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# SPATIAL AND ECOMORPHOLOGICAL DIVERGENCE OF *PLECOTUS* SIBLING SPECIES (MAMMALIA) IN SYMPATRY ZONE IN EASTERN EUROPE

*Загороднюк I., Постава Т.* **Просторова та екоморфологічна дивергенція видів-двійників *Plecotus* (Mammalia) у зоні симпатрії у Східній Європі** // Науч. зап. Гос. природоведч. музея. – Львов, 2007. – Вып. **23**. – С. 215-224.

Рід вуханів представлений у фауні регіону двома видами, *P. auritus* та *P. austriacus*, що формують широку зону симпатрії у західних областях України. За краніометричними ознаками (таких 23) види є дуже подібними і мають середню відмінність за коефіцієнтом дивергенції Майра *CD*=2,42, а за відношенням Хатчінсона — *HR*=1,076. Максимальні розходження видів за обома показниками стосуються лише 4-х: довжини слухового барабану Bul (*CD*=4,60, *HR*=1,16), довжини верхнього зубного ряду CM3 (*CD*=4,10, *HR*=1,112) та нижнього зубного ряду, im3 (*CD*=4,04, *HR*=1,12). Ці дані свідчать про початкові стадії диференціації видів за ознаками, явно пов'язаними з трофікою та загалом з харчодобувною активністю. Досягнення і перевищення критичних значень має місце лише за однією (першою) ознакою, що свідчить про значну схожість видів за екологічними преференціями.

*Zagorodniuk, I., Postawa, T.* **Spatial and ecomorphological divergence of *Plecotus* sibling species (Mammalia) in sympatry zone in Eastern Europe** // Proc. of the State Nat. Hist. Museum. – Lviv, 2007. – **23**. – P. 215-224.

Genus *Plecotus* is presented in the fauna of region by two sibling species, *P. auritus* and *P. austriacus*, which form wide sympatry zone in the western provinces of Ukraine. By craniometrical characters (23 characters were investigated), the species are much closed and have average distance by Mayr's coefficient of divergence *CD*=2.42, and by Hutchinsonian ratio *HR*=1.076. Maximal displacements of species in both indices are concerning just four characters: length of auditory bulla Bul (CD=4,60, *HR*=1.16), length of upper toothrow CM3 (*CD*=4.10, *HR*=1.12), and lower toothrow im3 (*CD*=4.04, *HR*=1.12). All the data abundantly evidence of earlier stages of species differentiation in characters, which clearly related with trophism as well as hunting activity in a whole. Exceeding of critical values take place just in one (first among mentioned) character, that suggest considerable similarity of species in ecological preferences.

## Introduction

Sibling species represent unique model to investigate mechanisms of early taxonomic differentiation of species. Just in the territory of Eastern Europe there are about 15 superspecies groups, which include two or more morphologically closed, sibling or cryptic species, or different taxa of unclear rank [10–11, 20–21, 25].

One of the most "hard" groups is long-eared bats, genus *Plecotus*, which represented more than six problematic taxa. Long times genus *Plecotus* was considered a polytypic group, but in the middle of XX century all long-eared bats were joined into the only species, *P. auritus* (s. l.), which was split recently again on the several species. During long time of investigation in the territory of post-soviet countries, just the only polytypic species was recognize, *Plecotus auritus* (sensu lato).

Due to pioneer investigations of Ju. Krochko [13–12], A. Ruprecht [18–19] and P. Strelkov [22–23] in 1984–1988, East European *Plecotus* were revised in a whole. It was shown, that this genus is represented in the studied region by two closed species, *P. auritus* (s. str.) and *P. austriacus*, which were recognized in most following studies.

Change of traditional polytypic species concept (PSC) on the concept of "small" species (CSS) [7, 25] allows to analyze pattern of genus on species level and to form the hypotheses about historical dynamics of closed species, like to *Plecotus auritus* and *P. austriacus*. East-European populations of studied species are more similar, than Central-European ones, that is explained mainly by increasing of sizes of *Plecotus auritus*. Closing in morphology of related species in a zone of their sympatry corresponds to the model of opposite isomorphism as a way of formation of sibling-species.

## Materials and methods

Collections of 6 zoological museums of Ukraine were investigated: State Natural History Museum in Lviv (SNHM), National Natural History Museum in Kyiv (NNHM), Zoological Museum of Lviv National University (ZMLU), Museum of Nature of Kharkiv National University (MNKU), Zoological Museum of Kyiv National University (ZMKU), Zoological Museum of Uzhgorod National University (ZMUz).

All samples were re-identified using morphological and skull characters, described in special publications [6, 8, 18, 22, 34]. Both species of *Plecotus* were identified in collections with ratio: 35 *P. austriacus* and 55 *P. auritus*. Collected specimens of *P. austriacus* are listed in Annex 1, and records of both species are presented on map (Fig. 1). Data on species distribution based on investigations of bats in collections as well as in the field were partially described in special articles [5, 26–27].

