tend to have relatively narrow skull and long tooth rows. The dentition of durophagous *Myotis* is composed by relatively enlarged second and reduced third molars.

K e y   w o r d s: *Myotis*, hardness of food, skull, teeth.

Связь между твердостью пищи и краниодентальными признаками девяти видов ночниц, *Myotis* (Chiroptera, Vespertilionidae). Гхазали М., Дзеверин И. — Для анализа связи между твердостью пищи и значениями черепных и зубных признаков исследовано 8 черепных и 42 зубных промера у девяти видов ночниц (*Myotis myotis, M. blythii, M. bechsteinii, M. dasycneme, M. emarginatus, M. nattereri, M. daubentonii, M. brandtii, M. mystacinus*). Вопреки общим для летучих мышей закономерностям у ночниц, специализированных к поеданию объектов питания с твердыми покровами, выявлена тенденция к сужению черепа и удлинению зубных рядов. В зубном аппарате такие ночницы имеют относительно увеличенные вторые и редуцированные третьи моляры.

К л ю ч е в ы е   с л о в а: *Myotis*, твердость пищи, череп, зубы.

Introduction

Skull and dental morphologies are in close association with the trophic specializations of most animals. Dietary adaptations are among the clearest changes that can be traced in fossils. Diversification rates of mammals are connected with diet: herbivores have relatively the highest rates and diversity, carnivores are in between, and omnivores have the slowest rates and lowest diversity (Price et al., 2012).

Bats are the second largest group in number of species after rodents (Simmons, 2005). They have a variety of feeding strategies that presumably evolved from an insectivorous bat ancestor (Slaughter, 1970). Diversification can occur during dietary niche shift, when animals change morphologically and fill new adaptive zones, as exemplified by transition from insectivory to frugivory in phyllostomids (Dumont et al., 2011). Within frugi- and insectivore feeding strategies, minor specializations of the skull, muscles and dentition to soft and hard objects have been distinguished. Freeman has thoroughly studied the bats from this point of view (Freeman, 1979; 1981a; 1981b; 1998; 2000). She found that cranial morphology closely correlates with the hardness of food and type of echolocation in bats. Bats that prey mostly on hard-shelled items have strong muscles that allow them to develop a force sufficient to crush those items. Such oral-emitting durophagous bats usually have reduced number of teeth, high coronoid processes, short faces and wide skulls (Freeman, 1981b; 2000).

Myotis (Chiroptera, Vespertilionidae) species retain the ancestral dental formula (38 teeth with upper third premolars (P3) being present) and are rather diverse in body size and trophic preferences. They feed on arthropods with variable body size and integumental characteristics (Dietz et al., 2009; see also references in table 1), and rarely on fish (e. g., *M. vivesi*: Blood, Clark, 1998). *Myotis myotis* is the most durophagous among the European *Myotis* species. It feeds mostly on Coleoptera (Bauerová, 1978) and has more reduced premolars (P3), which could enhance mechanical efficiency of the jaws (Ghazali, Dzeverin, 2004). A few other ves-

pertilionids have lost one or both small premolars on the maxilla and mandible during their evolution (Slaughter, 1970). P3 is lost in the dentition of *Plecotus*, upper and lower third premolars are lost in *Pipistrellus*, and *Eptesicus* has lost one more tooth — the upper second premolar. Some vespertilionid genera have additionally lost one of their upper incisors. These trends indicate that there could be a relationship between size of the animal and efficiency of the jaws' construction, e. g., *Eptesicus serotinus* is almost as large as *Myotis blythii*, but its diet is similar to the evidently larger *M. myotis,* mostly composed by hard-shelled Coleoptera (Gajdošík, Gaisler, 2004).

Given the lack of prior research on this area, the main purpose of our research is to explore how the shape and size of the *Myotis* skull and teeth are connected with the hardness of their diet.

Material and methods

We studied nine species of *Myotis*: 45 specimens of *Myotis myotis* (Borkhausen, 1797), 115 *M. blythii* (Tomes, 1857), 2 *M. nattereri* (Kuhl, 1817), 30 *M. daubentonii* (Kuhl, 1817), 2 *M. bechsteinii* (Kuhl, 1817), 14 *M. mystacinus* (Kuhl, 1817), 13 *M. dasycneme* (Boie, 1825), 15 *M. emarginatus* (Geoffroy, 1806) and 2 *M. brandtii* (Eversmann, 1845).

We measured 5 paired skull traits (CBL — condylobasal length, MXT and MDL — length of upper and lower toothrows, GMDL — length of mandibula, HCP — height of coronoid process), 3 skull breadth traits (ZYGB — zygomatic breadth, ORB — anterior between orbital breadth, MASTB — mastoid breadth), and 42 tooth traits from both sides of jaw. Measurements were taken according to Wołoszyn (1987) and Gromov et al. (1963). Left and right sides were denoted with prefix S and D, respectively. Upper teeth are denoted with capital letters (I for incisors, C for canine, P for premolars, M for molars), and lower teeth are labelled with lower-case letters. Height of upper canines (C1he) and length and width (for lower molars, width of trigonid and talonid) of each tooth were measured (fig. 1). A proxy for area (abbreviated as A) of each tooth was estimated as a product of length and width. For each of the lower molars, A was estimated as the product of length and mean width of trigonid and talonid. Sum of all upper and lower teeth areas is denoted as 'sumup' and 'sumlw', respectively.

