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Variability of Daubenton's Bat and Distribution of the nathalinae Morphotype in Poland

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In collections of *Myotis daubentoni* (Kuhl, 1819) from Poland (n=41) a morphotype P^4 analogical with that in *Myotis nathalinae* Tupinier, 1977 has been found. It forms 31.7% of all the skulls examined. Comparison of body and skull dimensions of the morphotype distinguished revealed its complete morphological similarity to Daubenton's bat. Bats representing the *nathalinae* morphotype occur in 10 localities (in 3 places sympatrically with *M. daubentoni*), situated in: the Pomeranian Lake Region, the Wielkopolska-Kujawy and Masovian Lowlands, the Małopolska Upland and in the Białowieża Primeval Forest.

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INTRODUCTION

The very small number of publications confirming the taxonomic separateness of the recently described *Myotis nathalinae* Tupinier, 1977, is still surprisingly persistent. Lesser Daubenton's bat is known from only a few localities in the south and north-east of Spain, and north and east of France, and also Switzerland. Further verification of identifications of specimens in museum collections of Daubenton's bat has resulted in new localities being found for *M. nathalinae* in Switzerland (Aellen, 1978) and Spain (Hutterer, 1978). After the appearance of Tupinier's publication (1977) species identification was verified for all available individuals of Daubenton's bat in Poland. Thirteen skulls with P^4 structure analogical with that in *M. nathalinae* were found in the collections, but they were treated as *M. daubentoni* morphotypes. The distribution of all localities of this morphotype has been given in the "Atlas of Polish Mammals" (Ruprecht, in press).

The purpose of the present study was to make a comparative morphological analysis of the Polish *M. daubentoni* material available and to discuss the credibility of the status as a separate species of *M. nathalinae*.

MATERIAL AND METHODS

Of the 41 skulls of Daubenton's bat used, 13 had been identified as *nathalinae* morphotype. The material was obtained from collections in the Mammals Research

Institute PAS at Białowieża (n=27), Department of Systematic and Experimental Zoology PAS in Kraków (n=6), Institute of Zoology PAS in Warsaw (n=4) and the author's own collection (n=4).

The last upper large premolar (P^4) in skulls was examined under a microscope for the presence of the protoconus which characterizes the teeth of Daubenton's bat. The protoconus usually takes the shape of a prominent cone similar to a small pyramid located orad and linguad. The skulls were measured with a vernier caliper, making the following six standard measurements with accuracy to 0.1 mm: (1) condylobasal length (*CbL*), (2) maxillary tooth-row length ($C—M^3$). (3) zygomatic breadth (*ZyB*), (4) interorbital constriction (*IC*), (5) mandible length (*MdL*) and 6) height of *ramus mandibulae* (*HRM*). A further additional 11 measurements were made of teeth using a measuring microscope, with accuracy to 0.01 mm, in accordance with the method adopted by Tupinier (1977). The following were also taken into consideration: the available body dimensions of Daubenton's bat from Poland, and measurements of the forearm in 83 males and 89 females of *M. daubentoni* from the population at Nietoperek (Gorzów Wielkopolski Palatinate), obtained when ringing the bats. The baculum was transluced in KOH and stained with alizarin after the method described by White (1951).

In studies on geographical, dimorphic and interspecies differentiation the Student *t* test was used for comparing averages of independent groups.

RESULTS

1. Variability of M. daubentoni from Poland

Representative material relating to the forearm length of Daubenton's bat from the population at Nietoperek reveals the wide range of lengths of this feature in both sexes (35.3—41.0 mm), with a low coefficient of variation of 2.6 and 2.7% in males and females respectively. The minimal class of variation in this feature, of 35.5 mm, potentially capable of including the lesser Daubenton's bat, consists of 4.8% of the males and 2.2% of the females from this same population (Fig. 1). The two peaks in the curves for forearm length, more strongly marked in females, are also remarkable. It may be that this is due to age differences in the sample. A highly statistically significant dimorphic difference was found, visible in the greater dimensions of the forearm in females ($P<0.001$).