For craniometrical analysis, samples were added by specimens from collection of Institute of Animal Systematics and Evolution PAS (Krakow). Totally, 23 skull and mandible measurements (Annex 2) were make using caliper to within 0.1 mm. All statistical operations were calculated in MS Excel. Two indices were use for species comparison, Mayr's coefficient of divergence (*CD*) and Hutchinsonian ratio (*HR*), given below. Peculiarities of their application for sibling species were described earlier [29, 32]:

$CD = (AVE_1 - AVE_2) / s.d.; \; HR = AVE_1 / AVE_2,$

where $AVE_1$ and $AVE_2$ are average values of metric character in compared samples, and *s.d.* is standard deviation of character's values.

## Distribution pattern

All classical faunal reviews mention the only species of long-eared bats in Eastern Europe, *Plecotus auritus* [1, 12]. Traditional views on taxonomy of *Plecotus* in our region were initially changed concerning Thranscarpathians, where *P. austriacus* was identified among *P. auritus* samples [13–14, 19]. Later *P. austriacus* was registered in some localities of Podolian Upland [5, 16], south-western part of Byelorussia [3], in northern Black sea region [23], in the Crimea and neighboring parts of Black sea and Azov sea regions [27]. In the Central and Eastern Ukraine just *P. auritus* are known up today [26].

In all the cases, a zone of sympatry of these two species concerns to the Southern and Western parts of Eastern Europe. There is the following correlation in distribution of a *Plecotus auritus* and its zone of a sympatry with in East Europe.

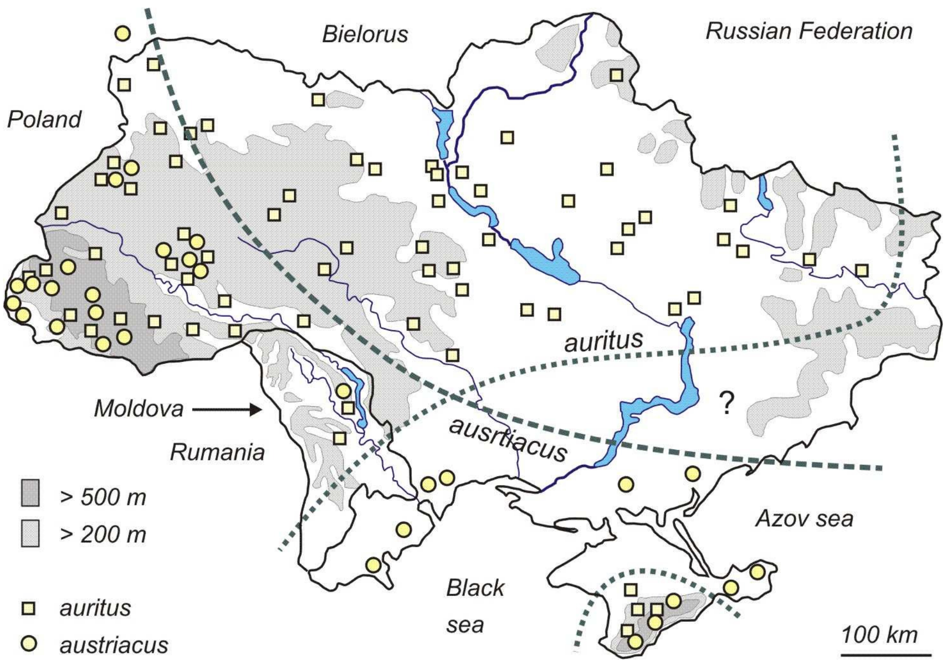


Fig. 1. Geographical distribution of two *Plecotus* species in Ukraine after analysis of collections and field investigations. Squares indicate known records of *P. auritus*, circles – *P. austriacus* (after [26], with additions according to [4, 17, 24, 33, 34] and new data). Lines are borders of ranges.

Most findings of *Plecotus* in Ukraine belong to species *Plecotus auritus* (Fig. 1). Geographical range of *P. austriacus* covers just south-western and southern parts of the region. Records of *P. austriacus* are listed below and presented in the map. Majority of *Plecotus austriacus* records come from the western regions of Ukraine. Here, wide sympatry zone with *P. auritus* exists. Known collected specimens of *P. austriacus* from the Ukraine are listed in the Annex 1. There are 30 records from 6 provinces, totally 48 specimens of this species. All other records belong to *P. auritus*. Distribution of all records in a time has shown some increasing of portion of *P. austriacus* during XX century (Fig. 2).

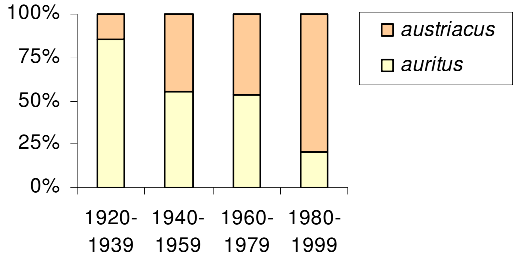


Fig. 2. Distribution of number of known collected samples of *Plecotus* sibling species in a time (data from Ukrainian museums). Totally, there are 53 records of *P. auritus* and 43 records of *P. austriacus* (for listed periods data distributed as 7, 51, 32, and 5 specimens).

