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MICROEVOLUTION OF BECHSTEIN'S BAT *MYOTIS* *BECHSTEINII* (KUHLE, 1817) (MAMMALIA: CHIROPTERA) IN THE HOLOCENE OF SOUTHERN POLAND

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Abstract. Bechstein's bat was one of the most common species in the Middle and Late Holocene of Southern Poland. It dominated in Kraków – Częstochowa Upland, but was also frequent in Tatra Mountains. Bone material from thanatocoenoses, dated by ^{14}C AMS method, was analysed. The aim of studies was to investigate the direction of changes in skull and mandible morphology of *Myotis bechsteinii* during the period from 5710 BC till present day and to answer the question which environmental parameters significantly correlates with these microevolutionary processes and frequency of species in different thanatocoenoses. Mandibles and skulls were analysed separately. Morphology was correlated with climate characteristics, temperatures, and percentage pollen of such species of trees as hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*), oak (*Quercus*) and elm (*Ulmus*) in investigated time limits.

Résumé. On a étudié les tendances microévolutives du crâne de la chauve-souris de Bechstein. Malgré le fait que les différences entre les groupes ne sont pas remarquables du point de vue statistique, les tendances microévolutives morphologiques sont visibles. Les changements de chaque paramètre ont un cours individuel, mais les tendances sont à peu près similaires. L'analyse statistique a rendue possible la réponse à la question quels facteurs de niche ont une influence importante sur la morphologie du crâne et quelle est la direction de ces influences. La température moyenne du mois de janvier, le pourcentage de *Fraxinus excelsior*, la fréquence de la chauve-souris de Bechstein et la fréquence des inondations déterminent la majeure partie des changements morphologiques.

Key words: Holocene, Bechstein's bat, microevolution, Southern Poland.

INTRODUCTION

Holocene is the last warm period of Quaternary, with the beginning dated to 10 200 ^{14}C BP (Starkel, 1999). In this relatively short period, many fluctuations in climate and changes in vegetation (Cheddadi & Bar-Hen, 2009; Raible et al., 2006; Ralska-Jasiewiczowa et al., 2004) occurred. Holocene is the best known geological period, in which present flora and fauna was moulded on the North of the Carpathian Mountains (Pawłowski, 1999).

Bechstein's bat is actually restricted to southern and central Poland and considered rare in the country. While during the Atlantic and Subboreal period its frequency in thanatocoenoses varied from 2-65%, it have been almost completely eliminated from recent fauna of Polish Tatras (Postawa, 2004; Piksa & Wołoszyn, 2001). Forest complexes dominated by old hollowed deciduous trees are typical natural biotops of this species. In the diet of *Myotis bechsteinii* (Kuhl, 1817) moths, beetles, spiders etc. dominate, caught mostly low between dense thickets (Beck, 1995). It inhabitates similar ecological niche as *Myotis nattereri* (Fenton & Bogdanowicz, 2002). If the competition for the best habitat is significant between these two species, it can have influence on their microevolution.

Morphology of population can be modified by age and sex structure (Krebs, 2001), despite the fact that investigated subfossil remains are from winter

hibernacula (Postawa, 2004; Piksa & Wołoszyn, 2001), and sexual dimorphism of small bats is not evident (Bogdanowicz, 1992). Analysis of Bechstein's bat recent population makes possible the investigation of these problems.

The aim of this study is to investigate microevolutionary trends in cranial skeleton morphology of Bechstein's bat and to answer to the question which of several factors (such as temperature, height above sea level, habitat structure) have significant influence on the morphology and which is the direction of this influence (positive or negative correlation).

MATERIALS AND METHODS

Study is based on morphometric analysis of 402 cranial skeleton elements: 190 skulls and 212 mandibles (Tabs 1, 2). The material, housed in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków (ISEA, PAS), came from 17 thanatocoenoses, dated with ^{14}C AMS method (Tab. 3).

Time scale includes the period from 5710 BC – 5570 BC (6725 ± 50 bp before calibration) to the recent time. ^{14}C dates, calibrated in OxCal programme, are given with 60% probability (standard in zoological analysis) (Walanus & Goslar, 2004).

For statistics, the following computer programmes were used: Microsoft Excel, Past, Statistica 6.0, and Canoco 4.52. For Discriminant Analysis (DA) and for making diagrams of changes morphological parameters during the Middle and Late Holocene, samples of unless 9 cranial skeleton elements were used.

Abbreviations

Analysed morphological parameters:

Skull dimensions: GLS - greatest length of skull; CLS - condylobasal length of skull; PM_1 - palate width at M_1 ; MSW - maximum skull width; MZB - maximum zygomatic breadth; PSW - posterior skull width; COW - condylus occipitalis width; TPL - total palate length; $\text{L}(\text{C}-\text{P}_3)$ - canine to third premolar length; LRT - toothrow length; $\text{L}(\text{P}_4-\text{M}_3)$ - P_4 to M_3 length; $\text{L}(\text{M}_1-\text{M}_3)$ - M_1 to M_3 length; PC - palatal width at canine (C_1); FCW - fossa condylaris width; $\text{L}(\text{P}_1-\text{P}_3)$ - P_1 to P_3 length;

Mandible dimensions: MDL - mandible length; MBTR - mandible toothrow length; LPA - length of processus angularis; HCP - height of coronoid process; HP_4 - height of mandible at P_4 ; HM_3 - height of mandible at M_3 .

