

# A CRANIOMETRIC COMPARISON OF HOLOCENE POPULATIONS OF *MYOTIS MYSTACINUS* (KUHL, 1817) AND *M. BRANDTII* (EVERSMANN, 1845) (CHIROPTERA, MAMMALIA)

by

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## ABSTRACT

This paper presents the results of an analysis of about four hundred skulls of *Myotis mystacinus* and *M. brandtii* of the Holocene age from the Záskočie Cave (Central Slovakia). A review of criteria for species determination is presented, including a new criterion concerning the morphology of P<sup>4</sup> roots, as well as the results of a statistical survey of skull dimensions and correlation and regression analyses. The author concludes that the above mentioned bats are not sibling species, but that they belong to different subgenera of the genus *Myotis*.

## INTRODUCTION

Until recently, the Brandt's Bat (*Myotis brandtii*) was considered to be just a subspecies of the Whiskered Bat (*M. mystacinus*). It was only in 1958 that Topál speculated, proceeding to the basis of a study of the morphology of the baculum (os penis) about the possibility that the two forms might constitute two separate species. A number of authors (cf. Baagøe, 1973) have dealt with this problem. After some initial doubts (cf. Hanák, 1965), the existence of two separate forms was confirmed (Hanák, 1970, 1971a; Vlček, 1970; Gauckler & Kraus, 1970). The sympatric occurrence of the species all the year round and the subsequently found morphological differences provided the final proof.

If the recognition of *Myotis brandtii* was "an unexpected result of detailed taxonomic research of a common species" (Hanák & Danko, 1975: 33), a minute taxonomic analysis of a large amount of material is necessary for final evaluation. However, most authors based their conclu-

sions on studies dealing with only a few dozen individuals at the most; only Baagøe (1973) and Ruprecht (1974) presented analyses of about one hundred individuals of both species.

During an investigation in the Liptov karst (Central Slovakia, Č.S.S.R.) I found 396 skulls of *Myotis mystacinus* and *M. brandtii*, i.e. material very suitable for taxonomic evaluation using statistical methods. The results of my work also provide a contribution towards a better understanding of the Central European Holocene bat fauna.

## MATERIAL AND METHODS

The Holocene material comes from Czechoslovakia's deepest cave, Záskočie. This cave is situated on a hillside of Mt. Krakova hola in the Lower Tatra Mts. (opening is at 1,332 m above sea level); the animal remains were collected from the surface of cave fills in 1973. Among 615 skulls of eight species which were collected there, *M. brandtii* (282 skulls, i.e. 45.8% + 107 mandibles) and *M. mystacinus* (114 skulls, i.e. 18.5% + 53 mandibles) were the two most frequently represented taxa. The facial parts of fragmental skulls (rostra) constituted about 25% of the sample, the remainder were relatively complete skulls. In the majority of cases, only the bullae ossae, incisors, canines and first two premolars were missing.

Skulls and mandibles were fixed in a gelatine solution and 23 dimensions were measured using calipers under a binocular microscope. The ac-

curacy of 0.05 mm was adequate for the degree of preservation of the material and also for the statistical validity of the sample sizes.

About nine thousand measurements were analyzed using an Odra 1204 computer. The arithmetic means (including their 95% confidence limits), range and standard deviations were calculated. Interspecific differences of the arithmetic means were examined by *F*- and Student's *t*-tests. To determine the correlation ratio of the skull dimensions, the correlation coefficient *r* was established (0 = linear independence, 0.10–0.39 = slight dependence, 0.40–0.69 = medium dependence,  $\geq 0.70$  = strong dependence); hundredfold of its square, the index of determination indicates the influence of the argument on the function in per cent. Conforming with Sigmund (1964b), the 95% confidence limits of the correlation coefficient were established. At the same time, the null hypothesis was tested, whether or not the correlation coefficients originate from random sampling. In order to determine the allometric ratios, linear regressions were calculated as well as the coefficients *a* and *b* of the regression lines and their 95% confidence limits. Carrying out the linearity regression test was considered as a precondition for all computations.

## RESULTS AND DISCUSSION

### Species determination

A reliable specific identification of the skulls was a first problem. This matter requires detailed analysis and evaluation of a large portion of the material. Because of this I will deal with species determination first.