### Craniometry

Variation of 23 craniometrical characters was studied (Table 1). These measurements completely characterized size and proportions of skull a whole, all parts of the skull (rostrum, teeth, brain-case) and all types of dimensions (length, width, height). Data from the Table 1 clearly shown, that studied measurements play very different role in species differentiation. No measurement reaches critical values of the Mayr's coefficient of divergence (*CD* > 6.0) and Hutchinsonian ratio (*HR* > 1.26). There are 5 characters with relatively high *CD* > 3.5, and 5 ones with *HR* > 1.10.

To compare the contribution of different characters in general differences of species, all values of *CD* and *HR* were normalized. Most significant characters are the following 7 (last column in Table 1): canine-basal length of skull (*CCL*) upper and lower toothrows (*CM3, PM3, im3u, cm3u*), length of auditory bulla (*Bul*).

Data on *HR* distribution confirm the rule known as "character displacement". Differences between closed species appear in features related to feeding niche, and these differences should reach the value *HR* = 1.26 [9, 15]. In our case, highest value reach just *HR* = 1.16 for bulla length (*Bul*), and another best values are *HR* = 1,15 in mandible height (*MaH*), and 1.12 in length of both upper (*CM3*) and lower (*cm3*) toothrow.

Table 1

Skull measurements of *Plecotus auritus* and *P. austriacus* (average ± st. dev.)

| Metric character | Character values | | Difference values* | | Normalized deviate | | |
|---|---|---|---|---|---|---|---|
| | *auritus* n=60 | *austriacus* n=57 | *CD* | *HR* | *CD* | *HR* | Aver. |
| *CRA* | 16.24 ± 0.35 | 17.31 ± 0.37 | 2.96 | 1.066 | 0.42 | -0.24 | 0.09 |
| *CBL* | 15.07 ± 0.32 | 16.20 ± 0.34 | 3.39 | 1.075 | 0.76 | -0.01 | 0.37 |
| *CCL* | 14.43 ± 0.30 | 15.59 ± 0.33 | **3.70** | 1.081 | **1.00** | 0.13 | **0.56** |
| *IOR* | 3.65 ± 0.15 | 3.55 ± 0.09 | 0.79 | 1.027 | -1.27 | -1.22 | -1.25 |
| *Zyg* | 8.71 ± 0.22 | 9.16 ± 0.23 | 2.05 | 1.052 | -0.29 | -0.59 | -0.44 |
| *BCr* | 8.88 ± 0.25 | 9.36 ± 0.21 | 2.08 | 1.053 | -0.27 | -0.55 | -0.41 |
| *IM3* | 6.22 ± 0.19 | 6.76 ± 0.20 | 2.78 | 1.087 | 0.28 | 0.29 | 0.29 |
| *CM3* | 5.31 ± 0.13 | 5.95 ± 0.18 | **4.10** | **1.120** | **1.30** | **1.12** | **1.21** |
| *PM3* | 3.95 ± 0.16 | 4.36 ± 0.09 | 3.06 | **1.104** | 0.49 | **0.70** | **0.60** |
| *M33* | 6.25 ± 0.16 | 6.40 ± 0.21 | 0.79 | 1.024 | -1.27 | -1.30 | -1.28 |
| *CC* | 3.71 ± 0.12 | 4.09 ± 0.17 | 2.47 | 1.100 | 0.03 | 0.61 | 0.32 |
| *HRo* | 3.76 ± 0.22 | 4.03 ± 0.19 | 1.27 | 1.071 | -0.90 | -0.12 | -0.51 |
| *RZg* | 3.70 ± 0.19 | 3.88 ± 0.16 | 1.05 | 1.050 | -1.07 | -0.64 | -0.85 |
| *PAL* | 6.53 ± 0.23 | 6.95 ± 0.26 | 1.70 | 1.063 | -0.56 | -0.31 | -0.43 |
| *HCr* | 5.62 ± 0.24 | 5.73 ± 0.24 | 0.43 | 1.019 | -1.55 | -1.42 | -1.48 |
| *HCB* | 7.37 ± 0.20 | 7.66 ± 0.26 | 1.24 | 1.039 | -0.92 | -0.91 | -0.92 |
| *BOc* | 5.10 ± 0.19 | 5.21 ± 0.19 | 0.61 | 1.023 | -1.41 | -1.32 | -1.36 |
| *Bul* | 4.07 ± 0.15 | 4.72 ± 0.13 | **4.60** | **1.161** | **1.70** | **2.14** | **1.92** |
| *MaL* | 10.52 ± 0.25 | 11.36 ± 0.26 | 3.21 | 1.079 | 0.61 | 0.09 | 0.35 |
| *MaH* | 2.95 ± 0.15 | 3.40 ± 0.12 | 3.17 | **1.151** | 0.58 | **1.88** | **1.23** |
| *im3* | 6.64 ± 0.17 | 7.26 ± 0.15 | **3.79** | 1.094 | **1.07** | 0.46 | **0.76** |
| *cm3* | 5.69 ± 0.18 | 6.40 ± 0.17 | **4.04** | **1.124** | **1.26** | **1.20** | **1.23** |
| average | | | 2.42 | 1.076 | 5 best: | 5 best: | 5 best: |
| st. dev. | | | 1.28 | 0.040 | ≥1.00 | ≥0.70 | ≥0.56 |

* Values for 5 most differenced characters are bolded: *CD* > 3.5 and *HR* > 1.10.