Table 1

Mean, minimum and maximum values of skull dimensions of Bechstein's bat (*Myotis bechsteinii*) from thanatocoenoses dated with ^{14}C AMS method.

^{14}C bp	N	Value	Skull measurements [cm]														
			GLS	CLS	PM_1	MSW	MZB	PSW	COW	TPL	$\text{C}-\text{P}_3$	LTR	P_4-M_3	M_1-M_3	PC	FCW	P_1-P_3
6725	14	mean	17.27	16.31	5.72	4.22	11.16	8.40	4.92	8.05	2.25	6.74	4.69	3.75	3.76	3.91	1.23
		minimum	17.16	16.22	5.59	4.17	11.12	8.30	4.52	7.88	2.17	6.40	4.63	3.54	3.60	3.68	1.01
		maximum	17.42	16.43	6.20	4.30	11.22	8.51	5.31	8.25	2.38	6.94	4.80	3.91	4.00	4.01	1.41
5990	10	mean	17.53	16.46	5.77	4.30	10.88	8.28	4.93	8.89	2.34	6.69	4.71	3.62	3.77	4.13	1.32
		minimum	17.23	16.28	5.66	4.21	10.58	8.18	4.70	7.98	2.22	6.53	4.67	3.48	3.54	3.88	1.11
		maximum	17.83	16.67	5.84	4.40	11.23	8.46	5.22	9.92	2.40	7.00	4.73	3.83	3.97	4.27	1.42
4925	25	mean	17.43	16.48	5.67	4.43	10.91	8.31	4.94	8.52	2.35	6.80	4.73	3.84	4.02	4.03	1.39
		minimum	17.19	16.24	5.49	4.19	10.59	8.16	4.72	7.68	2.21	6.48	4.52	3.64	3.77	3.79	1.10
		maximum	17.99	16.87	6.00	4.97	11.20	8.52	5.17	8.99	2.47	7.21	4.92	4.74	4.22	4.38	1.68

Table 1 (continued)

¹⁴ C bp	N	Value	Skull measurements [cm]														
			GLS	CLS	PM ₁	MSW	MZB	PSW	COW	TPL	C-P ₃	LTR	P ₄ -M ₃	M ₁ -M ₃	PC	FCW	P ₁ -P ₃
4345	5	mean	17.42	16.67	5.82	4.80	10.87	8.28	4.78	8.70	2.37	7.05	4.64	3.91	3.80	4.18	1.49
		minimum	17.39	16.44	5.51	4.50	10.71	8.19	4.67	8.62	2.02	6.72	4.52	3.86	3.77	4.06	1.42
		maximum	17.46	16.86	6.01	5.00	11.00	8.41	4.83	8.75	2.71	7.33	4.78	4.01	3.86	4.29	1.58
3725	12	mean	17.40	16.51	5.71	4.48	10.73	8.33	4.90	9.44	2.39	7.04	4.66	3.73	3.79	4.10	1.45
		minimum	17.12	16.41	5.56	4.30	10.50	8.23	4.72	8.77	2.30	6.81	4.42	3.51	3.53	3.80	1.31
		maximum	17.81	16.62	5.82	4.68	11.00	8.46	5.01	10.09	2.49	7.21	4.85	3.88	4.66	4.23	1.62
3545	12	mean	17.39	16.91	5.82	4.32	10.60	7.97	4.96	9.77	2.43	6.98	4.60	3.69	4.00	4.24	1.84
		minimum	17.21	16.60	5.60	4.01	10.26	7.60	4.74	8.98	2.23	6.70	4.41	3.63	3.67	4.00	1.40
		maximum	17.61	17.19	5.92	4.90	10.90	8.33	5.21	10.31	2.58	7.25	5.01	3.79	4.23	4.36	2.24
2890	20	mean	17.70	16.57	5.80	4.54	10.88	8.49	4.91	9.47	2.47	6.94	4.45	3.46	3.66	3.95	1.40
		minimum	17.46	16.39	5.67	4.29	10.70	8.21	4.70	8.72	2.24	6.52	4.23	3.22	3.50	3.79	1.33
		maximum	17.90	16.73	5.93	5.00	11.04	8.83	5.10	10.02	2.74	7.45	4.73	3.83	3.78	4.28	1.48
2120	24	mean	17.58	16.40	5.67	4.39	10.78	8.34	4.85	9.07	2.42	6.69	4.26	3.32	3.55	3.86	1.35
		minimum	17.45	16.22	5.59	4.29	10.63	8.21	4.70	8.52	2.21	6.45	3.82	3.19	3.40	3.62	1.27
		maximum	17.77	16.66	5.77	4.63	11.00	8.44	5.02	9.56	2.68	6.88	4.58	3.45	3.66	4.18	1.40
1490	6	mean	17.36	16.33	5.76	4.32	10.95	8.30	5.20	8.23	2.24	6.92	4.68	4.43	3.80	3.94	1.19
		minimum	17.29	16.25	5.66	4.20	10.80	8.21	5.12	8.17	2.16	6.84	4.65	3.70	3.76	3.80	1.06
		maximum	17.42	16.41	5.82	4.45	11.11	8.41	5.30	8.30	2.32	7.00	4.71	7.79	3.82	4.02	1.37
1470	15	mean	17.44	16.35	5.84	4.29	11.00	8.35	5.00	8.18	2.21	6.89	4.79	3.80	3.80	4.00	1.08
		minimum	17.29	16.20	5.31	4.20	10.75	8.21	4.82	7.96	2.15	6.80	4.62	3.70	3.76	3.90	1.00
		maximum	17.67	16.42	6.20	4.40	11.22	8.41	5.22	8.30	2.31	7.00	6.66	3.89	3.83	4.12	1.18
1320	21	mean	17.55	16.54	5.83	4.41	10.84	8.47	4.97	8.74	2.27	6.79	4.52	3.68	3.78	4.00	1.21
		minimum	17.31	16.35	5.66	4.30	10.52	8.31	4.78	8.18	2.18	6.53	4.25	3.34	3.61	3.76	1.00
		maximum	17.88	16.73	6.12	4.63	11.22	8.83	5.22	9.94	2.41	7.00	4.78	3.86	3.89	4.22	1.40
595	14	mean	17.73	16.60	5.74	4.42	10.75	8.05	5.28	8.30	2.30	6.91	4.76	3.66	3.85	4.06	1.36
		minimum	17.49	16.33	5.00	4.27	10.56	7.69	5.11	8.11	2.18	6.74	4.48	3.45	3.61	3.79	1.29
		maximum	18.12	16.77	5.99	4.66	10.99	8.43	5.40	8.62	2.42	7.04	6.60	3.88	4.01	4.35	1.50
1	12	mean	17.70	16.95	5.71	4.43	10.81	7.95	5.45	9.70	2.32	6.95	4.63	3.76	4.02	4.33	2.17
		minimum	17.17	16.64	5.01	4.17	10.47	7.63	5.12	8.87	2.23	6.80	4.48	3.66	3.88	4.19	1.93
		maximum	18.09	17.28	5.99	4.62	11.02	8.40	5.79	10.22	2.40	7.24	4.87	3.93	4.13	4.49	2.36
Σ	190																