### Dimensions. —

Formerly, only the skull dimensions were used as a criterion for the separation of the two forms, particularly using the condylobasal length: specimens with a condylobasal length over 13.4 mm had been considered as *brandtii* and under 13.3 mm as *mystacinus* (cf. Hanák, 1965). In later papers more critical values were presented, but some bats could not be determined in this manner (Baagøe, 1973; Ruprecht, 1974; etc.). In my opinion (cf. table I) condylobasal lengths ranging between 12.00–13.00 mm indicate *M. mystacinus*, and those from 13.30 to 14.40 mm *M. brandtii*; the intermediate zone (13.05–13.25 mm) includes about 5% of the total material. Slight overlap occurs also in the total length and width of the skull and in the infraorbital width (cf. Baagøe, 1973).

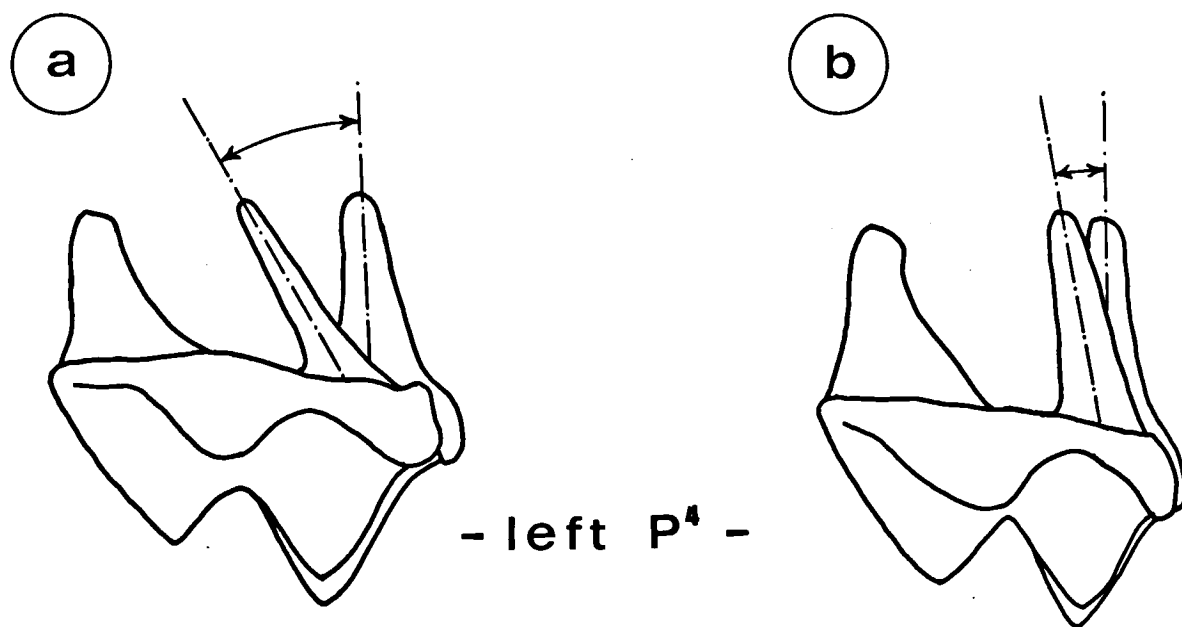


Fig. 1. The morphology of  $P^4$  roots as a criterion for species determination: (a) *Myotis mystacinus*; (b) *M. brandtii*.

### Morphology. —

Relatively slender skulls and evident bending of their frontal parts occur in both species. Skull shape helps identifying a major portion of the material: *M. mystacinus* has a large concavity of the frontal profile and its braincase is elongated (egg-shaped) from the dorsal view; the profile of the *M. brandtii* skull is rather flat and elongated, the braincase is shaped like a polygon inserted in a circle.

### Teeth. —

The standard criteria — i.e. the ratio of  $P_2$  and  $P_3$  sizes ( $P_3$  are rather lower than  $P_2$  in *M. mystacinus*, see Gauckler & Kraus, 1970; Hanák, 1970, 1971a), or their position (inward suppression of  $P_3$  in *M. mystacinus*) — are not suitable for fossil material with fragmental denture. Some authors (Stubbe & Chotolchu, 1968; Gauckler & Kraus, 1970; Baagøe, 1973) consider the occurrence of small protoconules on the frontal edge of upper molars to be characteristic of *M. brandtii*, others (e.g. Hanák, 1971a) deny the reliability of these criteria. These characters are not suitable for critical identification especially of fragmented fossil material. Also the secondary cone on the inner margin of  $P^4$  (according to some authors a reliable determining criterion; cf. Topál, 1963; Gauckler & Kraus, 1970; Hanák, 1970, 1971a) is relevant only to the determination of some *M. brandtii*; in some samples of the population it is inconspicuous while a portion of *M. mystacinus* has a relatively pronounced cone.

