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Pliocene bats of the genus *Myotis* (*Mammalia*: *Chiroptera*) from Podlesice (Poland) and Osztramos 9 and 13 (Hungary)

Joanna GODAWA

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Abstract: Twelve Pliocene species from Podlesice (Poland) and Osztramos 9 and 13 (Hungary) were examined by stepwise discriminant analysis and cluster analysis. Three fossil species, previously not recorded from Poland were found in Podlesice. The use of stepwise discriminant analysis for distinguishing species within groups of fossil and recent bats is discussed. Status of all fossil species has been maintained till now because of lack the data from Gundersheim collection.

Key words: Chiroptera, *Myotis*, discriminant analysis, Pliocene, Poland, Hungary.

Joanna GODAWA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland.

I. INTRODUCTION

Remains of bats of the genus *Myotis* KAUP, 1829, are relatively abundant in fossil faunas. Up to now the following seven Pliocene species of this genus have been described from Poland: (1) *Myotis danutae* KOWALSKI, 1956 originally described from Podlesice (KOWALSKI 1956, 1959, 1990: WOŁOSZYN 1988, 1989) was also found in Węże 1 (KOWALSKI 1962, 1964, 1990), Mała Cave (SULIMSKI et al. 1979) and Przymiłowice 3 (NADACHOWSKI et al. 1991), (2) *Myotis dasycneme subtilis* KOWALSKI, 1956 was recorded exclusively from Podlesice (KOWALSKI 1956, 1959, 1990; WOŁOSZYN 1988, 1989), (3) *Myotis exilis* HELLER, 1936 was collected from three localities: Podlesice (KOWALSKI 1956, 1959, 1964, 1990; RABEDER 1972; TOPÁL 1985; WOŁOSZYN 1988, 1989, Węże 1 (KOWALSKI 1962, 1964, 1990; WOŁOSZYN 1988, 1989), Kadzielnia 1 (KOWALSKI 1958, 1959) and Mokra 1 (WOŁOSZYN 1988, 1989), (4) *Myotis cf. aemulus* HELLER, 1936 was found in Podlesice (KOWALSKI 1956, 1959, 1962, 1964) and Węże 1 (KOWALSKI 1962), (5) *Myotis helleri* KOWALSKI, 1962 was noted in Węże 1 (KOWALSKI 1962, 1964, 1990; WOŁOSZYN 1988, 1989) and Przymiłowice 1, 3 (NADACHOWSKI et al. 1991), (6) *Myotis podlesicensis* KOWALSKI, 1956 was described from Podlesice (KOWALSKI 1956, 1959, 1990; WOŁOSZYN 1988,1989 and later was recorded from Mała Cave

(SULIMSKI et al. 1979, WOŁOSZYN 1988, 1989), Wężе 1 (KOWALSKI 1962, 1990; WOŁOSZYN 1988, 1989), Zamkowa Dolna Cave (WOŁOSZYN 1989) and Przymiłowice 1 (NADACHOWSKI et al. 1991), (7) *Myotis gundersheimensis* HELLER, 1936 was found in Podlesice (KOWALSKI 1990; WOŁOSZYN 1988, 1989) and Wężе 1 (KOWALSKI 1990; WOŁOSZYN 1988, 1989).

The fossil remains of bats described in this paper come from Podlesice near Kroczyce, Poland, the reference locality of MN (mammalian zone) 14 (DE BRUIJN et al. 1992). The fauna is of lower- Ruscinian age, lower Pliocene (NADACHOWSKI et al. 1989). Materials of similar age from Osztramos 9 and 13 (Hungary) were examined for comparison and they comprised eleven species (Table I). JÁNOSSY (1973, 1974) placed the fauna of Osztramos between the typical Upper and Lower Pliocene faunas of Europe. *Myotis paradaubentoni* TOPÁL, 1983, *Myotis janossyi* TOPÁL, 1983, and *Myotis estramosensis* TOPÁL, 1983 were represented by type populations.

The objective of this paper was to study the fossil material representing the genus *Myotis* from Podlesice. The status of some species from this locality is not clear and many of the previous determinations require revision. The author studied phenetic relationships among fossil species using biometrics methods.

The stepwise discriminant analysis was also used to study recent European species of the genus *Myotis* was to find if the number of characters used for fossil species is sufficient for taxa discrimination.