**Topography of best characters**

Topography of characters with large diagnostic values is very regular: all leading characters, in which best differences between species are registered, deal with dental and mandibular apparatus, and with sound system (Fig. 3, *a-b*).

Data on the species differentiation in the skull measurements allows considering that main trends in morphological divergence of *Plecotus* sibling species are in the differentiation of feeding niche. All main differences consist in primary divergence of species in "trophic" set of characters: the length of toothrow, mandible, and bulla. No significant features like width or height of neurocranium part of skull were found.

Data presented on Figure 3 clearly shown, that all the best characters have relations with feeding characters, and all of them are connected with main axis of skull. Maximal displacements of species in both indices are concerning with the following cranial characters (after Table 1): length of auditory bulla, *Bul* (*CD*=4.60, *HR*=1.16), main length of upper toothrow, *CM3* (*CD*=4.10, *HR*=1.12), and lower toothrow, *cm3* (*CD*=4.04, *HR*=1.12). Also, Mayr's index shown high values for two related characters: "canine" skull length, *CCL* (*CD*=3.70) and length of lower toothrow, *im3* (*CD*=3.79). By the same way, Hutchinson ratio shown high values for two another characters related to food catch: length of check toothrow, *Pm3* (*HR*=1.10), and height of mandible, *MaH* (*HR*=1.15). All the data abundantly evidence of earlier stages of species differentiation in characters, which clearly related with trophism and hunting activity in a whole.

**Comparison of Hutchinsonian and Mayr's indices**

Data presented on Figure 4 demonstrate some coincidence between two estimations of differences in species characters. These both indices, Hutchinsonian ratio (*HR*) and Mayr's coefficient of divergence (*CD*), were compared with each other, using data from Table 1. Coefficient of correlation between these two variables (*HR* and *CD*) is very high ($r$=0,882), that indicates on their non-random relation.

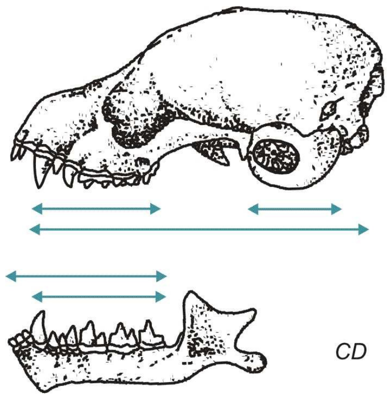


Fig. 3a. Topography of 5 most significant skull and mandible measurements according to Mayr's coefficient of divergence (*CD*>3.50).

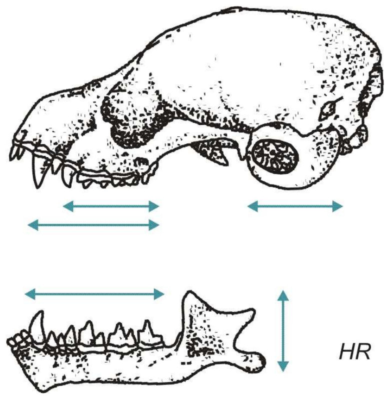


Fig. 3b. Topography of 5 most significant skull and mandible measurements according to Hutchinsonian ratio (*HR*>1.10).

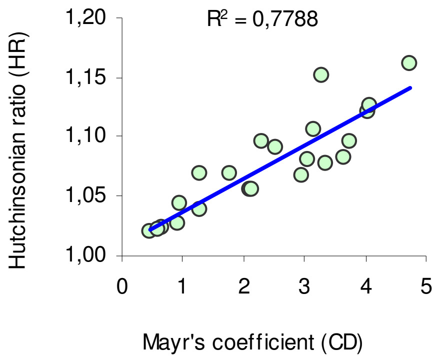


Fig. 4. Relationships between values of Hutchinsonian ratio (*HR*) and Mayr's coefficient of divergence (*CD*), that were estimated as level of species differences for total set of skull and mandible measurements. Plot was made after data from Table 1 (excluding four special characters listed in last rows of Table 1).

High correlation between these two indices can be explained by just one reason: non-random level of character's variation. Calculations shown mean coefficient of variation for all the characters *C.V.* = 3.19 % (3.35 in *Plecotus auritus* and 3.04 in *P. austriacus*). This linear equation is y = 0.0269x + 1.0104. Evidently, both indices *in pari causa* depend on difference between average values ($AVE_1$–$AVE_2$ or $AVE_1$/$AVE_2$), but regression slope fully determinates by *C.V.* In case of high variation (for example, 10 or 20 %) two coexisting species can reach high values of *HR* at smallest *CD*, and *vice versa*. Therefore, value of *C.V.* is significant and cannot be too small as well as too big.