In the course of my research I have found a new criterion for species identification, viz. the morphology of  $P^4$  roots (see fig. 1). The usefulness of this feature is based on the fact, that the roots are protected from outside influences (cf. the abrasion of the teeth crowns). The last of the upper premolars has two roots lying on the bucal side and one on the lingual side. From the frontal (rostral) view, the first bucal root of *M. brandtii* appears only slightly thinner in comparison with the second one and is slightly bent to the lingual side (i.e. axes of both roots are nearly parallel). By contrast, the first root of  $P^4$  in *M. mystacinus* is noticeably thinner than the second one, and its axis is bent to the lingual side. The  $P^4$  of *M. mystacinus* can be extracted from the upper jaw much more easily than in *M. brandtii*.

One basic criterion in the genus *Myotis* is the occurrence of 38 teeth ( $\frac{2-1-3-3}{3-1-3-3}$ ). However, in the

material of *M. brandtii* two anomalies occur: oligodonty (absence of both  $P^2$ ) and polydonty (supernumerary C on both sides of the upper jaw). Oligodonty in female *M. mystacinus* was noted by Baagøe (1973).

### Skull dimensions

Skull dimensions of the collection from the Záskočie Cave are given in table I. The skull of *M. brandtii* appears to be generally larger, although some overlap occurs with *M. mystacinus*.

Up to now, significant differences were established only for the total skull length, condylobasal length, width of skull, infraorbital width and length of the mandible. Therefore, most authors consider the dimensional differences between the two species to be minor. My results show, however, that the arithmetical means of these dimensions are highly significantly different (in most cases  $p < 0.001$  !); the length of  $M^1-M^3$  being the only exception (see table I).

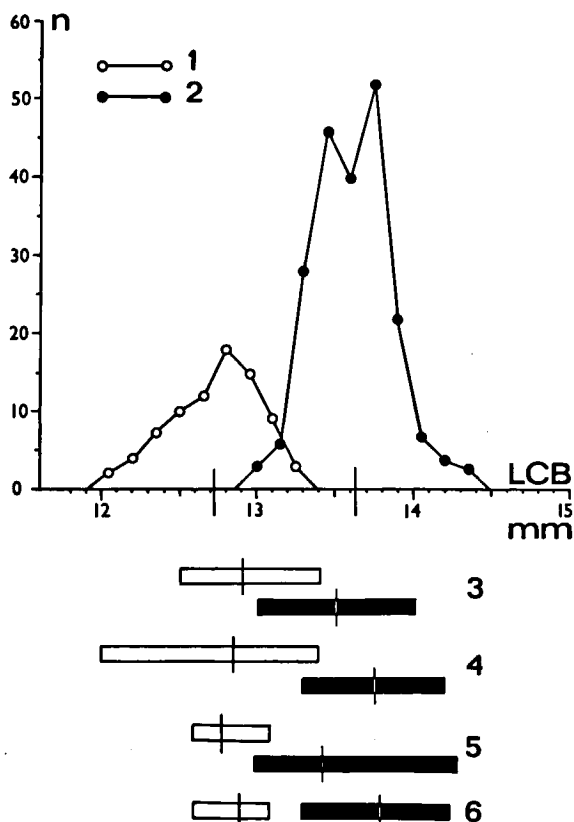


Fig. 2. Condylobasal length: (1) *Myotis mystacinus* and (2) *M. brandtii* from Záskočie Cave; (3) Gauckler & Kraus, 1970; (4) Hanák, 1971a; (5) Baagøe, 1973; (6) Ruprecht, 1974; (open columns = *M. mystacinus*, black ones = *M. brandtii*).

Table I. The statistical analysis of skull dimensions.