Table 2

Mean, minimum and maximum values of mandible dimensions of Bechstein's bat (*Myotis bechsteinii*) from thanatocoenoses dated with ^{14}C AMS method.

^{14}C bp	N	Value	Mandible measurements [cm]					
			MDL	MBTR	LPA	HCP	HP ₄	HM ₃
6725	19	mean	12.72	7.43	3.92	4.00	1.50	1.58
		minimum	12.16	6.36	3.37	3.73	1.32	1.43
		maximum	13.37	7.90	4.55	4.25	1.74	1.78
5990	9	mean	12.99	7.43	3.93	4.04	1.46	1.62
		minimum	12.91	6.93	3.46	3.78	1.35	1.40
		maximum	13.09	7.78	4.27	4.17	1.55	1.72
5225	20	mean	12.87	7.39	4.05	4.01	1.55	1.65
		minimum	12.45	6.98	3.52	3.42	1.42	1.52
		maximum	13.19	7.72	4.34	4.34	1.68	1.79
4345	20	mean	12.61	7.33	3.96	3.93	1.53	1.59
		minimum	12.22	6.99	3.52	3.44	1.35	1.36
		maximum	13.01	7.54	4.27	4.35	1.68	1.79
4110	12	mean	12.47	7.24	3.76	3.84	1.41	1.53
		minimum	11.93	7.00	3.50	3.33	1.31	1.36
		maximum	12.99	7.50	4.24	4.35	1.56	1.64
3905	9	mean	13.07	7.44	4.06	4.01	1.53	1.61
		minimum	12.72	7.34	3.77	3.80	1.45	1.56
		maximum	13.42	7.64	4.29	4.34	1.66	1.70
3545	26	mean	12.79	7.58	3.80	3.78	1.61	1.64
		minimum	12.60	7.29	3.60	3.65	1.49	1.58
		maximum	13.00	7.89	4.01	4.01	1.68	1.70
3535	20	mean	12.95	7.60	3.91	3.93	1.61	1.68
		minimum	12.80	7.29	3.68	3.65	1.57	1.62
		maximum	13.09	7.82	4.11	4.12	1.64	1.71
2890	24	mean	12.76	7.44	3.83	3.85	1.63	1.66
		minimum	12.36	7.23	3.51	3.45	1.43	1.59
		maximum	13.20	7.79	4.11	4.11	1.83	1.77
2415	21	mean	12.76	7.44	3.72	3.88	1.61	1.66
		minimum	12.47	6.90	3.51	3.58	1.50	1.59
		maximum	13.22	7.72	4.00	4.11	1.72	1.71
1470	5	mean	12.81	7.56	4.27	4.15	1.52	1.50
		minimum	12.69	7.49	4.12	4.01	1.44	1.47
		maximum	12.99	7.62	4.32	4.30	1.58	1.53

