Vespertilio 16: 139–147, 2012
ISSN 1213-6123

Morphometrics of *Myotis blythii* from Crete: A taxonomic transition or an island effect?

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Abstract. Taxonomy of the mouse-eared bats (*Myotis myotis* species group) in the western Palaearctic have undergone several revisions in the recent decades, under the light of distributional, morphological and genetic investigations. However, in many eastern Mediterranean islands, taxonomic questions regarding this complex remain open. Here we compare a large set of samples of *Myotis blythii* from Crete with conspecific population samples from the Lesvos island (North Aegean, Greece) and from the circum-Mediterranean region, incl. Europe, Middle East, and Central Asia, in order to elucidate the taxonomic position of the Cretan populations. Statistical analyses showed the Cretan lesser mouse-eared bats to have an intermediate forearm length and skull size, but the masticatory apparatus is significantly smaller than in the comparative populations. Our results suggest that the previous assignment of the Cretan populations of *M. blythii* to the Middle Eastern subspecies *M. b. omari* is not justifiable. Feeding ecology and genetic studies are needed in order to understand whether the Cretan mouse-eared bat is a taxonomic transition between the smaller *M. b. oxygnathus* occurring in southern Europe and the larger *M. b. omari* inhabiting the eastern Mediterranean including Iran and the Caucasus region as also formerly suggested, or whether it is shaped by the influence of the island effect and diet specialisation.

Mouse-eared bats, *Myotis*, Crete, morphology, taxonomy

Introduction

Systematics of the west-Palaearctic populations of the mouse-eared bats (*Myotis myotis* species group) have puzzled zoologists from the beginning of the 20th century. Since these bats are phylogenetically closely related, they exhibit high morphological resemblance and live in sympatry over wide areas of Europe and southwestern Asia (Miller 1912, Harrison & Lewis 1961, Strelkov 1972, Felten et al. 1977, Benda & Horáček 1995a, b, Arlettaz et al. 1997, Benda et al. 2006, Evin et al. 2008). Based on close similarities between the smaller representatives of the mouse-eared bats of the western Palaearctic, being originally assigned to the names *Myotis oxygnathus*, *Myotis myotis omari*, *M. m. risorius*, and *M. blythii*, Harrison & Lewis (1962), Topál (1971), and Strelkov (1972) suggested regarding them as three subspecies of a single species *M. blythii* (but see Bogdanowicz et al. 2009). The nominotypical subspecies *M. b. blythii* (Tomes, 1857) occurs in Afghanistan, northern India and Central Asia; *M. b. oxygnathus* (Monticelli, 1885) occupies continental Europe from Spain to Crimea; *M. b. omari* Thomas, 1905 occurs in the Caucasus region, Asia Minor, Levant including Cyprus, Iran, and western Turkmenistan. Moreover, *M. b. ancilla* Thomas, 1910 occurs in northeastern China (Strelkov 1972) and Altai, since Benda et al. (2011) synonymised also the newly described Altaic subspecies, *M. b. altaica* Dzeverin et Strelkov, 2008 with this name. Iliopoulou-Georgudaki (1984) suggested to attribute *M. blythii* populations from the Lesvos island to a separate subspecies, *M. b. lesviacus* Iliopoulou, 1984, however, her view was later doubted by Benda & Horáček (1995a, b), Arlettaz et al. (1997), Hanák et al. (2001) and Topál & Ruedi (2001).

In Europe, Asia Minor and in the Levant, *Myotis blythii* lives in sympatry with its larger relative, the greater mouse-eared bat, *Myotis myotis* (Borkhausen, 1797). The former and/or the latter species were thought to inhabit also the Maghreb and some western Mediterranean islands (Felten et al. 1977, Benda & Horáček 1995a), but recent genetic analyses justified a full species rank (*Myotis punicus* Felten, 1977) for these populations (Castella et al. 2000, Ruedi & Mayer 2001, Mayer et al. 2007). Additionally, based on these mitochondrial gene comparisons, several authors (Spitzenberger & Bauer 2001, Simmons 2005, Dietz et al. 2007) attributed the Mediterranean populations of *Myotis blythii* to a separate species, *M. oxygnathus* (Monticelli, 1885). However, *M. oxygnathus* is not widely accepted as a valid species (see e.g. Benda et al. 2009), since the Mediterranean populations of *M. blythii* were found to hybridize with *M. myotis* (Berthier et al. 2006), while geometric morphometrics showed that the *oxygnathus* samples are almost identical in skull shape with *M. b. omari* and *M. b. blythii* samples, but clearly differ from *M. myotis* and *M. punicus* (Evin et al. 2008).