Two such coexisting species have just two ways to reach minimal differences in some ecomorphological characters: (i) by increasing of linear differences, (ii) by reduction of variation [30]. Both ways separately are very expensive, because lead into heightened specialization. Thus, these two processes in accords can provide the minimal changes in evolutionary differentiations of closed species.

Both indices demonstrate different relations with levels of character variations (Fig. 4): *HR* doesn't depend and *CD* significantly depends on *C.V.* It can indicates on competence of author's hypothesis, that general differences between species don't depend on absolute value of character, but should succeed by means of reduction of character variation [28, 30]. Such result, first of all, appropriates in case of invasions and other changes of species geographical ranges. The latter are typical for natural history of most pairs of mammal sibling species in Eastern Europe [31]. Obtained data support idea, that differences are most expressed in small-sized characters (Fig. 5).

### Hypotheses on relations of *Plecotus* species

Diversity of viewpoints on differentiation of *Plecotus* sibling species occurring in Eastern Europe can be reduced to the two following concepts:

1. Wide-spread "western" concept based mostly on the known picture of geographical ranges: the gray bat distributed (prefer) in mountain regions, and the brown bat prefers lowlands. Most findings of *Plecotus auritus* come from northern (= lowland) regions, whereas *P. austriacus* known first of all from southern (= mountain) parts of the continent. Such interpretation likes to the idea of scale "cool-and-worm countries". On author's opinion, wide sympatry zone of these two species in Central Europe is secondary, due expansion of both species in quasi-natural landscapes of this region.

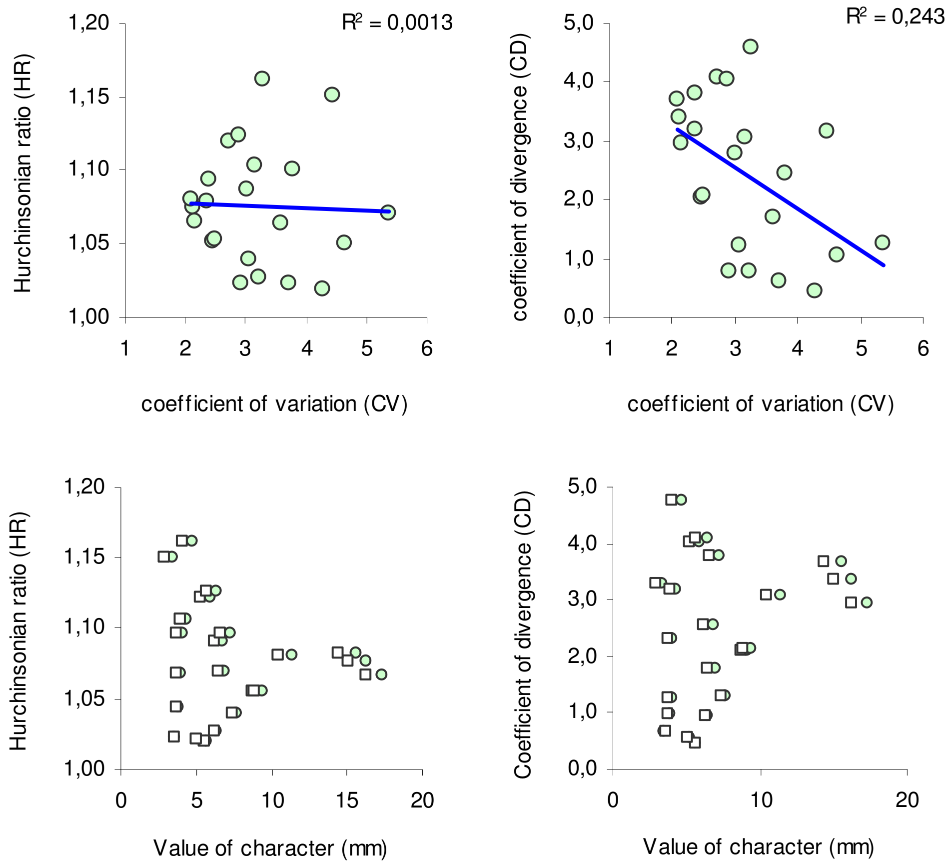


Fig. 5. Analysis of some quality of the Hutchinsonian ratio (*HR*) and the Mayr's coefficient of divergence (*CD*): relations of both indices with variation of characters (upper row) and with absolute values of characters (lower row). Plots were made using data from the Table 1.

2. "Eastern" ("soviet") concept deals with erroneous idea, that two *Plecotus* species (subspecies in former articles) are allopatric, and *Plecotus austriacus* ( "*P. a. wardi*" auct.) is the marginal in scale of East Europe "southern" species, and the Carpathians is considered as geographical border between two species (for example: [1]).