Dimension (abbreviation)	<i>Myotis mystacinus</i>				
	<i>n</i>	$\bar{x}$	95% confidence limits of $\bar{x}$	Range	S.D.
Total length of skull (LCr)	74	13.354	13.288—13.420	12.55—13.80	0.286
Condylobasal length (LCB)	80	12.715	12.653—12.777	12.00—13.25	0.277
Basal length (LBCr)	80	11.369	11.311—11.428	10.75—11.80	0.263
Width of braincase (LaN)	70	6.986	6.942— 7.031	6.60— 7.30	0.185
Zygomatic width (LaZ)	48	8.100	8.031— 8.170	7.20— 8.45	0.239
Rostral width (C—C)	95	3.179	3.152— 3.206	2.85— 3.45	0.130
Interorbital width (LaI)	93	3.555	3.529— 3.580	3.25— 3.85	0.124
Infraorbital width (LaInf)	98	3.268	3.239— 3.330	2.90— 3.55	0.142
Length of palate — including spina nasalis (LPa)	86	7.318	7.281— 7.355	6.85— 7.65	0.173
Alveolar length of I <sup>1</sup> -M <sup>3</sup>	100	5.992	5.964— 6.019	5.60— 6.30	0.140
Alveolar length of C-M <sup>3</sup>	105	4.889	4.867— 4.910	4.60— 5.20	0.111
Alveolar length of P <sup>1</sup> -M <sup>3</sup>	106	4.145	4.123— 4.168	3.80— 4.45	0.182
Crown length of P <sup>4</sup> -M <sup>3</sup>	46	3.687	3.661— 3.713	3.50— 3.85	0.086
Crown length of M <sup>1</sup> -M <sup>3</sup>	34	3.127	3.040— 3.213	2.85— 3.20	0.249
Height of braincase (AN)	71	4.835	4.801— 4.868	4.50— 5.25	0.140
Alveolar width of M <sup>3</sup> -M <sup>3</sup>	94	5.098	5.060— 5.136	4.75— 5.45	0.184
Condylar length of mandible (LMA)	21	9.598	9.498— 9.698	9.20— 9.90	0.219
Alveolar length of I <sub>1</sub> -M <sub>3</sub>	25	6.420	6.359— 6.482	6.00— 6.65	0.148
Alveolar length of C-M <sub>3</sub>	26	5.456	5.401— 5.510	5.15— 5.65	0.135
Alveolar length of P <sub>1</sub> -M <sub>3</sub>	25	4.806	4.754— 4.858	4.55— 5.10	0.126
Crown length of P <sub>1</sub> -M <sub>3</sub>	3	4.083	3.704— 4.463	3.95— 4.25	0.153
Crown length of M <sub>1</sub> -M <sub>3</sub>	7	3.429	3.313— 3.545	3.25— 3.60	0.125
Height of processus coronoideus (APC)	19	2.747	2.708— 2.787	2.60— 2.90	0.082

Measurements in mm.

The range of the skull dimensions of both species from the Záskočie Cave was similar to the recently published data for other Holocene and recent populations (Wołoszyn, 1970; Baagøe, 1973; Ruprecht, 1974).

In view of the extensive material available, bimodal curves of frequency distribution could be established for a number of dimensions (e.g. condylobasal length, M<sup>3</sup>-M<sup>3</sup>, C-M<sup>3</sup>, etc.). Their character remains constant even if classification grouping is made. This bimodality is probably due to sexual dimorphism, although Baagøe (1973) found smaller differences between the sexes (fig. 2; see also phylogenetic remarks).

Also remarkable were the statistically significant interspecific differences in variance of zygomatic width, rostral width, alveolar length of C-M<sup>3</sup> and alveolar width of M<sup>3</sup>-M<sup>3</sup>. A greater variance was found in *M. brandtii*.

#### Relation between the skull dimensions

References to the mutual relations of the skull proportions in *M. mystacinus* and *M. brandtii* are very infrequent. Sigmund (1965, 1966) presents

some somatic and skeleton allometries, but his results refer to *M. mystacinus* sensu lato, i.e. including *M. brandtii*. Only Baagøe (1973) provides some values for reliably identified material, useful for systematics. However, the importance of the allometries under discussion must not be overlooked, because they represent the results of selective processes in the course of evolution (Sigmund, 1964a, 1966) and thus contribute towards solving some evolutionary and other problems.

Correlation and regression analyses for 32 (and 64) pairs of values were examined of the Záskočie material. The most important results of correlation analysis are given in table II. A moderate to strong degree of interdependence of the dimensions under comparison could be established in most cases. Only a slight correlation is evident between the condylobasal length and the height of braincase in both species.

An important interspecific difference was established between the ratio of interorbital width and infraorbital width: a significantly lower correlation occurs in *M. mystacinus* than in *M. brandtii*. Furthermore, while in *M. mystacinus* the

Table I, continued.