Dietary items of bats are usually identified to the order level. Index of hardness (HARD) was calculated from the published data on diet of bats according to Freeman (1981b) from soft (1) to hard (5): 1 for Ephemeroptera, Isoptera, Trichoptera, Plecoptera, Neuroptera, Diptera; 2 for Araneae, Odonata, Homoptera, and Lepidoptera; 3 for Orthoptera; 4 for Hemiptera, Hymenoptera, Chilopoda, Diplopoda; and 5 for Coleoptera. Psocoptera, Dermaptera and Blattaria were not ranked by Freeman (1981b). We estimated hardness of their shells on the basis of their description. Psocoptera are small insects and we assigned HARD = 1 for them. Dermaptera have sclerotized forewings (Haas et al. , 2000) and we assigned HARD = 4. Hardness of Blattidae shells is close to the hardness of Orthoptera (Aguirre et al. , 2003) and we assigned HARD = 3.

Trophic data are usually expressed as percent volume or percent frequency of diet items in feces. Percent frequency is a percent of droppings that include specific dietary item. Percent volume is measured as the percentage of the area of Petri dish covered with the specific item (see Bauerová, 1986). When possible, we choose percent volume for calculating index of hardness. Otherwise, we use formula of Safi & Kerth (2004) to transform percent frequency (F) to percent volume (V): $V = -2.59F^3 + 3.20F^2 + 0.43F$. The estimated percent vol-
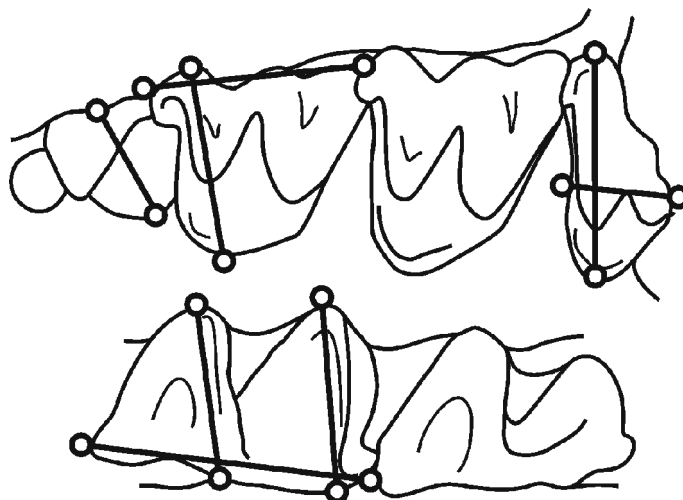

Fig. 1. Measurements of upper and lower molars.

Рис. 1. Промеры верхних и нижних моляров.

T a b l e 1. Characteristics of diet of the studied *Myotis*: Dominant item — up to 3 arthropod orders with the biggest volume percentages; Prey size — in mm, NA — data were not available; HARD — index of hardness

Т а б л и ц а 1. Особенности питания исследованных *Myotis*

| Species	Dominant item	Prey size	HARD	Source
M. myotis [myo]	Coleoptera	13−25	4.59	Bauerová, 1978; Beck, 1995; Arlettaz, 1996; Zahn et al., 2006; Whitaker, Karataş, 2009
M. blythii [bly]	Orthoptera	NA	3.48	Arlettaz, 1996; Whitaker, Karataş, 2009
M. nattereri [nat]	Diptera	2−20	2.20	Taake, 1992
M. daubentonii [dau]	Diptera	2−18	1.53	Taake, 1992; Beck, 1995
M. bechsteinii [bec]	Diptera, Arachnida, Coleoptera	3−26	2.37	Taake, 1992; Wolz, 1993
M. mystacinus [mys]	Arachnida, Diptera	2−20	1.67	Taake, 1992; Beck, 1995
M. dasycneme [das]	Diptera	NA	1.58	Britton et al., 1997
M. emarginatus [ema]	Arachnida	NA	1.80	Bauerová, 1986; Beck, 1995
M. brandtii [bra]	Diptera	3−20	1.50	Taake, 1992

umes in sum for each dietary item were higher than 100 %, thus we rescaled these percent volumes so that they cumulatively made 100 %.

According to Freeman (1981b), HARD index for the whole diet of each species is a multiplication of HARD of the dietary item and its percent volume. For those species with multiple dietary descriptions, we averaged index of hardness (table 1). Thus, we calculated index of hardness for the average animal with no regard to regional and seasonal differences. We visualized interspecies differences in diets with correspondence analysis (in PAST software) of the prepared dataset of percent volumes.