New investigations have shown a presence of wide sympatry zone of these two species (see map on Fig. 1). Moreover, this new point of view on species relations in Eastern Europe is based not only on recent records, but also on re-identifications of the old collection samples. It is likely, that two *Plecotus* species had initially allopatric distribution, and had form sympathry zone in recent time. It appears most likely just after human colonization of the most part of Europe, and both species had extended their ranges and abundance due to their evident bent to synanthropy, especially in case of *P. austriacus*.

Saving initial trends in geographic variation, species of *Plecotus* form morphologically differentiated sympatric populations (according to author's model of autogenetical mechanisms of speciation in sibling complexes [28]). It is clear, that levels of character displacements in investigated pair of species are relatively small against prospective displacement for sympatric pairs of related species. But in all the cases these differences cover the nonrandom set of characters, related with prey activity of species.

***Acknowledgments.*** The investigations is carried out due to support of Prof. A. Nadachowski and Prof. B. Wołoszyn (Institute of Animal systematics and evolution PAS), and due to help of our colleagues from zoological museums of Lviv and Kyiv.

**Annex 1. Records of *Plecotus austriacus* confirmed by museum samples**

**Lviv province:** ♦ Lviv city, Medovi caves, n=1 (1♂, 4.03.61, Kushniruk, ZMLU #504 skin). ♦ (ibidem), n=1 (1♀, 18.03.69, Kysil, ZMLU #496 skin [ident. not precise]). ♦ (ibidem), n=2 (2♂, 30.01.54, Opalatenko, SNHM #1057/3-4 skin+skull). ♦ Lviv city (pub), n=1 (1♀, 20.02.51, Khomjak, SNHM #1062/2 skin+skull). ♦ Lviv city (centre), n=1 (1♂, 04.04.52, Grichishyn, SNHM #1062/3 skin+skull). ♦ Lviv city (Radjanska str. (=Vinnychenko)), n=1 (1♀, 03.02.54, Tatarynov, SNHM #1062/5 skin+skull). ♦ Lviv city (Block str.), n=1 (1♂, 23.03.61, Maznova, NNHM #12591 skin [ident. not precise]). ♦ Ugniv vil. (90 km NW of Lviv), n=4 (2♀+1♂+1○, 11.03.67, leg.?, ZMLU 494, 495, 497, 498 skin+skull [just 2 skull]). ♦ Yavoriv dstr., Stradch (cave), n=1 (1♂, 13.02.55, Tatarynov, SNHM #1058/6 skin+skull). ♦ Yavoriv dstr., Ivan-Frankove, n=1 (1♂, 12.02.02, Gyzij, ZMLU #508 skin+skull). ♦ Drogobych (Suvorova str.), n=1 (1♂, 26.10.67, Dumanski, ZMLU #12593 skin+skull). **Ternopil province:** ♦ Nyzhnje Kryvche vil., cave [Kryshtaleva?], n=1 (1♂, 12.60, Maznova, ZMLU ST509). ♦ Borschiv dstr., Bilche-Zolote [Verteba cave?], n=3 (1♂+2♀, 02.02.51, Antonenko, SNHM #1059/1-3 skin+skull). ♦ (ibidem), n=1 (1♂, 27.03.52, Lysenko, SNHM #1059/4 skin+skull). ♦ Borschiv dstr., Vysichka (castle), n=3 (3♂, 30.03.52, Lysenko, SNHM #1061/1-3 skin+skull). **Zakarpatska province[1]:** ♦ Beregy city, n=5 (3♂+2♀, Abelentsev, 23.07.47, NNHM #303–307 skin+skull). ♦ Uzhgorod (church), n=2 (1♂+1♀, Abelentsev, 9.08.47, NNHM #310, 8791 skin+skull). ♦ Uzhgorod (city), n=1 (1○, leg.?, 4.05.49, ZMUz #102, skin). ♦ Uzhgorod (cellar), n=1 (1♂, Chonka, 17.02.66, ZMUz #4z, skin). ♦ Uzhgorod dstr., Glyboke (cave), n=1 (1♀, leg.?, 20.12.72, ZMUz #5z skin). ♦ Onokivsky dstr., Domanynci, n=2 (2♀, Abelentsev, 13.08.47, NNHM #308–309 skin+skull). ♦ Mukacheve dstr., Glynjanci (cave), n=1 (1♂, leg.?, 16.06.73, ZMUz #7z skin+skull). ♦ Mukacheve dstr., Rosvygove (church), n=2 (2○, leg.?, data?, ZMUz #no (X, Y) skin+skull). ♦ Tyachiv dstr., Solotvyne (cellar), n=1 (1♂, leg.?, data?, ZMUz #2z skin+skull). ♦ Beregy dstr., Popove (church), n=1 (1○, leg.?, 28.11.95, ZMUz #1z skin+skull). ♦ Beregy dstr., Ivanivtsi (cellar), n=2 (2○, leg.?, 12.71, ZMUz #22, 24 skin). ♦ Vynogradiv dstr., Koroleve (garret), n=2 (1♂+1○, Mikhel, 09.06.71, 17.05.72, ZMUz #3z, 6z skin+skull). **Odessa province:** ♦ Odessa city, n=1 (1♀, leg.?, 08.27, NNHM #9204 skin+skull). **Crimea:** ♦ Lenine dstr., Simpheropol highway, n=1 (1♂, Tkach, 10.02.93, NNHM #14319 skull). **Kherson province:** ♦ Askania-Nova, n=1 (1♂, 18.09.98, Polischuk, NNHM #14476 skull).