<i>Myotis brandtii</i>					F-test		t-test	
n	$\bar{x}$	95% confidence limits of $\bar{x}$	Range	S.D.	F	significance level	t	significance level
187	14.255	14.216—14.295	13.60—15.10	0.273	1.098	0.6103	23.72	0.0000***
209	13.615	13.581—13.649	13.05—14.40	0.250	1.229	0.2511	26.54	0.0000***
215	12.159	12.126—12.191	11.40—12.85	0.244	1.163	0.3964	24.16	0.0000***
184	7.560	7.536— 7.584	7.15— 8.00	0.167	1.235	0.2712	23.74	0.0000***
121	8.725	8.691— 8.759	8.30— 9.10	0.188	1.618	0.0386*	16.23	0.0000***
257	3.365	3.351— 3.378	3.10— 3.95	0.110	1.405	0.0389*	12.35	0.0000***
241	3.816	3.801— 3.831	3.55— 4.15	0.118	1.094	0.5836	17.86	0.0000***
268	3.693	3.678— 3.708	3.40— 4.10	0.125	1.281	0.1267	27.70	0.0000***
244	7.740	7.718— 7.763	7.25— 8.20	0.179	1.065	0.7477	19.00	0.0000***
271	6.406	6.389— 6.423	6.05— 6.80	0.141	1.026	0.8976	25.10	0.0000***
278	5.229	5.213— 5.245	4.85— 5.85	0.139	1.587	0.0068**	24.94	0.0000***
278	4.434	4.420— 4.447	4.20— 4.80	0.113	1.088	0.5824	22.04	0.0000***
230	3.858	3.845— 3.875	3.55— 4.10	0.099	1.336	0.2450	10.86	0.0000***
209	3.186	3.170— 3.202	2.90— 3.45	0.116	4.629	0.0000***	1.37	0.1801
187	4.912	4.892— 4.933	4.55— 5.40	0.140	1.005	0.9580	3.99	0.0001***
264	5.350	5.332— 5.368	5.00— 5.80	0.148	1.542	0.0082**	12.00	0.0000***
48	10.296	10.239—10.352	9.90—10.70	0.195	1.264	0.4992	13.17	0.0000***
54	6.773	6.734— 6.812	6.50— 7.20	0.142	1.094	0.7637	10.15	0.0000***
55	5.732	5.699— 5.765	5.45— 6.05	0.123	1.208	0.5515	9.14	0.0000***
55	5.056	5.022— 5.091	4.85— 5.35	0.126	1.002	1.0000	8.23	0.0000***
18	4.233	4.182— 4.285	4.00— 4.40	0.104	2.178	0.2956	2.18	0.0422*
28	3.605	3.552— 3.659	3.45— 4.50	0.138	1.206	0.8845	3.09	0.0041**
50	2.975	2.942— 3.008	2.75— 3.20	0.116	1.985	0.1127	7.81	0.0000***

\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ .

correlation ratios of  $M^1-M^3$  to  $P^4-M^3$  (or  $C-M^3$ ) are not significant, in *M. brandtii* higher correlations of  $M^1-M^3$  to  $P^4-M^3$  and still higher of  $M^1-M^3$  to  $C-M^3$  are characteristic. Probably, this can be considered to be a result of the phylogenetic development of the  $P^2-P^3$  zone during the Holocene.

Table II also presents some of the results of the regression analysis. The interspecific transposition of regression lines could be established in most cases (see also fig. 3). Like in sibling species (cf. Šachlová, 1966), the regression lines of longitudinal dimensions are very nearly parallel and not significantly different ( $I^1-M^3 / LCB$ ,  $I_1-M_3 / LMa$ ,  $C-M_3 / LMa$ ). However, the important difference in skull shape influences the more substantial differences between the allometric ratios of longitudinal proportions to latitudinal ones, mutual ratios of latitudinal proportions and the ratio of the height of the skull to the condylobasal length (significant difference of parallel regression lines of  $LaN/LCB$ ,  $LaZ/LCB$ ,  $LaZ/LaI$ ,  $AN/LCB$  and significantly unparallelled regression lines for  $LaIn/LaI$  and  $M^3-M^3 / LPa$ ), i.e., in *M. brandtii* the longer skulls are relatively

more slender at rostral parts, but they have relatively higher and wider braincases.