Before doing the main statistic analyses we tested whether similarity between species was due to their phylogenetic relationships. The phylogenetic signal was estimated using Blomberg's K statistics (Blomberg et al., 2003) that is implemented in phylosig function in R package phytools (Revell, 2012). Randomization test with 1000 permutations was conducted to test significance of K. The calculations were performed using R software (version 2.15.1, R Core Development Team 2012)

For the sake of brevity, we do not explain our phylogenetic hypothesis here (fig. 2), for details see Dzeverin, Ghazali (2010) and the references there. However we did not mention *M. mystacinus* in that paper. In the present paper, this species is treated in the wide sense (Mayer, Helversen, 2001) and is placed in the phylogeny according to the reconstruction of Stadelmann et al. (2004).

As the generalized descriptor of size and shape, we calculated principal components using variance-covariance matrix for skull measurements, upper teeth areas, and lower teeth areas. Missing values were replaced with iterative imputation algorithm that is implemented in PAST software (PAST 2.03, Hammer et al., 2001). We used a Spearman coefficient to study the correlation of traits with hardness of food. These statistical calculations were made using PAST software (PAST 2.03, Hammer et al., 2001). Corrections for multiple comparisons were made using R software (version 2.15.1, R Core Development Team 2012) with p. adjust function. We employed false discovery rate (fdr) procedure, which is powerful for large number of comparisons and does not require strong control of family-wise error rate (Benjamini, Hochberg, 1995).
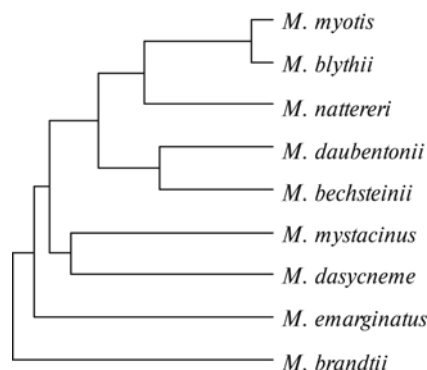
Fig. 2. Phylogenetic tree of the studied *Myotis* species.

Рис. 2. Филогенетическое дерево исследованных видов *Myotis*.

Results

Correspondence between dietary items and *Myotis* is well seen on fig. 3. Both correspondence axes explain 60.8 % of total variation (Axis 1 = 39.6 %, eigenvalue = 0.808; Axis 2 = 21.2 %, eigenvalue = 0. 433). Since bats usually hunt abundant insects, their diet is rather diverse; it depends greatly on region and season. Nevertheless, distinction of the diets is preserved: species for which we have several points group together. Large-sized gleaners *M. myotis* and *M. blythii* have evident correspondence with Coleoptera and Orthoptera, the insects that are to lesser extent available for other *Myotis*. Small and medium-sized *Myotis* with different foraging strategies (aerial hawking, gleaning, trawling) mostly choose other arthropods (fig. 3).

Testing for the correlation of hardness index with each morphological trait was redundant. So, we decided to analyze principal components of different sets of traits (skull, upper teeth areas, lower teeth areas). The first principal component explained more than 99 % of total variance, since it is mostly connected with animals' body size and associated shape differences. The second principal components explained less than 1 % of the variance. Position of bats on principal components biplots agrees with the peculiarities of *Myotis* skull and teeth (fig. 4). Two extremes between which other bats are placed are clear. *M. bechsteinii* has relatively long skull with well-developed small premolars and relatively small molars. *M. dasycneme* has wider skull with well-developed molars and more reduced small premolars.

Usually, morphological differences in *Myotis* species agree with the species ecology, and the genus taxonomy was formerly based on both morphological and ecological data (Findley, 1972; Tate, 1941). However, molecular genetic studies (Ruedi, Mayer, 2001) showed a considerably high degree of morphological convergence in evolution of *Myotis* lineages. Thus, phylogeny and morphology are supposed to be uncoupled in *Myotis*. We assume Brownian motion to be a plausible pattern for evolution of the traits under study
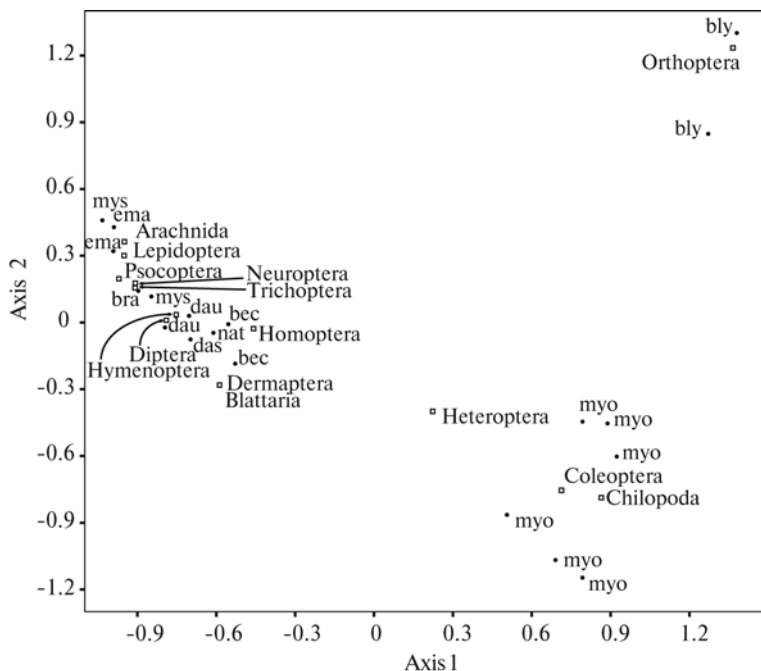