Taxonomy of the Cretan populations of the mouse-eared bats has also been rather complicated and controversial. The earlier authors (Raulin 1869, Bate 1905) considered Cretan populations to be a part of the European *M. myotis* (which at that time covered also *oxygnathus*), but Miller (1912) distinguished *M. blythii* as a separate species in Europe (originally as *M. oxygnathus*), including the Cretan samples collected by Bate (1905). This approach was followed by von Wettstein (1942) and Ondrias (1965), while Pohle (1953) and Kahmann (1959) considered the Cretan mouse-eared bats to be a part of the large European mouse-eared species under the name *M. myotis oxygnathus*.

Topál (1971), Strelkov (1972) and Iliopoulou-Georgudaki (1979, 1984) classified a small number of examined Cretan specimens as *M. blythii omari*. However, a further morphological analysis on a limited number of 15 samples from Crete showed that the Cretan population slightly overlaps in dimensional ranges with *M. punicus*, but largely with both *M. b. oxygnathus* and *M. b. omari*, and is dimensionally intermediate between the latter two subspecies and thus represents a 'taxonomic transition' between the two continental forms (Benda et al. 2009).

In this study we compare an extensive set of museum specimens of *Myotis blythii* from Crete with a series of samples from the Lesvos island (Greece), continental Europe (*M. b. oxygnathus*), from the Middle East (from Cyprus to Azerbaijan and SE Iran, *M. b. omari*) and from Central Asia and Kashmir (*M. b. blythii*), aiming to elucidate the taxonomic status of the Cretan mouse-eared bats.

Material and Methods

We took nine cranial dimensions, viz. LCr = greatest length of skull, LaZ = zygomatic width, LaI = width of interorbital constriction, LaN = neurocranium width, LaM = mastoidal width, ANc = neurocranium height, CM^3 = length of upper tooth-row between C and M^3 (incl.), CC = rostral width between upper canines (incl.) and M^3M^3 = rostral width between third upper molars (incl.); and forearm length (LAt) in 711 specimens, collected from 101 sites in the western Palaearctic, from Kirghizstan to Portugal (Table 1; for origin of the material see Benda et al. 2006: 300–302 and Benda et al. 2011: 221–222). Most (308 out of 317) Cretan samples were measured by S.K., all other samples were measured by P.B.

The majority of Cretan samples (235 out of 317) are skulls of animals which perished in six roosts (four hibernacula and two others) and they are deposited in the collection of the Natural History Museum of Crete. Most (73 out of 79) of the forearm lengths were obtained from specimens trapped while emerging from 10 roosts, which were released in

Table 1. Origin of the osteological material investigated for cranial and external morphology; subspecies identification after Benda et al. (2009)

country	subspecies	number of collection sites	number of the specimens examined
Afghanistan	*blythii*	4	5
Albania	*oxygnathus*	1	6
Armenia	*omari*	1	1
Azerbaijan	*omari*	1	14
Bulgaria	*oxygnathus*	8	30
Czech Republic	*oxygnathus*	7	10
Greece (Crete)	transient	20	317
Greece (Lesvos)	transient	2	7
Greece (mainland)	*oxygnathus*	5	16
India	*blythii*	3	3
Iran	*omari*	7	45
Kazakhstan	*blythii*	1	12
Kirghizstan	*blythii*	9	102
Lebanon	*omari*	1	2
Portugal	*oxygnathus*	1	1
Romania	*oxygnathus*	2	4
Slovakia	*oxygnathus*	12	91
Spain	*oxygnathus*	4	5
Syria	*omari*	6	19
Tajikistan	*blythii*	2	2
Turkey (Thrace)	*oxygnathus*	2	13
Uzbekistan	*blythii*	2	6
total		101	711

situ immediately after processing. Additionally, nine examined specimens come from collections of the Natural History Museum of Geneva (Switzerland) and the Zoological Institute and Museum Alexander Koenig (Bonn, Germany).