Examination of the last premolar (P^4) in the series of the Daubenton's bat skulls examined, regardless of the degree of wear of the crown, made it possible to distinguish the following variants: (1) protoconus strongly developed, equal in height to that of the crown of premolar P^3; (2) protoconus of intermediate development, equal in height to half the height of the crown of P^3; (3) protoconus weakly developed, lower in height than half the height of the crown of P^3, sometimes in the form of a fold of enamel, only visible from certain positions of the tooth; (4)

complete absence of protoconus. The fourth variant, which corresponds to the diagnosis of *Myotis nathalinae* Tupinier, 1977, was found in 13 cases (31.7%). It may therefore be said that the formation of protoconus of P^4 does not have the properties of a completely alternative characteristic, but is distinguished by continual variation as in the examples of variants 1—3.

Skull dimensions of Polish specimens are distinguished by very little variability, both in the case of Daubenton's bat (C.v.=2.4—6.2%), and of the *nathalinae* morphotype (C.v.=1.2—3.9%), which is evidence of the considerable homogeneity of samples (Table 1). In no case out of 17 comparisons of averages for skull measurements were differences between the two forms of bats from Poland statistically significant ($P>0.05$; Table 1).

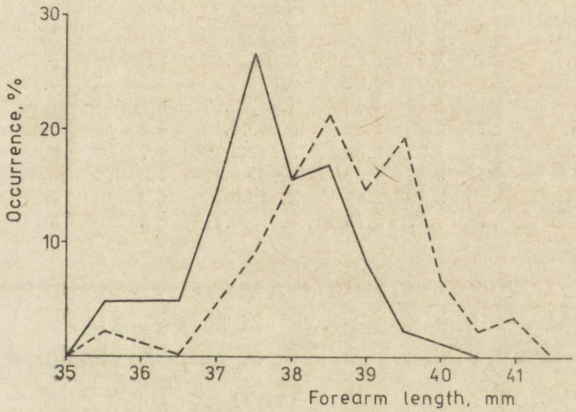

Fig. 1. Variability in forearm length in *Myotis daubentoni* (Kuhl, 1819) from Nietoperek. Material may contain both forms of Daubenton's bat. Continuous line — males, mean — 37.66±0.98; broken line — females, mean — 38.68±1.04.

Among skull dimensions the two Polish forms differ most (although not significantly) in respect of extreme *CbL* dimensions. The correlation between *CbL* and forearm length was examined, but the calculated coefficient of correlation ($r=0.26$) proved statistically insignificant ($P>0.05$). On the other hand, the relation of *CbL* and *MdL* is expressed by a highly significant ($P<0.001$) coefficient of correlation ($r=0.76$), which makes it possible to estimate the condylobasal length of the skull (y) on the basis of the dimension of mandible length (x) from the following regression equation: $y=1.02x+3.14$.

The degree of differentiation between selected skull measurements of *M. d. daubentoni* from Western, Southern and Central Europe is given in Table 2. Although material from Hungary, Czechoslovakia and Yugoslavia was not divided into the two forms of Daubenton's bat, the

Table 1
Ranges of variation in body and skull dimensions of the two forms of Daubenton's bat from Poland.

Measurements	Daubenton's bat n	min—max	x̄±SD	C.v.	*nathalinae* morphotype n	min—max	x̄±SD	C.v.
Head and body	7	44.0—57.4	49.95±4.57	9.1	3	45.0—50.0	47.00±2.64	5.6
Tail	7	31.4—40.0	36.25±3.11	8.6	3	35.0—38.3	37.10±1.82	4.9
Ear	8	11.0—14.9	13.07±0.93	7.1	4	12.5—14.0	13.30±0.81	6.1
Forearm	12	35.0—39.7	36.86±1.29	3.5	4	34.0—38.2	36.57±1.85	5.0
Body weight	7	5.7—12.9	7.61±2.48	32.6	3	6.4—8.5	7.55±1.06	14.0
CbL	23	13.3—14.6	13.67±0.33	2.4	8	13.2—13.8	13.58±0.19	1.4
C—M^3	28	4.8—5.5	5.11±0.17	3.3	13	4.9—5.3	5.12±0.10	1.9
ZyB	22	8.3—9.6	8.94±0.38	4.2	8	8.7—9.2	8.95±0.17	1.9
IC	26	3.7—4.2	4.03±0.13	3.2	12	3.7—4.1	4.00±0.10	2.5
MdL	26	9.7—10.9	10.18±0.27	2.6	10	10.0—10.3	10.20±0.12	1.2
HRM	25	2.7—3.2	2.99±0.13	4.3	11	2.8—3.2	3.01±0.12	3.9
C—P^4 length	28	2.00—2.48	2.24±0.11	4.9	13	2.19—2.37	2.27±0.05	2.2
P^4*—M*^{3} length	28	3.55—4.14	3.83±0.13	3.4	13	3.71—3.98	3.86±0.07	1.8
M^1*—M*^{2} length	28	2.24—2.60	2.42±0.09	3.7	13	2.33—2.57	2.44±0.06	2.4
M^1*—M*^{3} length	28	2.84—3.45	3.15±0.12	3.8	13	3.01—3.25	3.18±0.06	1.9
M^3 length	28	0.68—0.85	0.76±0.03	3.9	13	0.70—0.82	0.76±0.03	3.9
M^3 breadth	28	1.14—1.48	1.30±0.07	5.4	13	1.19—1.37	1.27±0.05	3.9
C—M$_3$ length	22	5.20—5.83	5.54±0.18	3.2	10	5.35—5.71	5.50±0.12	2.2
C—P$_4$ length	22	1.92—2.30	2.14±0.10	4.7	10	2.03—2.22	2.13±0.07	3.3
P$_4$*—M*$_3$ length	22	3.87—4.39	4.08±0.12	2.9	10	3.90—4.17	4.05±0.08	1.9
M$_1$*—M*$_2$ length	22	2.23—2.99	2.41±0.15	6.2	10	2.27—2.47	2.37±0.05	2.1
M$_1$*—M*$_3$ length	22	3.27—3.73	3.47±0.11	3.2	10	3.13—3.55	3.41±0.12	3.5