Table 2 (continued)

¹⁴ C bp	N	Value	Mandible measurements [cm]					
			MDL	MBTR	LPA	HCP	HP ₄	HM ₃
1320	3	mean	12.78	7.61	4.35	4.26	1.56	1.54
		minimum	12.77	7.60	4.33	4.20	1.55	1.53
		maximum	12.79	7.63	4.37	4.30	1.57	1.54
595	6	mean	12.73	7.58	4.28	4.21	1.57	1.52
		minimum	12.70	7.52	4.20	4.19	1.55	1.50
		maximum	12.77	7.62	4.36	4.24	1.60	1.53
1	18	mean	12.80	7.52	4.29	4.38	1.57	1.52
		minimum	12.69	7.35	4.20	4.30	1.51	1.48
		maximum	12.93	7.81	4.41	4.54	1.60	1.55
Σ	212							

Table 3

Thanatocoenoses dated with ¹⁴C AMS method (1-3, 5-7 and 10 from Kraków-Częstochowa Upland; 4, 8, 11 and 13-17 from Tatra Mts.; 9 from Świętokrzyskie Mts.; 12 from Sudety Mts.; 18 - recent specimens from uplands of southern Poland).

Nr.	Thanatocoenoses	¹⁴ C bp AMS	¹⁴ C BP AMS Calibrated date
1	Cave Na Świniuszcze	6725±50 BP	5710 BC - 5570 BC
2	Cave Studnisko II	5990±40 BP	4940 BC - 4800 BC
3	Cave Maurycego	5225±45 BP	4150 BC - 3960 BC
4	Cave Bandzioch Kominiarski	4925±35 BP	3760 BC - 3650 BC
5	Cave Studnisko I	4345±45 BP	3020 BC - 2900 BC
6	Cave Kryształowa	4110±45 BP	2860 BC - 2580 BC
7	Cave Małotowa	3905±45 BP	2470 BC - 2340 BC
8	Cave Miętusia Wyżnia	3725±30 BP	2200 BC - 2040 BC
9	Cave Zbójecka w Łagowie	3545±35 BP	1940 BC - 1780 BC
10	Cave Na Tomaszówkach Dln.	3535±35 BP	1930 BC - 1770 BC
11	Cave Wysoka Za Siedmioma Progami	2890±30 BP	1120 BC - 1015 BC
12	Cave Niedźwiedzia w Kletnie	2415±30 BP	530 BC - 400 BC
13	Cave Zakosista	2120±30 BP	200 BC - 100 BC
14	Cave Szczelina Chochotowska	1490±30 BP	545 AD - 605 AD
15	Cave Piwnica Miętusia	1470±30 BP	565 AD - 630 AD
16	Cave Zimna	1370±30 BP	640 AD - 670 AD
17	Cave Czarna	595±30 BP	1305 AD - 1405 AD
18	Recent specimens	*marked as 1	

At each skull 15 and at each mandible six morphological parameters were taken, using Nikon MM200 measurement microscope. Each result was given with precision up to 0.001 mm (Tabs 1, 2).

To divide Middle and Late Holocene population of *M. bechsteinii* into general groups, and to see eventually mistakes in description of specimens as Bechstein's bat, Principal Component Analysis (PCA) was made.

Discriminant Analysis (DA) gives an answer to which of several cranial dimensions have significant and the strongest influence on differentiated investigated populations. Than changes of each morphological parameter significantly discriminating these groups was examined. 28 environmental factors were chosen to investigate their correlation with morphological parameters. Those are: age of sample, temperature of January, general climate characteristic, a.s.l. hight, frequency of Bechstein's bat, frequency of Natterer's bat, percentage of pollen of: fir, maple, hornbeam, beech, ash, spruce, pine, oak, willow, lime, elm, sum of herb pollen, etc. (Tab. 7).

To see which of environmental variables (Tab. 4) have significant influence to morphology and if it correlates with morphology positively or negatively, Redundancy Analysis (RDA) with gradient selection was made (Lepš & Šmilauer, 1999; Ter Braak & Prentice, 1988). To make results clearer, time limits are given separately for Holocene: Atlantic (8200-5115 ^{14}C BP), Subboreal (5115-2800 ^{14}C BP), and Subatlantic period (2800 ^{14}C BP till now). In Redundancy Analysis (RDA) length and direction of the arrows say about strength and character of correlation with morphological parameters (the longer arrow = the stronger influence on environmental parameter to morphology).

RESULTS

For skulls as well as for mandibles percentage of variance for the first with the second canonical axis in PCA does not exceed 50%: there is no doubt that all specimens belong to the species *M. bechsteinii* (Tab. 5). Results of PCA are given on figures 1 and 2. Differently marked lines connect extreme points of each group, dated with ^{14}C method. Influence of sexual dimorphism to differences between populations of Bechstein's bat from radiocarbon dated thanatocoenoses are excluded by researching recent population of the species. Principal Component Analysis did not show significant differences between males and females (variance = 38%).