Fig. 3. Correspondence analysis of dietary preferences of the studied *Myotis* species. Species acronyms as in table 1.

Рис. 3. Анализ соответствий пищевых предпочтений исследованных видов *Myotis*. Акронимы видов как в табл. 1.
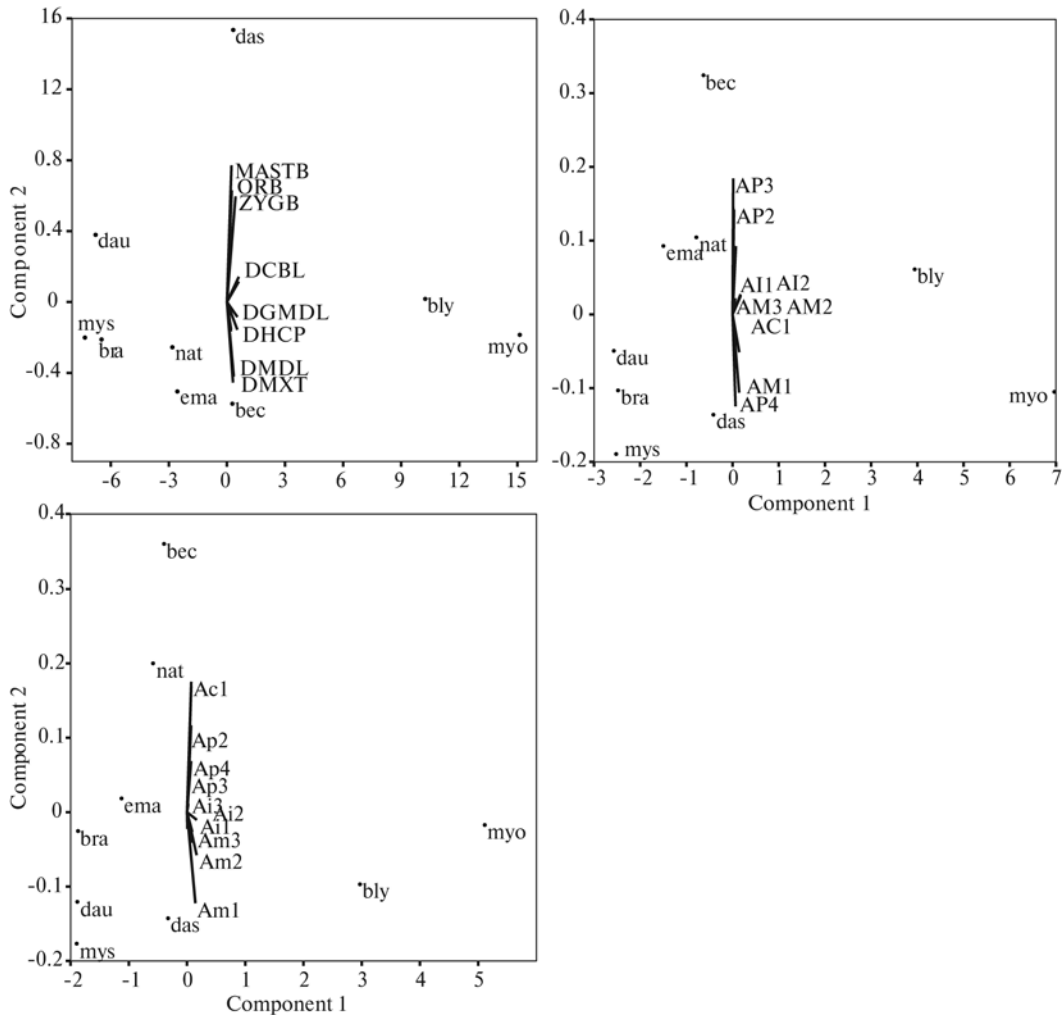
Fig. 4. Principal components analysis of skull traits and teeth areas. Only right measurements are named.
Рис. 4. Анализ главных компонент промеров черепа и площадей зубов. На рисунках обозначены только промеры правой стороны.

in *Myotis* (Dzeverin, 2008; Dzeverin, Ghazali, 2010), i. e. changes in sister lineages were independent.