**Annex 2. Skull and mandible measurements of *Plecotus* samples**

**Overall skull measurements:** LCr — overall length of skull, CBL — condylobasal length of skull, CCL — "canine" length of skull, IOR — infraorbital width, Zyg — zygomatic width of skull, BCr — width of neurocranium. **Rostrum section:** IM3 — general length of upper toothrow, CM3 — basic length of toothrow (from canine), PM3 — length of upper cheek toothrow, M33 — width between toothrow (on level of $M^3$), CC — width between toothrow (on level of C), HRo — height of rostrum, RZg — height of rostrum (from zygomatic arc), Pal — length of palatine. **Occipital section:** HCr — main height of skull, HCB — height of skull with bulla, BOc — occipital width, Bul — length of bulla. **Mandible:** MaL — length of mandible (with incisive), MaH — height of mandible, im3 — length of lower teethrow, Proc — length of mandible processus.

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[1] Records of "*Plecotus*" from Verkhnje Vodyane (Rakhiv dstr.) mentioned recently in revision of bat collection of Uzhgorod University by T. Bashta [2], actually concern to another species of "long-eared bats" from another genus, namely *Myotis bechsteinii* [35].

1. *Abelentsev V. I., Popov B. M.* Order of handwingings, or bats — Chiroptera // Fauna of Ukraine. — 1956. Kyiv: Naukova Dumka, 1956. — Vol. 1 (Mammals), Issue 1. — P. 229-446.
2. *Bashta A.-T.* Bats in the collection of Zoological museum of the Uzhgorod National University: description and general analyzes // Scientific Bulletin of the Uzhgorod University. Series Biology. — 2007. — Vol. 21. — P. 120-127.
3. *Demyanchick M. G., Demyanchick V. T.* The problems of preserving of frontier population of Chiroptera in the South-West of Belarus // Bats & man: million years of coexistence: Abstracts VIIIth European Research Symposium. — Krakow: PLATAN Publ. House, 1999. — P. 15.
4. *Godlevska E. V.* Data on bats from the Kerch peninsula (Crimea) // Plecotus et al. — 2003. — № 6. — P. 29-36.
5. *Godlevska L., Petrushenko Ya., Tyschenko V., Zagorodniuk I.* Winter communities of the bats (Chiroptera) in the caves of the Central Podillia (Ukraine) // Vestnik zoologii. — 2005. — Vol. 39, N 2. — P. 37-45.
6. *Hanák V.* Zur Systematik und Verbreitung der Gattung *Plecotus*, Geoffroy, 1818 (Mammalia, Chiroptera) // Lynx (series nova). — 1966. — Fasc. 6. — P. 57-66.
7. *Häuser C. L.* The debate about the biological species concept — a review // Z. zool. Syst. Evol.-forsch. — 1987. — Vol. 25. — S. 241-257.
8. *Horaček I.* Notes on the ecology of bats of the genus *Plecotus* Geoffroy, 1818 (Mammalia, Chiroptera) // Vést. Čs. spol. zool. — 1975. — Vol. 39. — P. 195-210.
9. *Hutchinson G. E.* Homage to Santa *Rosalia* or why are there so many kinds of animals? // The American Naturalist. – 1959. – Vol. 93, № 870. – P. 145-159.
10. *Juste J., Ibanez C., Munoz J. et al.* Mitochondrial phylogeography of the long-eared bats (*Plecotus*) in the Mediterranean Palaearctic and Atlantic islands // Molecular Phylogenetics and Evolution. — 2004. — Vol. 31. — P. 1114-1126.
11. *Kiefer A., Mayer F., Kosuch J. et. al.* Conflicting molecular phylogenies of European long-eared bats (*Plecotus*) can be explained by cryptic diversity // Molecular Phylogenetics and Evolution. — 2002. — Vol. 25, N 3. — P. 557-566.
12. *Korneev O. O.* Key to mammals of Ukrainian SSR (2nd edition). — Kyiv: Naukova Dumka Press, 1965. — P. 1-236.
13. *Krochko Ju. I.* On the records of the European subspecies of the long-eared bat (*Plecotus auritus austriacus*) from the Zakarpatska province // Nature protection and rational using of natural resources. — Kyiv: Naukova Dumka Press, 1980. — P. 181-182.
14. *Krochko Ju. I.* Bats of Ukraine and some aspects of their protection // Scientific Bulletin of the Uzhgorod State University. Series Biology. — 1995. — Vol. 2. — P. 96-98.
15. *Meszéna G., Gyllenberg M., Pásztor L., Metz J. A. J.* Competitive exclusion and limiting similarity: a unified theory // Theoretical Population Biology. — 2006. — Vol. 69. — P. 68–87.
16. *Petrushenko Ya.* Finding of the gray long-eared bat (*Plecotus austriacus*) in Podolia // Vestnik zoologii. — 2000. — Vol. 34, № 1–2. — P. 20.
17. *Petrushenko Ya., Godlevska L., Zagorodniuk I.* Investigations on bat communities in the Siversky Donets flood-lands // Visnyk of Luhansk Pedagogical University. Biological Sciences. — 2002. — № 1 (45). — P. 121-124.
18. *Ruprecht A.* Metody wyrozniania *Plecotus austriacus* Fischer, 1829 i nowe stanowiska tego gatunku w Polsce // Acta Theriologica. — 1965. — Vol. 10. — P. 215-220.
19. *Ruprecht A. L.* Data on the findings of the gray long-eared bat (*Plecotus austriacus*) in the Zakarpatska province of Ukraine // Vestnik zoologii. — 1998. — Vol. 32, № 4. — P. 104-105.
20. *Spitzenberger F., Pialek J., Haring E.* Systematics of the genus *Plecotus* (Mammalia, Vespertilionidae) in Austria based on morphometric and molecular investigations // Folia Zoologica. — 2001. — Vol. 50, № 3. — P. 161-172.
21. *Spitzenberger E., Strelkov P., Haring E.* Morphology and mitochondrial DNA sequences show that *Plecotus alpinus* Kiefer & Veith, 2002 and *Plecotus microdontus* Spitzenberger, 2002 are synonyms of *Plecotus macrobullans* Kuzjakin, 1965 // Natura Croatica. — 2003. — Vol. 12, № 2. — P. 39-53.