### Phylogenetic remarks

According to current opinion, *M. mystacinus* is a younger evolutionary species and its evolution is closely connected with an older species *M. brandtii*. This view of its origin has never been explicitly stated, although the notion seems to be implied in several papers (e.g. Hanák, 1971b; Baagøe, 1973). The presumption, that *M. mystacinus* is a more advanced species is substantiated by indisputable facts:

— Morphology of the teeth, above all the more advanced reduction of  $P_3$ . (The progressive tendency in the genus *Myotis* has its source in the reduction of the rostral part of the skull including the teeth, above all the premolars — Miller & Allen, 1928; Kuzjakin, 1950; Wołoszyn, 1969.)

— Recent (cf. Baagøe, 1973) as well as historic distribution of the species in Central Europe (*M. brandtii* occurred in the Pleistocene, *M. mystacinus* appears later, during the Holocene — Wołoszyn, 1970; Hanák, 1971b; Schaefer, 1974).

Table II. The correlation and regression analysis of skull measurements.

Dimensions		<i>Myotis mystacinus</i>				
Function (y)	Argument (x)	N	r	index of determination (%)	Linear regression $y' = a + bx$	
			95% confidence limits of r		95% confidence limits of a	95% confidence limits of b
LaN	LCB	65	0.553	30.62	2.383	0.363
			0.362—0.705		0.635—4.130	0.225—0.500
LaZ	LCB	45	0.564	31.80	1.652	0.508
			0.330—0.739		—1.252—4.556	0.279—0.737
LPa	LCB	75	0.724	52.42	1.154	0.484
			0.598—0.818		—0.214—2.523	0.376—0.591
I <sup>1</sup> -M <sup>3</sup>	LCB	79	0.771	59.39	0.858	0.403
			0.665—0.849		—0.105—1.820	0.327—0.478
C-M <sup>3</sup>	LCB	79	0.658	43.33	1.325	0.280
			0.515—0.769		0.399—2.250	0.207—0.353
C-M <sup>3</sup>	I <sup>1</sup> -M <sup>3</sup>	100	0.750	56.22	1.299	0.599
			0.651—0.826		0.664—1.935	0.493—0.705
AN	LCB	67	0.270	7.31	3.079	0.139
			0.034—0.481		1.526—4.632	0.016—0.261
LaZ	LaI	47	0.365	13.34	5.683	0.678
			0.091—0.593		3.836—7.530	0.159—1.592
LaInf	LaI	88	0.290	8.42	2.054	0.340
			0.088—0.472		1.201—2.908	0.099—0.580
M <sup>3</sup> -M <sup>3</sup>	LPa	29	0.523	27.31	1.037	0.555
			0.344—0.669		—0.466—2.541	0.349—0.760
M <sup>1</sup> -M <sup>3</sup>	C-M <sup>3</sup>	34	nonsignificant correlation	—	—	—
P <sup>4</sup> -M <sup>3</sup>	M <sup>1</sup> -M <sup>3</sup>	34	nonsignificant correlation	—	—	—
I <sub>1</sub> -M <sub>3</sub>	LMa	21	0.754	56.89	1.132	0.550
			0.493—0.899		—1.077—3.340	0.320—0.781
C-M <sub>3</sub>	LMa	21	0.790	62.35	0.610	0.504
			0.557—0.914		—1.194—2.414	0.316—0.691
I <sub>1</sub> -M <sub>3</sub>	C-M <sub>3</sub>	25	0.852	72.60	1.206	0.957
			0.698—0.935		—0.176—2.588	0.704—1.211
P <sub>4</sub> -M <sub>3</sub>	M <sub>1</sub> -M <sub>3</sub>	3	—	—	—	—
APC	LMa	18	0.486	23.57	0.970	0.185
			0.038—0.782		—0.729—2.669	0.008—0.362

All correlations are significant at the 5% level of significance.

However, at the same time, the following facts must not be overlooked:

— In older forms a stabilization of variability in dimensions, morphology, etc. occurs. However, some skull dimensions of *M. brandtii* (cf. table I) are significantly more variable than comparable *M. mystacinus* measurements.

— The correlation between some dentition measurements points to a progressive development of morphology in *M. brandtii* during the Holocene. It is also possible that the conspicuous bimodal character of frequency curves of some skull

measurements was not due to sexual dimorphism but reflects the above mentioned development (cf. *Myotis bechsteini* — Rybář, 1976).

— Significant differences were found in some allometries (see continuation of table II) and not, as usually found in sibling species, merely a transposition of regression lines.