Phylogenetic signal of HARD and other traits and morphological indices was not significant. K for principal components ranged from 0.542 to 1.003. For morphological indices K ranged from 0.311 to 1.114 (table 2). Since we found no significant phylogenetic signal, we could use standard statistical methods without phylogenetic corrections. The main trend is evident — the bigger is an animal, the harder food it can process. However, HARD does not significantly correlate with the first principal components, if adjusted probability is calculated (table 3). Shape differences expressed with second principal components in skull and teeth did not correlate with HARD, that is proved with both significance tests.

For detailed correlation analysis we chose several morphological indices of skull and teeth (table 2). We expected durophagous species have more mechanically effective skull: with relatively shorter tooth rows and more reduced small premolars that put canines closer to the craniomandibular joint. Instead, we observed that relative length of tooth row (MXT/CBL) increased with the increase of hardness of diet, while relative facial breadths

T a b l e 2. Blomberg's K statistic for index of hardness, morphological indices and principal components
Т а б л и ц а 2. К-статистика Бломберга для индекса твердости пищи, морфологических индексов и главных компонент

Trait	N	K	p
HARD	9	0.790	0.333
PC1 Skull	9	1.003	0.138
PC2 Skull	9	0.832	0.342
PC1 Upper teeth	9	0.848	0.301
PC2 Upper teeth	9	0.542	0.503
PC1 Lower teeth	9	0.878	0.256
PC2 Lower teeth	9	0.633	0.476
ORB/CBL	9	0.840	0.199
ZYG/CBL	9	0.980	0.103
MASTB/CBL	9	1.063	0.072
MXT/CBL	9	1.076	0.072
HCP/GMDL	9	0.602	0.445
C1he/MXT	9	0.869	0.275
I12/sumup	9	0.593	0.504
i123/sumlw	8	0.848	0.181
C1/sumup	9	0.790	0.242
c1/sumlw	8	0.643	0.523
P23/sumup	9	0.780	0.283
p23/sumlw	8	0.840	0.295
P4/sumup	9	0.864	0.224
p4/sumlw	8	0.311	0.823
M12/sumup	9	1.086	0.063
m12/sumlw	8	0.758	0.271
M3/sumup	9	0.958	0.153
m3/sumlw	8	0.860	0.223
M1/M123	9	0.836	0.250
m1/m123	8	0.832	0.298
M2/M123	9	1.114	0.063
M2/m123	8	1.035	0.070

almost did not change (ORB/CBL, ZYG/CBL), and relative mastoid breadth (MASTB/CBL) decreased. As was expected, *Myotis* that eat hard-shelled prey had relatively higher coronoid processes (HCP/GMDL). Relative height of upper canines (to the length of upper tooth row as in Freeman, 1981b) has been supposed to correlate with the hardness of diet, but not in case of *Myotis* (C1he/MXT).

The relative contribution of small premolars to the sum of areas of all upper or lower teeth did not correlate with HARD (P23/sumup, p23/sumlw). Other vestigial teeth, third molars, were inversely related to HARD (M3/sumup, m3/sumup). Part of lower incisors also decreases (i123/sumlw). Relative area of large teeth, first and second molars, in total teeth area do not correlate with diet. In particular, the contribution of the first molar area to the total area of molars (M1/M123, m1/m123) do not correlate with HARD, whereas second molar area (M2/M123, m2/m123) increase with the index of hardness.

Discussion

Cranial and dental anatomy are thought to reflect the feeding adaptations of animals. The mastoid process and lambdoidal crest are the sites of attachment for head-moving muscles. However, mastoid breadth and height of the skull at bullae still correlate with diet adaptations; they are relatively bigger in carnivorous and sanguivorous bats in com-

T a b l e 3. Spearman correlation coefficients (RS) of index of hardness with principal components and morphological indices: p and p (fdr) — traditional and fdr-adjusted significance test. The significant results are shown in bold

Т а б л и ц а 3. Коэффициенты корреляции Спирмена (RS) индекса твердости пищи с главными компонентами и морфологическими индексами: p и p (fdr) — традиционный и fdr-скорректированный метод оценки достоверности. Значимые результаты выделены полужирным шрифтом

Trait	R_S	p	p (fdr)
PC1 Skull	0.717	0.031	0.069
PC2 Skull	-0.217	0.552	0.615
PC1 Upper teeth	0.767	0.021	0.056
PC2 Upper teeth	0.333	0.359	0.495
PC1 Lower teeth	0.733	0.031	0.069
PC2 Lower teeth	0.467	0.194	0.281
ORB/CBL	0.233	0.521	0.615
ZYG/CBL	0.267	0.463	0.584
MASTB/CBL	**-0.933**	**<0.001**	**0.003**
MXT/CBL	**0.833**	**0.006**	**0.029**
MDL/GMDL	**0.800**	**0.011**	**0.035**
HCP/GMDL	**0.817**	**0.008**	**0.030**
C1he/MXT	0.238	0.536	0.615
I12/sumup	-0.611	0.087	0.169
i123/sumlw	**-0.905**	**0.002**	**0.013**
C1/sumup	**0.783**	**0.014**	**0.040**
c1/sumlw	0.619	0.115	0.184
P23/sumup	0.583	0.097	0.175
p23/sumlw	0.643	0.083	0.169
P4/sumup	-0.567	0.121	0.184
p4/sumlw	0.619	0.115	0.184
M12/sumup	0.283	0.463	0.584
m12/sumlw	0.095	0.840	0.840
M3/sumup	**-0.933**	**<0.001**	**0.003**
m3/sumlw	**-0.857**	**0.007**	**0.030**
M1/M123	0.183	0.644	0.691
m1/m123	-0.095	0.840	0.840
M2/M123	**0.983**	**<0.001**	**<0.001**
m2/m123	**0.905**	**0.002**	**0.013**