ranges of variation obtained and mean values for five skull dimensions exhibit considerable reciprocal similarity. The almost identical mean values for Daubenton's bat from Spain, Czechoslovakia and Poland are very striking, only individuals of *M. daubentoni* from Yugoslavia having slightly smaller *CbL*.

Table 2
Variability of some skull dimensions of *Myotis d. daubentoni* from the geographical aspect.

Country, Author	*CbL* min—max Avg. (n)	*C—M*^{3} min—max Avg. (n)	*ZyB* min—max Avg. (n)	*IC* min—max Avg. (n)	*MdL* min—max Avg. (n)
Spain, Tupinier, 1977	13.5—14.0 13.7 (7)	5.12—5.50 5.27 (7)	8.8—9.0 8.9 (7)	3.4—4.2 3.9 (7)	10.0—10.8 10.39 (7)
Yugoslavia[1], Mirić, 1971	12.9—13.8 13.38 (7)	5.0 —5.4 5.12 (7)	8.6—9.1 8.91 (7)	3.9—4.3 4.05 (7)	9.4—10.5 9.96 (6)
Hungary[1], Topal, 1969	13.2—14.0	5.5 —6.1	8.8—9.4	—	9.9—10.6
Czechoslovakia[1], Feriancová-Masárová & Hanák, 1965	13.4—14.3 13.7 (55)	5.5 —6.0 5.3 (55)	8.5—9.6 9.0 (55)	3.7—4.3 4.0 (55)	—
Poland, Author's own data	13.3—14.6 13.67 (23)	4.8 —5.5 5.11 (28)	8.3—9.6 8.95 (22)	3.7—4.2 4.03 (26)	9.7—10.9 10.18 (26)

[1] The material may contain both forms of Daubenton's bat.

Bats of the *nathalinae* morphoytpe from Poland are significantly larger in respect of *CbL* than individuals of the lesser Daubenton's bat from Spain ($0.01<P<0.05$), and also in respect of forearm length ($0.01>P>>0.001$).

It is clear from these comparisons that the nominative subspecies of Daubenton's bat inhabiting Central and Western Europe is distinguished by very small geographical differentiation in the 5 skull dimensions examined. The small skull dimensions of Spanish *M. nathalinae*, on the other hand, would appear to be characteristic of that local population.

The author's opinion that he had to do with the morphotype of *M. daubentoni* would appear to be confirmed by the lack of statistically significant differences in the mean values from skull measurements of the two forms of Daubenton's bat from Poland.

2. Occurrence of the nathalinae Morphotype in Poland

The available material of the *nathalinae* morphotype originates from different parts of Poland — these are thus new localities of this form

Table 3

Documentation of the *nathalinae* morphotype of Daubenton's bat from Poland.