22. *Strelkov P. P.* Brown (*Plecotus auritus*) and gray (*Plecotus austriacus*) long-eared bats (Chiroptera, Vespertilionidae) in USSR. Communication 1 // Zoologichesky Zhurnal. — 1988a. — Vol. 67, № 1. — P. 90-101.
23. *Strelkov P. P.* Brown (*Plecotus auritus*) and gray (*Plecotus austriacus*) long-eared bats (Chiroptera, Vespertilionidae) in USSR. Communication 2 // Zoologichesky Zhurnal. — 1988b. — Vol. 67, № 2. — P. 287-292.
24. *Vasiliev A., Andreev S.* Species composition, abundance and distribution of bats (Chiroptera) occurring in the undergrounds near village Sakharna (Moldova) // Plecotus et al. — 1998. — №1. — P. 48-54.
25. *Zagorodnyuk I. V.* Polytypic species: a concept and the presence in mammal fauna of the East Europe // Reports Natl. Acad. Sci. Ukr. — 1998. — № 7. — P. 171-178.
26. *Zagorodniuk I.* Brown long-eared bat — *Plecotus austriacus*. Gray long-eared bat — *Plecotus austriacus* // Mammals of Ukraine, protected by Bern Convention. — Kyiv, 1999. — P. 61-71.
27. *Zagorodniuk I.* Species of the genus *Plecotus* in the Crimea and neighbouring areas in the Northern Black Sea Region // Woloszyn B. W. (ed.). Proceedings of the VIII$^{th}$ ERBS. — Krakow: PLATAN, 2001. — Vol. 2. — P. 159-173.
28. *Zagorodniuk I. V.* Autogenic regularities of speciation in sibling complexes of mammals // Reports Natl. Acad. Sci. of Ukraine. — 2003. — № 11. — P. 179-187.
29. *Zagorodniuk I.* Levels of morphological differentiation in closed species of mammals and the concept of hiatus // Visnyk of Lviv University. Biology Series. — 2004a. — Vol. 38. — P. 21-42.
30. *Zagorodniuk I. V.* Biological species as amplify essence: attributes of buffering and modes of shifting // Scientific Bulletin of the Uzhgorod University. Series Biology. — 2004b. — Issue 14. — P. 5-15.
31. *Zagorodniuk I.* Biogeography of mammals' cryptic species in the Eastern Europe // Scientific Bulletin of the Uzhgorod University. Series Biology. — 2005. — Issue 17. — P. 5-27.
32. *Zagorodniuk I.* Conflict through coincidence of niches in sibling species: estimation using Hutchinsonian ratio // Scientific Bulletin of the Uzhgorod University. Series Biology. — 2007. — Vol. 21. — P. 5-13.
33. *Zagorodniuk I., Godlevska L.* Bats on the collections of zoological museums of Ukraine: phenological review of data // Migration status of bats in Ukraine. — Kyiv, 2001. — P. 122-156.
34. *Zagorodniuk I., Godlevska L., Tyshchenko V., Petrushenko Ya.* Bats of Ukraine and adjacent countries: a guide for field investigations. — Kyiv, 2002. — 110 pp.
35. *Zagorodniuk I., Zizda Ju.* Records of three rare bat species in Transcarpathian Ukraine // Vestnik zoologii. — 2007. — Vol. 41, № 3. — P. 226.



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