parison with insectivorous and frugivorous bats (Van Cakenberghe et al., 2002). This could be related with the distribution of bite stresses during mastication.

Relative mastoid breadth and relative tooth row length are negatively correlated in *Myotis* (fig. 5, $R_S = -0.903$, $p = 0.001$). Relatively wide skulls and short tooth rows in soft-eating bats may be the result of their higher masticatory demands as could be predicted from their body size. Larger bats also need to improve their prey detection system to hunt larger prey, meanwhile smaller bats usually hunt in air and are "opportunists to small-prey items" (Barclay, Brigham, 1991). In comparison with other vespertilionids *Myotis* have variable, but interspecifically similar echolocation signals (Obrist et al., 2004). So, prey of large and small *Myotis* are similar in size, but due to different functional abilities of their masticatory apparatus, these differ in exoskeleton properties. We assume that relatively wide braincase and short rostrum in small *Myotis* is an adaptation to relatively big and hard prey items. This makes sense, because a relatively big prey item would be "hard" in relation to the bite force a small bat can produce, thus a wide and short skull would have a better mechanical advantage (Santana, personal communication).

Tooth size also correlates with functional demands of mastication. In the dentition of insectivorous bats, molars usually occupy half of the toothrow (Freeman, 1998). Certain diminution of incisors and third molars is the most vivid trend in the dentition of the *Myotis*
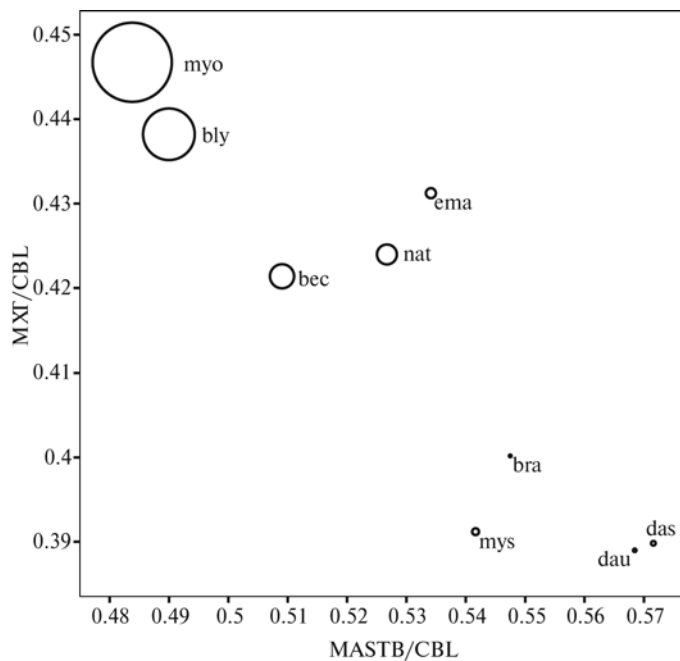
Fig. 5. Relative breadth of skull at mastoids (MASTB/CBL) decreases with relative elongation of the rostral part of skull (MXT/CBL). Size of bubbles is proportional to HARD.

Рис. 5. Относительная ширина черепа между сосцевидными отростками (MASTB/CBL) уменьшается с относительным удлинением ростральной части черепа (MXT/CBL). Размер пузырьков пропорционален HARD.

species studied. Although a portion of areas of the first two molars with respect to the total area of teeth does not change, the contribution of the 2nd molar to the total area of molars increases significantly with the increase of hardness of diet. Maximal bite forces are applied at post-canine teeth (Dumont et al., 2005). In functional terms, as the point of bites approaches to the fulcrum, the out-lever is shortening and bite force increases. Large second molars may indicate displacement of the maximal bite force from first to second molar.

Bite force in bats is rather associated with absolute size than with specific traits of skull; along with increasing of skull length, fiber length of mastication muscles (especially m. masseter and m. temporalis, Herrel et al., 2008). The moment at the temporo-mandibular joint is generated mainly by three muscles (m. temporalis, m. masseter, m. pterygoideus medius). The relative importance of these muscles is associated with the peculiarities of diet. The contribution of the temporalis to the jaw moment is dominant in bats with hard diets, masseter muscles input is important in bats with soft diets, and medial pterygoid increases in importance in bats with liquid diet (Santana et al., 2010).