Discriminant analysis shows morphological parameters significantly differentiating examined populations. In skull morphology those are: P^1 - P^3 length [$L(P^1-P^3)$], length from the first to the third molar [$L(M_1-M_3)$], maximum zygomatic breadth (MZB), total palate length (TPL), condylus occipitalis width (COW), posterior skull width (PSW), greatest length of skull (GLS), tooththrow length (LTR), palatal width at canine (C^1) [$L(C^1-C^1)$], canine to third premolar length [$L(C-P^3)$], condylobasal of skull (CLS), maximum skull width (MSW), fossa condylaris width (FCW), P^4 to M^3 length [$L(P^4-M^3)$] and in mandibles: height of coronoid process (HCP), height of mandible at third molar (HM_3), height of mandible at fourth premolar (HP_4), length of processus angularis (LPA), mandible length (MDL) and mandible tooththrow length (MBTR) (Tab. 7).

Table 4
Values of environmental factors in investigated time scale.

¹⁴ C bp AMS	T _j [K]	<i>Populus</i>	<i>Fagus</i>	<i>Acer</i>	<i>Abies</i>	<i>Alnus</i>	<i>Betula</i>	<i>Fraxinus</i>	<i>Corylus</i>	<i>Salix</i>	<i>Ulmus</i>	<i>Quercus</i>	<i>Tilia</i>	<i>Carpinus</i>	<i>Pinus</i>	<i>Picea</i>	<i>Artemisia</i>	Cyperaceae	Poaceae	<i>Typha</i>	Herbs	Climate	Ft MBE	Ft MYN	Ft Floods	Floods	T _y [°C]	H a.s.l.
6725	268.15	0.1	0.50	0.50	0.10	15.00	15.00	3.00	20.00	0.50	7.00	10.00	3.00	0.10	30.00	5.00	0.70	5.00	5.00	0.20	10.00	1	25.76	5.30	0.0002	0	8.5	450
5990	266.65	0.1	0.50	0.50	0.10	20.00	15.00	3.00	15.00	0.50	7.00	10.00	3.00	0.50	30.00	5.00	0.50	3.00	5.00	0.20	10.00	1	26.34	52.41	0.0002	0	9.2	346
5225	266.15	0.1	0.50	0.50	0.50	15.00	15.00	2.00	15.00	0.50	5.00	10.00	3.00	0.50	30.00	5.00	0.70	3.00	5.00	0.70	20.00	1	28.33	33.67	0.0006	1	9.2	340
4925	265.65	0.1	1.00	0.50	1.00	15.00	10.00	3.00	20.00	0.50	10.00	7.00	3.00	1.00	20.00	20.00	1.00	3.00	3.00	0.20	10.00	2	11.96	0.96	0.0005	1	3.0	1456
4110	267.15	0.1	2.00	0.50	1.00	20.00	10.00	2.00	15.00	0.50	3.00	10.00	5.00	2.00	25.00	10.00	0.70	5.00	3.00	0.20	10.00	2	38.27	9.22	0.0002	1	8.7	325
4345	266.15	0.1	1.00	0.50	0.50	15.00	10.00	2.00	15.00	0.50	5.00	10.00	3.00	1.00	30.00	7.00	0.50	5.00	5.00	0.20	10.00	2	4.17	56.25	0.0003	0	8.7	346
3905	267.15	0.1	2.00	0.50	1.00	20.00	10.00	2.00	15.00	0.50	3.00	10.00	5.00	2.00	25.00	15.00	0.70	7.00	3.00	0.20	20.00	2	47.17	3.77	0.0001	0	8.7	384
3725	267.65	0.5	5.00	0.50	7.00	15.00	7.00	3.00	15.00	0.50	7.00	7.00	3.00	3.00	20.00	25.00	1.00	3.00	3.00	0.20	10.00	2	15.20	1.60	0.0001	0	4.0	1393
3545	267.65	0.1	3.00	0.50	2.00	25.00	20.00	1.00	7.00	1.00	2.00	10.00	2.00	5.00	40.00	5.00	1.00	2.00	3.00	0.20	7.00	2	29.63	22.96	0.0003	0	8.5	312
3535	267.65	0.5	5.00	0.50	7.00	20.00	10.00	2.00	10.00	0.50	3.00	10.00	3.00	7.00	25.00	10.00	0.70	5.00	5.00	0.20	20.00	2	52.45	9.98	0.0003	0	8.2	435
2890	269.15	0.1	7.00	0.50	5.00	15.00	7.00	2.00	7.00	0.50	5.00	7.00	2.00	7.00	20.00	25.00	1.00	1.00	3.00	0.20	7.00	2	3.92	0.00	0.0004	0	3.0	1488
2415	269.15	0.5	15.00	0.50	7.00	15.00	15.00	1.00	5.00	0.50	2.00	7.00	1.00	7.00	25.00	7.00	1.00	3.00	5.00	0.20	10.00	3	65.22	10.86	0.0003	1	5.4	800
2120	268.65	0.1	15.00	0.50	10.00	15.00	10.00	1.00	5.00	0.50	3.00	7.00	1.00	7.00	25.00	10.00	1.00	2.00	3.00	0.20	10.00	3	41.86	0.00	0.0004	1	3.0	1275
1490	267.15	0.5	10.00	0.10	15.00	20.00	15.00	0.50	5.00	1.00	2.00	7.00	1.00	7.00	20.00	7.00	1.00	3.00	3.00	0.20	20.00	3	20.00	0.00	0.0009	0	4.2	1051
1470	267.15	0.5	10.00	0.10	15.00	20.00	15.00	0.50	5.00	1.00	2.00	7.00	1.00	7.00	20.00	7.00	1.00	3.00	3.00	0.20	20.00	3	53.47	0.99	0.0009	0	2.5	1392
1370	267.15	0.5	10.00	0.10	15.00	20.00	15.00	0.50	5.00	1.00	2.00	7.00	1.00	7.00	20.00	7.00	1.00	3.00	3.00	0.20	20.00	3	20.34	0.00	0.0004	1	2.2	1120
595	266.65	0.1	10.00	0.50	3.00	15.00	15.00	0.50	3.00	2.00	1.00	5.00	0.50	5.00	30.00	2.00	2.00	5.00	10.00	0.20	30.00	3	4.94	1.04	0.0008	1	2.5	1326
1	270.15	0.5	5.00	0.10	5.00	10.00	10.00	0.50	3.00	2.00	1.00	5.00	0.50	2.00	40.00	2.00	2.00	10.00	20.00	0.20	40.00	4	0.38	25.65	0.0001	1	7.0	288