— Some sources (Topál, 1958; Vlček, 1970; Baagøe, 1973) give important differences in os penis morphology, which do not correspond to sibling species.

These contradictions would seem to indicate the

Table II, continued. On the right hand side a comparison of allometric ratios is given (i.e. the linear regressions  $y' = a + bx$ ) in *Myotis mystacinus* and *M. brandtii*.

<i>Myotis brandtii</i>					<i>t</i> -test for identity of two regression coefficients <i>b</i>		<i>t</i> -test for identity of two linear regressions	
<i>N</i>	<i>r</i> 95% confidence limits of <i>r</i>	index of determination (%)	Linear regression $y' = a + bx$		<i>t</i>	significance level	<i>t</i>	significance level
			<i>a</i> 95% confidence limits of <i>a</i>	<i>b</i> 95% confidence limits of <i>b</i>				
172	0.594 0.489—0.684	35.32	2.071 0.946—3.196	0.403 0.320—0.486	0.5207	0.6031	5.430	0.0000***
114	0.441 0.282—0.580	19.48	3.973 2.165—5.782	0.350 0.217—0.483	1.291	0.1986	4.234	0.0000***
199	0.821 0.770—0.862	67.35	0.001 -0.757—0.759	0.569 0.513—0.625	1.397	0.1650	1.976	0.0482*
208	0.787 0.730—0.834	61.95	0.350 -0.302—1.003	0.445 0.397—0.493	0.9462	0.3449	1.602	0.1102
209	0.613 0.521—0.692	37.54	0.617 -0.199—1.434	0.339 0.279—0.399	1.239	0.2171	2.586	0.0097**
271	0.710 0.647—0.765	50.45	0.845 0.324—1.367	0.684 0.603—0.766	1.255	0.2106	4.073	0.0000***
181	0.343 0.208—0.466	11.74	2.325 1.278—3.373	0.190 0.113—0.267	0.7180	0.4734	2.442	0.0153*
117	0.487 0.336—0.615	23.67	5.627 4.600—6.654	0.812 0.542—1.082	0.4602	0.6468	9.053	0.0000***
235	0.596 0.507—0.673	35.46	1.290 0.872—1.709	0.630 0.520—0.740	2.183	0.0309*	—	—
238	0.353 0.237—0.460	12.45	2.997 2.198—3.797	0.304 0.200—0.407	2.312	0.0215*	—	—
209	0.299 0.171—0.418	8.92	1.852 1.267—2.436	0.255 0.143—0.366	—	—	—	—
208	0.559 0.459—0.647	31.24	2.216 1.171—3.261	0.230 0.154—0.307	—	—	—	—
48	0.704 0.531—0.826	49.61	1.366 -0.252—0.298	0.525 0.368—0.682	0.1889	0.8507	0.2642	0.7924
48	0.653 0.458—0.793	42.64	1.450 -0.256—2.926	0.416 0.273—0.560	0.7400	0.4619	0.3776	0.7069
54	0.812 0.699—0.889	65.93	1.346 0.260—2.432	0.946 0.756—1.135	0.0696	0.9447	2.744	0.0076**
15	0.819 0.549—0.941	67.08	2.310 1.490—3.129	0.537 0.312—0.763	—	—	—	—
48	0.362 0.091—0.589	13.13	0.716 -1.007—2.440	0.219 0.052—0.387	0.2459	0.8066	1.488	0.1418

\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ .

existence of a separate phylogenetic development of the two species. Thus, it may be necessary to exclude the species *M. brandtii* from the subgenus *Selysius* Bonaparte, 1841, to which *M. mystacinus* belongs. Naturally, it would be hardly possible to present the definitive solution of the subgenus determination of *M. brandtii* within the framework of the present paper. Nevertheless, some facts — e.g. the high frequency of protoconules on the  $M^{1-3}$  (cf. Tate, 1941) and the statistical analysis of the os penis dimensions (Viček, 1970) — would seem to indicate

that a relationship might exist to *M. daubentonii* (Kuhl, 1817), i.e. to the subgenus *Leuconoe* Boie, 1830.

### SUMMARY

This paper presents the results of a systematic survey of 114 skulls and 53 mandibles of *Myotis mystacinus* and 282 skulls and 107 mandibles of *M. brandtii* collected in the Záskočie Cave, Slovakia, Č.S.S.R.