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II. MATERIAL AND METHODS

More than three hundred mandibles from Podlesice and Osztramos 9 and 13 were examined and 280 were selected for father biometric studies (Table I). Following holo-

Table I

Numbers of egzamined fossil specimens from Osztramos and Podlesice.

Species egzamined	Number of specimens from Osztramos 9 and 13	Number of specimens from Podlesice
Myotis aemulus HELLER	15	20
Myotis danutae KOWALSKI	3	10
Myotis delicatus HELLER	5	9
Myotis estramosensis TOPÁL	9	–
Myotis exilis HELLER	17	27
Myotis gundersheimensis HELLER	20	38
Myotis helleri KOWALSKI	15	11
Myotis janossyi TOPÁL	20	12
Myotis kormosi HELLER	12	–
Myotis paradaubentoni TOPÁL	10	4
Myotis podlesicensis KOWALSKI	–	15
Myotis praevius HELLER	4	4

types were included: *Myotis podlesicensis* (no. MF/14/60), *Myotis danutae* (no. MF/17/60) from the Institute of Systematics and Evolution of Animals and *Myotis estramosensis* (no. V.82.173) from Osztramos 9 stored in the Hungarian Natural History Museum, Paleontological Dept. Because seven species of bats were originally described by HELLER (1936) on the basis of the morphology and dimensions of mandibles, the following measurements were used in the analyses: lengths of M_1, M_2, M_3, P_4, C-P_4, P_4-M_3, M_1-M_3, C-M_3, and mandible (LM) and the height of coronoid process (HP). All dimensions were taken with an eyepiece micrometer with an accuracy of 0.01 mm. Descriptive statistics are given in Table III. The same measurements were taken for recent species of the genus *Myotis* from Europe. All values were transformed to their natural logarithms. Biological size relationships are typically allometric and the log transformation results in a higher degree of linearity of the size component of the data (OWEN 1988). Twelve fossil species and ten recent ones were analyzed by stepwise discriminant analysis. Discriminant analysis was used to found distances between fossil species. The unweighted pair-group method using arithmetic centroids (SNEATH, SOKAL 1973) was performed on the matrix of Mahalanobis distances between taxa. It is not often to use the Mahalanobis distance as the basis for a cluster analysis of populations, however, there is no reason not to use it. The Mahalanobis distance is similar to the standard Euclidean distance measure, except that it takes into account the correlation between variables (THORPE 1976). Stepwise discriminant analysis and cluster analysis were computed using package CSS:STATISTICA (StatSoft, Inc. 1991).

III. RESULTS

The Mahalanobis distances between the taxa are given in Table II. Two first components were represented by a plot of component scores. The results show that the measurements used in discriminant analysis are good discriminators for both recent and fossil taxa (Fig 1a, b). The 90 % of the recent and and 81 % of the fossil species were classified correctly. The phenogram from the Mahalanobis distance matrix (Fig. 2) indicates two basic phenetic groups among the fossil species. The smaller Mahalanobis distance in the group of small species is between *Myotis exilis* and *Myotis janossyi* (4.62). *Myotis estramosensis* is different from all other species and separated from them by great distances. Bigger species like *Myotis kormosi*, *Myotis aemulus* and *Myotis podlesicensis* belong to the second group. Among them the smaller Mahalanobis distance is between *Myotis aemulus* and *Myotis podlesicensis* (7.17). These species overlap each other and their measurements are very similar (Fig. 1b). *Myotis gundersheimensis*, *Myotis delicatus* (HELLER, 1936) and *Myotis praevius* distinctly differ from the second group by their smaller measurements. The Mahalanobis distance between the last two species is 9.03. These species are easily distinguishable in the plot (Fig. 1b). The situation is different with the first group because *Myotis exilis*, *Myotis janossyi* and *Myotis paradaubentoni* overlap each other. In the phenogram only the first taxa have a small Mahalanobis distance.