Table 5

Results of Principal Components Analysis (PCA) for skulls and mandibles of Bechstein's bat.

Skulls N=190			Mandibles N=212		
PC	Eigenvalue	% variance	PC	Eigenvalue	% variance
1	0.500675	49.384	1	0.00114	39.061
2	0.160075	15.789	2	0.000977	33.503
3	0.074495	7.3477	3	0.000314	10.756
4	0.048561	4.7897	4	0.000297	10.183
5	0.039849	3.9305	5	0.000137	4.7084
6	0.029704	2.9298	6	5.22E-05	1.7883
7	0.029098	2.87			
8	0.024197	2.3866			
9	0.023374	2.3054			
10	0.021653	2.1357			
11	0.016346	1.6123			
12	0.015628	1.5415			
13	0.012366	1.2197			
14	0.010117	0.99784			
15	0.007712	0.76068			

Table 6

Results of Discriminant Analysis (DA) for skulls and mandibles of Bechstein's bat.

Skulls N=179			Mandibles N=198		
Parameter	F	p	Parameter	F	p
GLS	6.2874	0.0000	MDL	5.45687	0.00000
CLS	4.6849	0.0000	MBTR	2.88447	0.00229
PM ₁	1.4129	0.1793	LPA	5.67441	0.00000
MSW	3.4676	0.0004	HCP	8.72381	0.00000
MZB	7.9880	0.0000	HP ₄	6.47495	0.00000
PSW	6.9799	0.0000	HM ₃	6.84590	0.00000
COW	7.2200	0.0000			
TPL	7.8801	0.0000			
L(C-P ₃)	5.0741	0.0000			
LTR	6.1599	0.0000			
L(P ₄ -M ₃)	2.3565	0.0128			
L(M ₁ -M ₃)	9.6325	0.0000			
PC	5.2394	0.0000			
FCW	2.3864	0.0117			
L(P ₁ -P ₃)	13.6642	0.0000			

Table 7

Environmental factors correlated with Bechstein's bat morphology.

Nr.	Parameter
1	Age of sample (^{14}C bp)
2	Climate
3	Mean temperature of January (T_j)
4	Mean annual temperature (T_y)
5	High above sea level (H a.s.l.)
6	Floods
7	Frequency of floods (Fr floods)
8	Frequency of the species
9	Fir <i>Abies alba</i>
10	Maple <i>Acer</i>
11	Alder <i>Alnus</i>
12	Birch <i>Betula</i>
13	Hornbeam <i>Carpinus betulus</i>
14	Hazel <i>Corylus avellana</i>
15	Beech <i>Fagus silvatica</i>
16	Ash <i>Fraxinus excelsior</i>
17	Spruce <i>Picea abies</i>
18	Pine <i>Pinus</i>
19	Oak <i>Quercus</i>
20	Willow <i>Salix</i>
21	Lime <i>Tilia</i>
22	Elm <i>Ulmus</i>
23	Poplar and aspen <i>Populus</i>
24	<i>Artemisia</i>
25	Sedge family Cyperaceae
26	Grass family Poaceae (Gramineae)
27	Bulrush (cat-tail) <i>Typha latifolia</i>
28	Herbs

Figures 3-12 presents microevolution trends of cranial dimensions, with the strongest discrimination to the groups. Despite the fact that differences between groups are mostly not statistically significant, microevolutionary trends in morphology are visible. Changes of each parameter has individual course, but trends are mostly similar. GLS (Fig. 3), COW (Fig. 6), LTR (Fig. 8), and HCP (Fig. 10) increase espacially during Subatlantic period (from 2800 ^{14}C BP till recent time). At the same time MZB (Fig. 4), PSW (Fig. 5), and HM_3 (Fig. 12) decrease. Some of cranial parameters: TPL, $\text{L}(\text{M}_1\text{-M}_3)$, and HP_4 seem to be rather stable (Figs 7, 9, 11).