Wide and short skulls may lead to a relative increase of cross-sectional area of muscles and thus higher bite force (Swartz et al., 2003). We suppose that functional demands on eating tough prey are satisfied with the increased body-sized and associated expansion of muscles' cross-sectional area. However these changes may not be seen in relative scale of the traits, they may be masked under increase of body-size.

In spite of having a small sample of *Myotis* species, we consider our results to be representative since rather different trophic strategies and different body sizes were presented in the sample. However, we expect that more species would make a stronger analysis.

References

Aguirre L. F., Herrel A., Van Damme R., Matthysen E. The implications of food hardness for diet in bats // Functional Ecology. — 2003. — **17**, 2. — P. 201−212.

Arlettaz R. Feeding behaviour and foraging strategy of free-living mouse-eared bats, Myotis myotis and Myotis blythii // Anim. Behav. — 1996. — **51**. — P. 1−11.

Barclay R. M. R., Brigham R. M. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? // The American Naturalist. — 1991. — **137**, N 5. — P. 693−703.

Bauerová Z. Contribution to the trophic bionomics of Myotis emarginatus // Folia zoologica. — 1986. — **35**, 4. — P. 305−310.

Bauerová Z. Contribution to the trophic ecology of Myotis myotis // Folia zoologica. — 1978. — **27**, 4. — P. 305−316.

Beck A. Fecal analyses of European bat species // Myotis. — 1995. — **32−33**. — P. 109−119.

Benjamini Y., Hochberg Y. Controlling the false discovery rate: a practical and powerful approach to multiple testing // J. R. Statist. Soc. B. — 1995. — **57**, N 1. — P. 289−300.

Blomberg S. P., Garland T., Jr., Ives A. R. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile // Evolution. — 2003. — **57**, N 4. — P. 717−745.

Blood B. R., Clark M. K. Myotis vivesi // Mammalian Species. — 1998. — **588**. — P. 1−5.

Britton A. R. C., Jones G., Rayner J. M. V. et al. Flight performance, echolocation and foraging behaviour in pond bats, Myotis dasycneme (Chiroptera: Vespertilionidae) // J. Zool. — 1997. — 241, 3. — P. 503−522.

Dietz C., von Helversen O., Nill D. Bats of Britain, Europe and Northwest Africa. — London : A&C Black Publishers Ltd., 2009. — 400 p.

Dumont E. R., Dávalos L. M., Goldberg A. et al. Morphological innovation, diversification and invasion of a new adaqptive zone // Proc. R. Soc. B. — 2012. — **279**, 1734. — P. 1797−1805.

Dumont E. R., Piccirillo J., Grosse J. R. Finite-element analysis of biting behavior and bone stress in the facial skeletons of bats // The Anatomical Record Part A. — 2005. — 283 A. — P. 319−330.

Dzeverin I. The stasis and possible patterns of selection in evolution of a group of related species from the bat genus Myotis (Chiroptera, Vespertilionidae) // J. Mammal. Evol. — 2008. — **15**. — P. 123−142.

Dzeverin I., Ghazali M. Evolutionary mechanisms affecting the multivariate divergence in some Myotis species (Chiroptera, Vespertilionidae) // Evol. Biol. — 2010. — **37**. — P. 100−112.

Findley J. S. Phenetic relationships among bats of the genus Myotis // Systematic Zoology. — 1972. — **21**, 1. — P. 31−52.

Freeman P. W. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution // Fieldiana (Zoology). — 1981 a. — 7. — P. 1−173.

Freeman P. W. Correspondence of food habits and morphology in insectivorous bats // J. Mamm. — 1981 b. — **62**, 1. — P. 164−166.

Freeman P. W. Form, function, and evolution in skulls and teeth of bats // Bat Biology and Conservation / Ed. T. H. Kunz, P. A. Racey. — Washington, DC : Smithsonian Institution Press, 1998. — P. 140−156.

Freeman P. W. Macroevolution in Microchiroptera: recoupling morphology and ecology with phylogeny // Evol. Ecol. Res. — 2000. — 2. — P. 317−335.

Freeman P. W. Specialized insectivory: Beetle-eating and moth-eating molossid bats // J. Mamm. — 1979. — **60**, 3. — P. 467−479.

Gajdošík M., Gaisler J. Diet of two Eptesicus bat species in Moravia (Czech Republic) // Folia Zool. — 2004. — **53**, N 1. — P. 7−16.

Ghazali M. A., Dzeverin I. I. Biometrics of reduced elements of the dental system in some mouse-eared bats, Myotis (Vespertilionidae) // Plecotus et al. — 2004. — 7. — P. 7−17. — Russian : *Гхазали М. А. , Дзеверин И. И.* Биометрическая характеристика редукции элементов зубной системы некоторых видов ночниц, Myotis (Vespertilionidae).