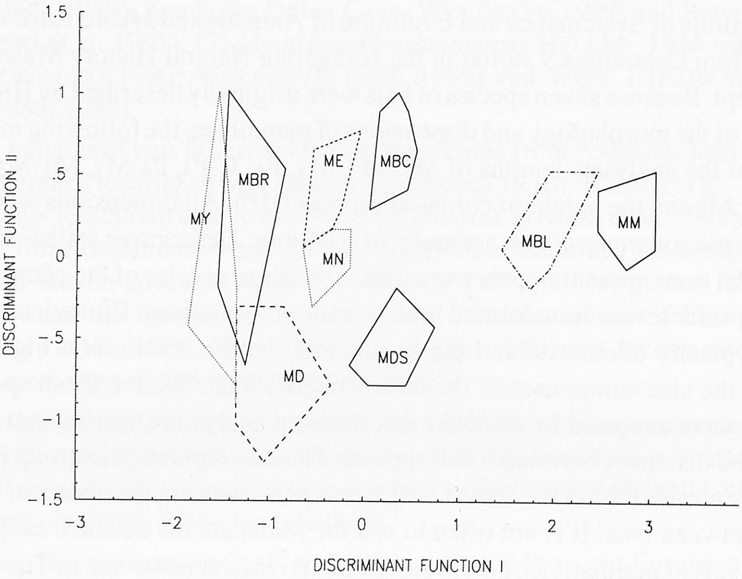

Fig. 1a. Plot of the first two discriminant functions of stepwise discriminant analysis. Components account for 42.73 % and 1.76 % of total variance. The first canonical component is highly correlated with P_4-M_3 (0.86), M_1-M_3 (0.78) and C-M_3 (0.70). Species are: MD – *M. daubentoni*, MC – *M. capaccini*, MBR – *M. brandti*, MY – *M. mystacinus*, MN – *M. nattereri*, ME – *M. emarginatus*, MDS – *M. dasycneme*, MBC – *M. bechsteini*, MBL – *M. blythi* and MM – *M. myotis*.

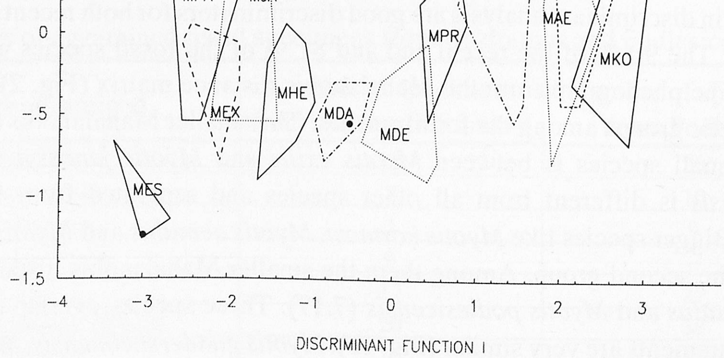

Fig. 1b. Plot of the first two discriminant functions of stepwise discriminant analysis. Components account for 54.18 % and 1.08 % of total variance. The first canonical component is highly correlated with C-M_3 (0.73), and LM (0.62). Species are: MES – *M. estramosensis*, MPA – *M. paradaubentoni*, MEX – *M. exilis*, MJA – *M. janossyi*, MHE – *M. helleri*, MDA – *M. danutae*, MDE – *M. delicatus*, MPR – *M. praevius*, MGU – *M. gundersheimensis*, MKO – *M. kormosi*, MPO – *M. podlesicensis* and MAE – *M. aemulus*. Dots indicate holotypes.

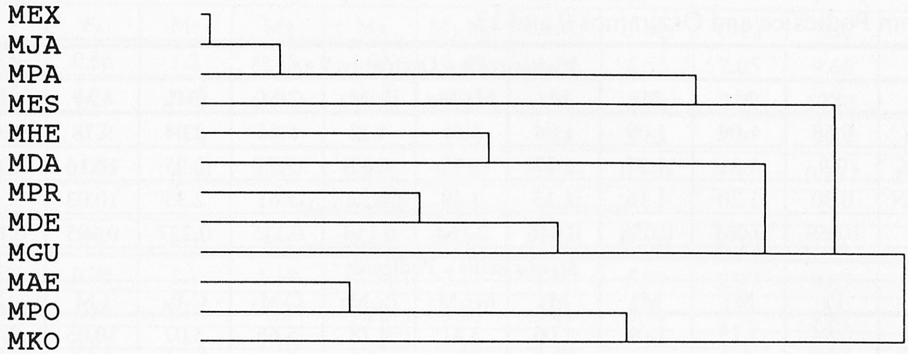

Fig. 2. The phenogram based on matrix of Mahalanobis distance.