During the Subboreal period (5115-2800 ^{14}C BP) four environmental variables have the strongest influence on skull morphology of investigated species. Those are: age of sample, mean temperature of January, and percentage of *Populus* and *Fagus silvatica* in vegetation (Fig. 13, tab. 8). In the same time range another four variables correlates significantly with mandible morphology: presence of floods, percentage of *Tilia* in vegetation, and frequency of *M. bechsteinii* and ecologically close species – *M. nattereri* (Fig. 15, tab. 9).

Fig. 1 - Principal Components Analysis (PCA) for *Myotis bechsteinii* skull dimensions. N=190 with diagram of % variance values for 1st, 2nd and 3rd canonical axis. Symbols: + specimens from Kraków-Częstochowa Upland thanatocoenoses, □ specimens from Świętokrzyskie Mts.: thanatocoenoses Zbójcka w Łagowie, ● specimens from Tatra Mts.

Fig. 2 - Principal Components Analysis (PCA) for *Myotis bechsteinii* mandible dimensions. N=212 with diagram of % variance values for 1st, 2nd, 3rd, 4th, 5th and 6th canonical axis. Symbols: + specimens from Kraków-Częstochowa Upland thanatocoenoses, ▲ specimens from Świętokrzyskie Mts.: thanatocoenoses Zbojcka w Łagowie, ○ specimens from Sudety Mts.: thanatocoenoses Niedzwiedzia w Kletnie, ● specimens from Tatra Mts.

Table 8

Results of gradient selection in Redundancy Analysis (RDA) for cranial skeleton of Bechstein's bat.

		Factor	Lambda	r	p	F	Nr of permutations
Skulls	Subboreal	Age of sample	0.03	-0.7536	0.004	3.88	499
		T_january	0.03	0.7175	0.004	3.88	499
		<i>Populus</i>	0.03	0.1735	0.004	3.88	499
		<i>Fagus silvatica</i>	0.03	0.6147	0.004	3.88	499
	Subatlantic	Age of sample	0.01	-0.3976	0.002	2.29	499
		T_january	0.01	0.8194	0.002	2.29	499
		<i>Populus</i>	0.01	-0.0532	0.002	2.29	499
		<i>Fagus silvatica</i>	0.01	-0.2918	0.002	2.29	499
		Frequency_MBE	0.01	-0.4454	0.002	2.29	499
Mandibles	Subboreal	Floods	0.12	0.5296	0.002	14.4	499
		Frequency_MBE	0.1	-0.3459	0.002	13.1	499
		<i>Tilia</i>	0.08	0.2142	0.002	11.3	499
		Frequency_MYN	0.02	0.2700	0.002	3.72	499
	Subatlantic	<i>Fraxinus excelsior</i>	0.62	0.9443	0.002	84.91	499
		H_a.s.l.	0.03	0.1872	0.004	4.13	499

In Subatlantic period (2800 ¹⁴C BP till now) five factors influence on skull morphology: age of sample, mean temperature of January, percentage of *Populus* and *Fagus silvatica* in vegetation, and frequency of *M. bechsteinii* (Fig. 14, tab. 8). The same time range characterizes correlation of high a.s.l. and percentage of *Fraxinus excelsior* in vegetation with mandible morphology of Bechstein's bat (Fig. 16, tab. 8).

Mean temperature of January, percentage of *F. excelsior*, frequency of Bechstein's bat and occurrence of floods determine morphology changes the most (Figs 13-16).

Fig. 3 - Changes in greatest length of skull (GLS) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 4 - Changes in maximum zygomatic breadth (MZB) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 5 - Changes in posterior skull width (PSW) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 6 - Changes in condylus occipitalis width (COW) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 7 - Changes in total palate length (TPL) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 8 - Changes in tooththrow length (LTR) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 9 - Changes in M_1 to M_3 length ($L(M_1-M_3)$) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 10 - Changes in height of coronoid process (HCP) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 11 - Changes in height of mandible at P_4 (HP_4) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 12 - Changes in height of mandible at M_3 (HM_3) (in mm) of *Myotis bechsteinii* in the Middle and Late Holocene. (□ - Mean; □ - Mean ± Standard error; | - Mean ± Standard deviation)

Fig. 13 - Diagram of Bechstein's bat skull dimensions in gradient of environmental factors having significant influence into morphology during the Subboreal period (5115-2800 ^{14}C BP) based on gradient selection redundancy analysis (RDA).