1. The morphology and proportions of skulls and

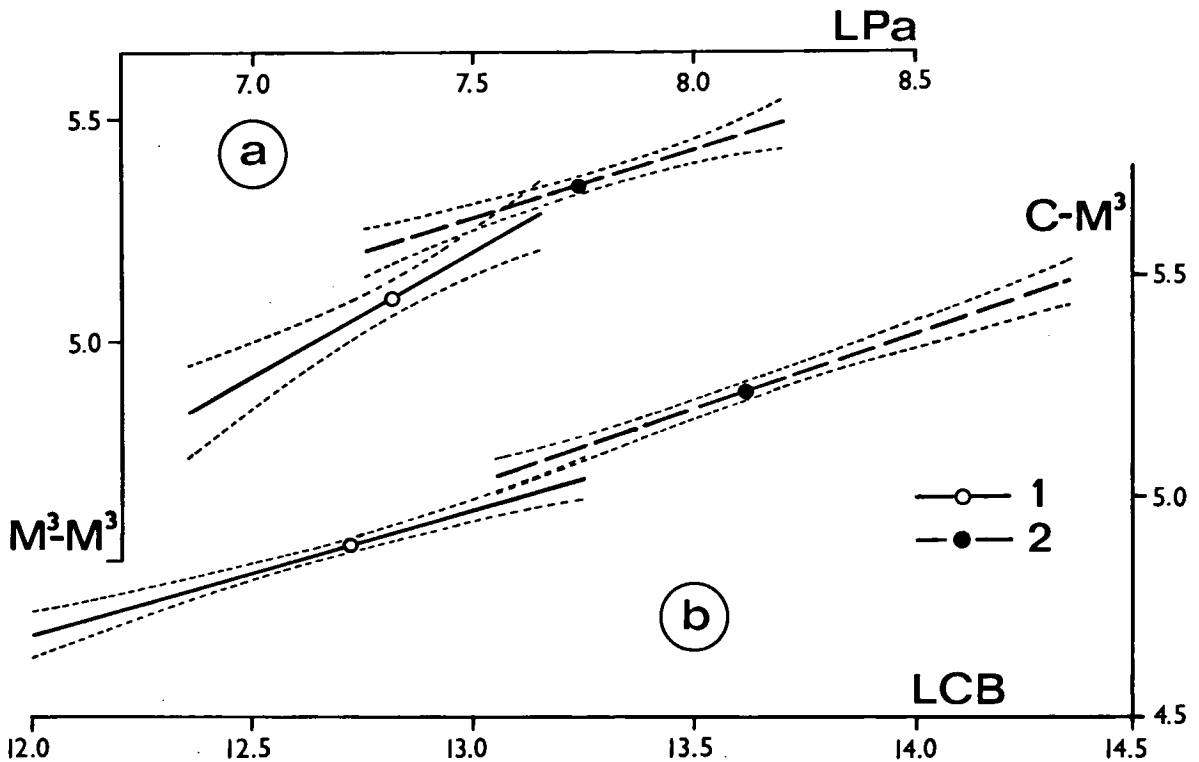


Fig. 3. Allometries of skull proportions in *Myotis mystacinus* (1) and *M. brandtii* (2) including their 95% confidence limits: (a) alveolar width of  $M^3-M^3$  as the function of length of the palate (an example of unparallel regression lines); (b) alveolar length of  $C-M^3$  as the function of condylobasal length (an example of significantly different parallel regression lines). All measurements in mm.

mandibles, frequency of protoconules on the upper molars, size ratio of the premolars or the degree of development of the secondary cone on  $P^4$  were determined and were found then to be adequate only for identifying part of the material under consideration. A new discriminative criterion, based on the  $P^4$  roots morphology is proposed.

2. The results of the statistical analysis of skull dimensions are presented in table I. Although overlap between species occurs, arithmetic means (with the exception of the crown length of upper molars) are significantly different. A significantly greater variance was established in case

of some dimensions in *M. brandtii* as compared to *M. mystacinus*.

3. The results of the correlation and regression analysis (table II) concern the interspecific differences in the allometries of latitudinal dimensions of skulls.

4. A contradiction was found between the geologically older age of *M. brandtii* and some of its evolutionary advanced features (in comparison with *M. mystacinus*). This may indicate that *M. brandtii* and *M. mystacinus* are not sibling species, but that they each belong to a different subgenus: *M. mystacinus* to *Selysius*, *M. brandtii* probably to *Leuconoe*.

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