Gromov I. M., Gureev A. A., Novikov G. A. et al. Mammals of the fauna of the USSR. Part 1. Moskva-Leningrad: Izdatelstvo Akademii Nauk SSSR, 1963. — 639 p. — Russian : *Громов И. М., Гуреев А. А., Новиков Г. А. и др.* Млекопитающие фауны СССР. Часть 1.

Haas F., Gorb S., Wootton R. J. Elastic joints in dermapteran hind wings: materials and wing folding // Arthropod Structure & Development. — 2000. — **29**. — P. 137−146.

Hammer O., Harper D. A. T., Ryan P. D. PAST: Paleontological Statistics software package for education and data analysis // Palaeontologia Electronica. — 2001. — **4**, 1. — P. 1−9. — http:// palaeo−electronica. org/2001_1/past/issue1_01. htm.

Herrel A., De Smet A., Aguirre L. F., Aerts P. Morphological and mechanical determinants of bite force in bats: do muscles matter? // J. Exp. Biol. — 2008. — **211**. — P. 86−91.

Mayer F., von Helversen O. Cryptic diversity in European bats // Proc. R. Soc. Lond. B. — 2001. — **268**. — P. 1825−1832.

Obrist M. K., Boesch R., Flückiger P. F. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach // Mammalia. — 2004. — **68**, N 4. — P. 307−322.

Price S. A., Hopkins S. S. B., Smith K. K., Roth V. L. Tempo of trophic evolution and its inpact on mammalian diversification // Proc. Natl Acad. Sci USA. — 2012. — **109**, 18. — P. 7008−7012.

R Development Core Team. R: A language and environment for statistical computing. — Vienna : R Foundation for Statistical Computing, 2012. — http: // www.R-project.org/.

Revell L. J. phytools: An R package for phylogenetic comparative biology (and other things) // Methods Ecol. Evol. — 2012. — **3.** — P. 217−223.

Ruedi M., Mayer F. Molecular systematics of bats of the genus Myotis (Vespertilionidae) suggests deterministic ecomorphological convergences // Molecular Phylogenetics and Evolution. — 2001. — **21**, N 3. — P. 436−448.

Safi K., Kerth G. A comparative analysis of specializations and extinction risk in temperate zone bats // Conservation Biology. — 2004. — **18**, 5. — P. 1293−1303.

Santana S. E., Dumont E. R., Davis J. L. Mechanics of bite force production and its relationship to diet in bats // Functional Ecology. — 2010. — **24**, N 4. — P. 776−784.

Slaughter B. H. Evolutionary trends of chiropteran dentitions // About bats: A chiropteran biology symposium / Eds B. H. Slaughter, D. W. Walton. — Dallas, Texas : Southern Methodist University Press, 1970. — P. 51−84.

Stadelmann B., Jacobs D. S., Schoeman C., Ruedi M. Phylogeny of African Myotis bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences // Acta Chiropterologica. — 2004. — **6**, N 2. — P. 177−192.

Swartz S. M., Freeman P. W., Stockwell E. F. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology // Bat Ecology / Eds T. H. Kunz, M. B. Fenton. — Chicago : The University of Chicago Press, 2003. — P. 257−300.

Taake K. H. Strategien der Ressourcennutzung an Waldgewässern jagender Fledermäuse (Chiroptera: Vespertilionidae) // Myotis. — 1992. — **30.** — P. 7−74.

Tate G. H. H. A review of the genus Myotis (Chiroptera) of Eurasia, with special reference to species occurring in the East Indies (Results of the Archbold expeditions, N 39) // Bull. Amer. Mus. Natur. Hist. — 1941. — **78**, 8. — P. 537−565.

Van Cakenberghe V., Herrel A., Aguirre L. F. Evolutionary relationships between cranial shape and diet in bats (Mammalia: Chiroptera) // Topics in Functional and Ecological Vertebrate Morphology / Eds P. Aerts et al. — Maastricht : Shaker Publishing, 2002. — P. 205−236.

Whitaker J. O., Karataş A. Food and feeding habits of some bats from Turkey // Acta Chiropterologica. — 2009. — **11**, 2. — P. 393−403.

Simmons N. B. Order Chiroptera // Mammal Species of the World. A Taxonomic and Geographic Reference / Ed. D. E., Wilson, D. M. Reeder. — 3rd ed. — Baltimore : Johns Hopkins University Press, 2005. — P. 312−529. — http: // bucknell.edu/msw3/

Wołoszyn B. Pliocene and Pleistocene bats of Poland // Acta Palaeontologica Polonica. — 1987. — **32**, N 3-4. — P. 207-325.

Wolz I. Das Beutespektrum der Bechsteinfledermaus Myotis bechsteini (Kuhl, 1818) ermittelt aus Kotanalysen // Myotis. — 1993. — **31.** — P. 27−68.

Zahn A., Rottenwallner A., Güttinger R. Population density of the greater mouse-eared bat (Myotis myotis), local diet composition and availability of foraging habitats // J. Zoology. — 2006. — **269**. — P. 486−493.