Fig. 14 - Diagram of Bechstein's bat skull dimensions in gradient of environmental factors having significant influence into morphology during the Subatlantic period (2800 ^{14}C BP till now) based on gradient selection redundancy analysis (RDA).

DISCUSSIONS

Bats are the only mammals able to active flight (Sachanowicz & Ciechanowski, 2005). This ability determining cranial morphology of bats as well as changes in climate, vegetation feedback and all modifications in ecological niche of the species (Horáček, 1976; Kordos, 1982; Obuch, 1995; Zahn, 1999).

During the Middle and Late Holocene cranial morphology of Bechstein's bat shows the following trends: greatest length of skull, condylus occipitalis width, tooth row length, and height of coronoid process increase. At the same time maximum

Fig. 15 - Diagram of Bechstein's bat mandible dimensions in gradient of environmental factors having significant influence into morphology during the Subboreal period (5115-2800 ^{14}C BP) based on gradient selection redundancy analysis (RDA).

Fig. 16 - Diagram of Bechstein's bat mandible dimensions in gradient of environmental factors having significant influence into morphology during the Subatlantic period (2800 ^{14}C BP till now) based on gradient selection redundancy analysis (RDA).

zygomatic breadth, posterior skull width and height of mandible ramus under third molar decrease, while total palate length, length from the first to the third molar, and height of mandible ramus under fourth premolar seem to be rather stable.

Those are trends in making cranial skeleton more slender, skull seem to become narrower and longer. Place of muscle attachment seem to become wider. Molar row length rather does not change, but skull and mandible became longer, being possible the effect of extending premolar row length. Surely, all these trends are the effect of optimizing the skeleton proportions to the muscle mass, which are saved, when there is assured high effectiveness of flight and biting of food, and low body mass at the same time (Czarnecki & Kallen, 1980; Smith & Savage, 1956). Presented microevolutionary trends in cranial skeleton of this species can possibly be part of long-term modifications, or reversible changes as morphological answer to the climate and ecological niche fluctuations (Futuyma, 2008).

Influence of sexual dimorphism to differences between populations of *M. bechsteinii* from radiocarbon dated thanatocoenoses are excluded by researching

recent population of the species. Differences between them can be rather a result coming from varied geographical regions (mountains, or uplands of southern Poland), where climatic changes and events have individual course.

Ten of 28 investigated environmental factors have significant influence on cranial morphology of Bechstein's bat. Influence of the age of sample on skull parameters can mean, that morphological changes are part of long-term directioned modifications (Smith & Savage, 1956).

Temperature of January is strongly correlated with mean temperature of the year and it's obvious factor, determining presence of the species in region (Krebs, 2001). For bats, which are warm-likely animals, living in colder region can mean worse condition of population. Individuals can be weaker than those from warmer regions (Wimsatt, 1970).

Frequency of investigated bat species, as well as frequency of Natterer's bat, can also be information about condition of population. Probably the higher frequency of Bechstein's bat, the better condition of population. Opposite direction can be with higher frequency of *M. nattereri*, as possible competitor for the same niche.

Percentage of pollen of beech, lime, ash, poplar and aspen gives information about participation of these species in forests. They correlates with morphology of *M. bechsteinii* possibly as good habitat. Especially beech is known as species important for Bechstein's bat. Old, hollowed trees are inhabited by this species very often during the summer (Sachanowicz & Ciechanowski, 2005).

Hight above sea level says a lot about differences between populations from uplands and mountains. It has to be factor determining not only frequency, but also morphology of bats. During the Atlantic and Subboreal period frequency of Bechstein's bat varied from 2-65% and was higher on uplands. Nowadays this species is almost completely eliminated from Polish mountain fauna (Postawa, 2004; Piksa & Wołoszyn, 2001).

Occurrence of floods is connected with cooler climate of Subboreal period (Starkel, 1999). It is also a resistant factor to the occurrence and morphology of *M. bechsteinii*. Neighbourhood of water reservoirs is an ecosystem typical for other bat species (for example Daubenton's bat *Myotis daubentonii*), not Bechstein's bat (Sachanowicz & Ciechanowski, 2005). It must be the reason why floods are correlating with morphology of *M. bechsteinii*.

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MICROEVOLUȚIA LILIAULUI LUI BECHSTEIN *MYOTIS BECHSTEINII* (KUHL, 1817) (MAMMALIA: CHIROPTERA), ÎN HOLOCENUL POLONIEI DE SUD

REZUMAT

S-au studiat tendințele microevoluționare ale craniului liliacului lui Bechstein. În ciuda faptului că diferențele dintre grupuri nu sunt deosebite din punct de vedere statistic, tendințele microevoluționare morfologice sunt vizibile. Schimbările fiecărui parametru au un curs individual, dar tendințele sunt aproape similare.

Analiza statistică a facut posibil răspunsul la întrebarea care din factorii de nișe au o influență importantă la morfologia craniului și care este direcția acestei influențe. Temperatura medie a lunii ianuarie, procentul lui *Fraxinus excelsior*, frecvența liliacului lui Bechstein și frecvența inundațiilor determină cel mai mult schimbările morfologice.

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