Locality in UTM grid	Date of capture	Coll. no.	Remarks
WU 30 Nietoperek	Apr. 9, 1980	135 945	Hibernating together with *M. daubentoni, M. myotis, P. auritus, M. nattereri, M. dasycneme, M. mystacinus* and *E. serotinus;* species in order of frequency of encounter. Female.
WU 38 Raduń	May 27, 1971	742	From pellets of the barn owl, found together with *P. pipistrellus* and *M. nattereri*
WV 55 Świdwin	Jan. 23, 1936	792	Female, in winter hibernation place
XU 30 Poznań	Feb. 15, 1942	899	In winter hibernation place
CD 56 Ciechocinek	July 29, 1964	672	In state of decomposition under a tree hollow inhabited by a bat colony in the city centre; cooccurring with *M. daubentoni*
EB 69 Puławy	?,	42 5?4	Collected by A. Krzanowski
EB 69 Włostowice	June 29, 1957	19	In barn owl pellets in addition to *P. austriacus, E. serotinus* and *M. dasycneme*
EC 71 Baranów	Aug. 28, 1961	346a	In barn owl pellet in addition to *P. austriacus, P. pipistrellus* and *M. mystacinus*
		346b	
	Mar. 29, 1963	829	In barn owl pellet; distinct absence of protoconus P^4 in all three specimens
FD 84 Białowieża Primeval Forest	Apr. 19, 1974	113 220	Male drowned in a well in sector 450 of the Białowieża Primeval Forest; baculum: length 0.63, breadth 0.54 mm
	Nov. 29, 1962	31 057	Male found in the Palace Park; cooccurring with *M. daubentoni*
FD 94 Białowieża	July 31, 1969	86 352	Female caught near the Narewka river

not as yet given in literature. They have been arranged in order of succession of readings from 10×10 km squares of the UTM grid, describing the circumstances under which the bats were found (Table 3).

The current distribution of the *nathalinae* morphotype in Poland includes the following regions: Pomeranian Lake Region, Wielkopolska — Kujawy and Masovian Lowlands, Małopolska Upland and the Białowieża Primeval Forest.

DISCUSSION

Discussion must begin with presentation of the taxonomic values of the available dimensional characteristics of the body and skull which are of assistance in differentiating between the two forms of Daubenton's bat.

Tupinier & Aellen (1978) give the following characteristics for the two forms of Daubenton's bat:

	M. daubentoni (Kuhl)	*M. nathalinae* Tupinier
Forearm	35.5—39.0 (Avg. 37.0 mm)	32.8 —36.0 (Avg. 34.5 mm)
Hind foot	9.0—10.2 (Avg. 9.8 mm)	7.8 — 9.5 (Avg. 8.7 mm)
Tibia/hind foot	1.6— 1.9	1.75— 2.1
CbL	13.3—14.2 mm	12.8—13.6 mm
Protoconus P^4	present	absent

Among body measurements only forearm length would appear to be of some taxonomic value when differentiating between the two forms of Daubenton's bat. In the available material from Poland ranges of variation in forearm length for *M. daubentoni* from Silesia are 35.0——40.8 mm (Haitlinger, 1976), from western Masovia 34.9—41.0 mm (Lesiński, pers. comm.) and from Nietoperek 35.3—41.0 mm (Fig. 1), and are decidedly greater than in other European populations. Far smaller ranges of forearm length were found in both Spanish representatives of Daubenton's bat (35.5—38.4 mm; Avg. 36.75) and lesser Daubenton's bat (32.8—36.4 mm; Avg. 34.48) (Tupinier, 1977). Hutterer (1978) also found very low values for forearm length in both *M. daubentoni* (34.1—34.3 mm) and *M. nathalinae* (31.5) when analyzing museum material collected in Spain. Low values for forearm length in *M. daubentoni* from Yugoslavia (33.7—39.1 mm) have also been given by Mirić (1971). This confirms the fact that more southern populations of Daubenton's bat are characterized by lower values for forearm length.

In order to obtain full comparability forearm length should always be measured under the same conditions, *i.e.*, on fresh material. The authors of taxonomic studies on bats do not usual give the conditions under which external measurements were made: whether they apply to fresh

material or were made on conserved or possibly dry material. Although the results of studies have shown that neither the age of bats (Baagøe, 1977b) nor the way in which they are conserved (Maeda, 1977), with the exception of sex dimorphism, exert any significant effect on forearm length, nevertheless it has been found that during the drying process forearm length, depending on the dimensions of the animals (large, medium or small) contracts by respectively 2.1, 2.8 and 3.4% (Arata, 1968).