IV. DISCUSSION

The characters used in discriminant analysis are good discriminators for recent and fossil bats. Recent species are relatively easily distinguishable on the basis of tooth and mandibular measurements. That is not the case as regards the fossil species and this is probably connected with the different concept of species assumed for the fossil taxa (chronospecies). Chronospecies may or may not have a direct relationship with biological

Table II

Squared Mahalanobis distances between fossil taxa. Species as in Fig. 1b

	MEX	MHE	MJA	MES	MPA	MDA	MPR	MDE	MGU	MAE	MKO
MEX	31.42										
MJA	4.62	24.26									
MES	32.38	66.93	43.34								
MPA	6.24	37.72	5.83	31.32							
MDA	87.37	18.72	72.55	150.98	98.35						
MPR	193.62	82.70	171.91	291.79	212.38	32.57					
MDE	163.54	55.01	141.60	232.76	175.88	17.17	9.03				
MGU	285.50	143.18	250.05	393.92	300.40	74.79	16.14	29.77			
MAE	435.76	253.76	399.66	567.97	458.26	150.36	49.21	78.64	23.90		
MKO	642.68	411.55	590.18	791.81	666.36	270.23	138.89	171.00	87.35	32.16	
MPO	571.78	363.98	527.51	730.51	599.82	235.12	104.75	144.89	58.28	7.17	27.36

Table III

Descriptive statistics for the measurements of the mandibles of Pliocene species from Podlesice and Osztramos 9 and 13

	Myotis exilis – Osztramos 9 and 13									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.68	1.09	1.09	1.04	3.31	4.12	5.45	2.04	9.78	3.06
MAX	0.9	1.31	1.27	1.22	3.95	4.67	5.78	2.95	10.16	3.59
MEAN	0.80	1.20	1.16	1.13	3.49	4.22	5.61	2.35	10.03	3.19
S.D.	0.059	0.061	0.058	0.046	0.164	0.159	0.115	0.277	0.105	0.139
	Myotis exilis – Podlesice									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.84	1.13	1.09	1.06	3.41	4.18	5.66	3.07	10.05	3.19
MAX	0.90	1.25	1.22	1.09	3.46	4.77	5.74	3.12	10.07	3.2
MEAN	0.87	1.19	1.16	1.08	3.44	4.48	5.7	3.1	10.06	3.2
S.D.	0.042	0.085	0.092	0.021	0.035	0.417	0.057	0.035	0.014	0.007
	Myotis helleri – Osztramos 13									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.7	1.15	1.1	1.1	3.6	4.2	5.85	2.25	10.59	3.13
MAX	0.89	1.3	1.36	1.3	3.9	4.8	6.2	2.8	11.12	3.68
MEAN	0.81	1.21	1.21	1.19	3.7	4.44	6.07	2.52	10.82	3.28
S.D.	0.055	0.044	0.075	0.053	0.114	0.165	0.121	0.164	0.199	0.172
	Myotis helleri – Podlesice									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.72	1.18	1.16	1.15	3.43	4.2	5.73	2.02	10.7	2.76
MAX	1.12	1.36	1.34	1.34	3.76	4.77	6.21	3.1	10.88	3.4
MEAN	0.84	1.26	1.25	1.21	3.65	4.4	6.04	2.74	10.8	3.09
S.D.	0.135	0.054	0.048	0.054	0.080	0.153	0.122	0.277	0.047	0.188
	Myotis janossyi Osztramos 9 and 13									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.65	1.1	1.05	1.05	3.45	4.15	5.58	2.0	9.7	2.7
MAX	0.9	1.85	1.7	1.4	3.85	4.5	6.2	3.03	10.95	3.7
MEAN	0.78	1.26	1.2	1.17	3.58	4.33	5.96	2.78	9.99	3.16
S.D.	0.075	0.197	0.167	0.103	0.112	0.122	0.235	0.386	0.325	0.224
	Myotis janossyi – Podlesice									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.7	1.11	1.18	1.07	3.43	4.1	5.47	2.23	9.85	2.9
MAX	0.94	1.37	1.36	1.31	3.7	4.77	6.12	3.07	10.06	3.2
MEAN	0.82	1.21	1.25	1.17	3.53	4.37	5.78	2.8	9.97	3.13
S.D.	0.087	0.066	0.054	0.068	0.076	0.279	0.189	0.311	0.076	0.084
	Myotis estramosensis – Osztramos 9									
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.63	1.11	1.09	0.95	3.12	3.7	5.3	2.28	9.91	2.41
MAX	0.92	1.2	1.1	1.2	3.5	4.83	5.4	3.23	9.95	2.8
MEAN	0.82	1.17	1.1	1.08	3.31	4.09	5.37	2.85	9.93	2.61
S.D.	0.165	0.052	0.006	0.126	0.190	0.638	0.058	0.501	0.020	0.195

Table III ctc.

Myotis paradaubentoni – Osztramos 13										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.68	1.2	1.18	1.03	3.43	4.14	5.52	2.05	9.66	2.9
MAX	0.74	1.36	1.31	1.18	3.73	4.45	5.78	2.09	10.05	3.32
MEAN	0.7	1.28	1.24	1.1	3.56	4.25	5.63	2.07	9.87	3.04
S.D.	0.035	0.080	0.067	0.075	0.154	0.176	0.133	0.021	0.197	0.242
Myotis paradaubentoni – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.78	1.1	1.18	1.2	3.41	4.77	5.59	2.97	9.87	2.9
MAX	0.9	1.14	1.2	1.22	3.56	5.01	5.74	3.12	9.87	2.96
MEAN	0.84	1.12	1.19	1.21	3.49	4.89	5.67	3.05	9.87	2.93
S.D.	0.085	0.028	0.014	0.014	0.106	0.170	0.106	0.106	0.000	0.042
Myotis danutae – Osztramos 9 and 13										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.7	1.22	1.2	1.18	3.73	4.54	6.2	2.3	11.4	3.46
MAX	0.99	1.27	1.31	1.4	3.9	4.73	6.55	2.66	11.5	3.49
MEAN	0.85	1.25	1.24	1.31	3.83	4.62	6.33	2.49	11.44	3.47
S.D.	0.145	0.025	0.059	0.117	0.091	0.097	0.194	0.180	0.051	0.017
Myotis danutae – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.7	1.17	1.15	1.25	3.7	4.45	6.47	2.65	11.28	3.42
MAX	0.87	1.33	1.3	1.33	3.88	4.77	6.57	2.83	11.52	3.46
MEAN	0.78	1.26	1.25	1.29	3.79	4.62	6.50	2.75	11.41	3.45
S.D.	0.075	0.072	0.069	0.039	0.074	0.141	0.046	0.075	0.103	0.020
Myotis praevius – Osztramos 9										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	1.04	1.31	1.27	1.22	3.96	4.92	6.53	2.53	12.12	3.94
MAX	1.04	1.36	1.49	1.31	4.0	5.0	6.75	2.57	12.3	3.95
MEAN	1.04	1.34	1.38	1.27	3.98	4.96	6.64	2.55	12.21	3.95
S.D.	0.000	0.035	0.156	0.064	0.028	0.057	0.156	0.028	0.127	0.007
Myotis praevius – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.85	1.37	1.31	1.2	4.0	4.77	6.65	2.33	11.92	3.83
MAX	1.05	1.54	1.51	1.56	4.2	5.17	6.85	2.53	12.32	3.96
MEAN	0.97	1.46	1.42	1.33	4.12	4.89	6.77	2.41	12.11	3.89
S.D.	0.068	0.058	0.057	0.101	0.078	0.168	0.060	0.078	0.175	0.040
Myotis delicatus – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.81	1.23	1.26	1.17	3.67	4.51	6.53	2.55	11.68	3.47
MAX	0.98	1.43	1.47	1.36	4.1	4.97	6.94	2.86	12.78	3.55
MEAN	0.91	1.33	1.35	1.27	3.85	4.75	6.7	2.77	11.98	3.51
S.D.	0.061	0.069	0.068	0.069	0.146	0.180	0.133	0.109	0.364	0.026

Table III ctc.