To sum up it may be said that it is essential, in comparative taxonomic studies of bats, in which the ranges of forearm length play so important a part, to pay particular attention to the conditions under which measurements are made.

Among skull measurements it is condylobasal length which is of the greatest importance in diagnosing the two forms of Daubenton's bat. Age differences, which have not been found in the case of mandible length in this species (Baagøe, 1977b), have an important influence on *CbL* length. The process of conservation in formalin contributes greatly to reduction in all skull measurements, including *CbL* in the age groups examined, when compared with analogical skull dimensions prepared from fresh material of Schreiber's bat (Maeda, 1977). Similarly the values of certain dimensions of the rostral part of the skull in Natterer's bat, kept for a considerable time in formalin, were 12% smaller in comparison with material conserved for a shorter time (Horáček, 1979).

In the light of the facts presented it would appear extremely risky to draw far-reaching conclusions of a taxonomic nature on the strength of results obtained from studies of museum specimens of bats conserved for a long time.

The dimensions of the baculum in one example of the *nathalinae* — morphotype from the Białowieża Primeval Forest correspond to the dimensions characteristic of age group V, defined by X-ray, of *M. daubentoni* from Denmark (Baagøe, 1977a). Baculum dimensions are subject to the effect of age variation in *M. daubentoni,* attaining maximum size in the oldest age groups (Vlček, 1970; Baagøe, 1977a). Ranges of variation in baculum dimensions for the two forms of Daubenton's bat given by Tupinier (1977) come completely within the ranges of variation for the Danish representatives of *M. daubentoni* analyzed in age classes. Males of *Myotis* attain sexual maturity in spring or autumn of the second calendar year, and consequently such considerable differences in baculum length in Danish *M. daubentoni* must arouse understandable interest. It is possible that differentiation of this population into the two forms of Daubenton's bat may lie at the basis of such differences.

The tooth characteristic most effectively separating the two species would appear to give rise to the greatest doubts. It is a fact that it exhibits continual variability and consequently cannot be treated as a fully alternative characteristic. It would seem that it is insufficient to base distinction of *M. nathalinae* on one character only. It is for this reason that specimens from Poland have been treated as morphotype P^4 analogical with *M. nathalinae*. This point of view, with the present state of knowledge on the European Daubenton's bat, would seem to be fully justified on rational grounds, and does not rule out their real taxonomic separateness. A similar opinion is held by Dr. V. Hanák (pers. comm.) after thorough examination of Daubenton's bat material from Czechoslovakia.

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ZMIENNOŚĆ NOCKA RUDEGO I ROZMIESZCZENIE MORFOTYPU *NATHALINAE* W POLSCE

Streszczenie

Opisano zmienność morfologiczną wymiarów ciała i czaszki dostępnych materiałów (n=41) nocka rudego z Polski (Tabela 1—2). Wśród czaszek tego gatunku zostało znalezionych 13 okazów (31,7%), których ostatni górny ząb przedtrzonowy (P^4) odznaczał się całkowitym brakiem protoconusa. Cecha ta jest właściwa zębom P^4 nowego dla Europy gatunku nietoperza — *Myotis nathalinae* Tupinier, 1977. Nie dysponując żadnymi innymi kryteriami pomocniczymi, jak również stwierdzając dużą zmienność w stopniu wykształcenia protoconusa na zębach polskich okazów nocka rudego, autor doszedł do wniosku, iż miał do czynienia z cechą polimorficzną. Zatem, nie umniejszając odrębności systematycznej nowej formy, autor uważał, iż właściwiej będzie traktować wyróżnione okazy z Polski, jako morfotyp P^4 analogiczny jak u *M. nathalinae*. Przeprowadzone porównania wymiarów czaszki nietoperzy morfotypu *nathalinae* z *Myotis daubentoni* (Kuhl, 1819) z Polski, wykazały znaczne ich podobieństwo morfologiczne (Tabela 1). Nietoperze reprezentujące morfotyp *nathalinae* występują na 10 stanowiskach (w 3 miejscowościach sympatrycznie z nockiem rudym), które są zlokalizowane na: Pojezierzu Pomorskim, Nizinie Wielkopolsko-Kujawskiej i Mazowieckiej, Wyżynie Małopolskiej i w Puszczy Białowieskiej.