Myotis delicatus – Osztramos 9										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.96	1.27	1.36	1.36	4.18	5.04	6.78	2.86	11.86	3.5
MAX	1.0	1.49	1.5	1.49	4.22	5.18	6.8	3.46	11.94	3.54
MEAN	0.98	1.38	1.43	1.43	4.2	5.11	6.79	3.16	11.9	3.52
S.D.	0.028	0.156	0.099	0.092	0.028	0.099	0.014	0.424	0.057	0.028
Myotis gundersheimensis – Osztramos 9										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	1.0	1.27	1.36	1.27	4.18	5.18	7.22	2.04	11.81	3.74
MAX	1.13	1.5	1.5	1.49	4.49	5.49	7.72	3.45	12.68	4.11
MEAN	1.08	1.43	1.42	1.35	4.28	5.29	7.52	2.85	12.28	3.85
S.D.	0.052	0.088	0.063	0.081	0.098	0.099	0.162	0.562	0.282	0.128
Myotis gundersheimensis – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.9	1.37	1.38	1.2	4.06	4.77	6.88	2.08	12.14	3.32
MAX	1.16	1.6	1.62	1.5	4.45	5.46	7.86	3.29	12.43	3.98
MEAN	1.01	1.5	1.49	1.4	4.32	4.88	7.34	2.25	12.25	3.77
S.D.	0.076	0.054	0.053	0.063	0.082	0.238	0.258	0.226	0.073	0.104
Myotis aemulus – Osztramos 9										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.9	1.5	1.45	1.36	4.49	4.67	7.0	1.90	13.18	4.25
MAX	1.22	1.63	1.63	1.59	4.68	5.72	7.68	3.49	13.74	4.67
MEAN	1.11	1.58	1.55	1.46	4.58	5.41	7.35	2.31	13.41	4.33
S.D.	0.111	0.046	0.058	0.076	0.075	0.431	0.235	0.601	0.213	0.146
Myotis aemulus – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.9	1.37	1.44	1.35	4.28	4.77	7.35	2.01	12.24	3.62
MAX	1.07	1.53	1.57	1.5	4.56	5.55	7.98	3.07	13.31	4.25
MEAN	1.01	1.47	1.51	1.43	4.47	5.27	7.6	2.33	13.05	4.12
S.D.	0.080	0.075	0.051	0.055	0.109	0.313	0.232	0.459	0.455	0.282
Myotis kormosi – Osztramos 9 and 13										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	1.0	1.5	1.54	1.49	4.59	5.63	7.78	2.85	13.4	4.12
MAX	1.22	1.68	1.72	1.77	5.09	6.13	8.48	3.69	14.4	4.9
MEAN	1.12	1.61	1.59	1.61	4.77	5.83	8.14	3.41	13.87	4.43
S.D.	0.071	0.058	0.061	0.082	0.183	0.185	0.238	0.248	0.373	0.266
Myotis podlesicensis – Podlesice										
	P_4	M_1	M_2	M_3	M_1-M_3	P_4-M_3	C-M_3	C-P_4	LM	HP
MIN	0.94	1.37	1.53	1.31	4.31	4.77	7.77	1.75	12.85	4.37
MAX	1.2	1.75	1.7	1.7	4.78	5.87	8.3	2.55	14.05	4.8
MEAN	1.05	1.52	1.6	1.49	4.53	5.07	8.03	2.06	13.67	4.54
S.D.	0.058	0.137	0.060	0.104	0.142	0.411	0.157	0.226	0.359	0.128

species. The main matter is to find a correlation between the fossil taxa and the recent, real species (NADACHOWSKI 1993).

The majority of fossil bats were described from Gundersheim on the basis of mandibular characters. The age of locality is Late Ruscinian (MN 15B) (KOENIGSWALD, TOBIEN 1990). HELLER (1936) described eight new fossil species of the genus *Myotis* from Gundersheim. Six of them were also found in Poland. *Myotis dasycneme subtilis* found in Podlesice is in TOPÁL's (1985) opinion a younger synonym of *Myotis delicatus* HELLER, 1936. There are slight differences between premolars but it may be connected with intraspecific variability. *Myotis podlesicensis* is known only from Podlesice. This taxon is very similar to *Myotis aemulus* and there are no differences between their lower teeth. *Myotis aemulus* has its coronoid process lower. These two species overlap each other in Fig. 1b. Their Mahalanobis distance is small, but their status should be maintained until the material from Gundersheim has been studied. *Myotis gundersheimensis* is very abundant in Podlesice but was not recognized by KOWALSKI, 1956 apparently because of the misleading measurements given by HELLER (1936).

Among the fossil materials from Podlesice three species new to Poland were found. They are *Myotis paradaubentoni* TOPÁL, 1983, *Myotis janossyi* TOPÁL, 1983 and *Myotis cf. praevius* HELLER, 1936. These species are similar to the populations from Osztramos 9 and 13. *Myotis estramosensis* TOPÁL, 1983 is absent from Podlesice and it has been found only in Osztramos 9 and 13.

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