We calculated descriptive statistics (mean, standard deviation, minimum and maximum) for each dimension in each subspecies or population sample. Subsequently, we performed ANOVA (for LaZ, LaN, LaM and LAt) followed by Hochberg's GT2 *post hoc* test to examine whether measurements from Crete are significantly different from any of the comparative samples. When the assumption of homogeneity of variance was violated (LCr), we calculated the Welch F-ratio (F_w) followed by Games-Howell *post hoc* test. In LaI, ANc, CM^3, CC and M^3M^3, the assumption of normal distribution was not satisfied, even after transformation and consequently we performed a Kruskal-Wallis test followed by multiple Mann –Whitney tests with a Bonferroni correction (Field, 2005).

Although the assumptions of parametric tests were violated, we performed a PCA (with a Varimax rotation with Kaiser Normalization) of the cranial measurements, in order to examine whether the Cretan population is separated from the established subspecies of *M. blythii* and the Lesvos population. All statistics were performed using the SPSS v. 15 software.

Results

Descriptive statistics of the obtained measurements (Table 2) showed that although LCr, LaI, LaN and LAt have intermediate mean values in the Cretan population in respect to the comparative samples, LaZ, LaM and ANc are among the largest and comparable to those of *Myotis blythii omari* from the Middle East (Fig. 1). On the contrary, mean values of measurements of the masticatory apparatus (CM^3, CC and M^3M^3) are the smallest of the samples examined.

The overall statistical comparisons are all highly significant (p<0.001, Table 3). All the upper mandible measurements of the Cretan sample had significantly lower means compared to the other samples (except CC in the Lesvos samples). Regarding the remaining cranial measurements, the

Table 2. Descriptive statistics (mean±standard deviation, minimum–maximum, number of samples) of the ten dimensions measured in five compared sample sets. For abbreviations see Material and Methods

dimension	Crete	Lesvos	*M. b. oxygnathus*	*M. b. blythii*	*M. b. omari*
LAt	57.75±1.557 54.7–62.2 79	59.10±1.273 58.2–60 2	57.22±4.229 51.4–63.6 99	57.07±1.882 53.2–61.5 118	59.98±2.114 56–66.7 38
LCr	21.61±0.474 20.12–22.78 158	21.84±0.509 21.08–22.65 7	21.35±0.466 20.15–22.42 173	21.09±0.382 20.2–22.47 128	22.25±0.386 21.43–23.2 80
LaZ	14.24±0.336 13.12–15.12 133	14.01±0.333 13.55–14.41 7	13.66±0.332 12.87–14.36 138	13.61±0.322 12.82–14.37 110	14.28±0.306 13.55–14.83 72
LaI	5.13±0.161 4.68–5.6 222	5.07±0.195 4.74–5.39 7	5.09±0.181 4.65–5.62 175	5.06±0.155 4.7–5.42 130	5.20±0.143 4.86–5.53 80
LaN	9.72±0.208 9.07–10.13 171	9.68±0.212 9.52–10.12 7	9.62±0.215 8.88–10.22 174	9.58±0.191 9.07–10.07 130	9.86±0.232 9.23–10.42 80
LaM	10.37±0.252 9.63–10.98 187	10.27±0.269 9.83–10.53 7	9.97±0.320 9.25–10.57 171	9.94±0.243 9.35–10.92 130	10.30±0.230 9.76–10.75 35
ANc	7.76±0.201 7.13–8.25 173	7.58±0.156 7.38–7.85 7	7.53±0.227 7.05–8.07 168	7.49±0.197 6.95–7.96 125	7.75±0.207 7.28–8.27 79
CM^3	8.62±0.225 8.1–9.23 231	9.00±0.188 8.65–9.22 7	8.79±0.227 8.06–9.37 171	8.73±0.198 8.28–9.32 130	9.33±0.185 8.88–9.75 81
CC	5.59±0.198 5.13–6.1 203	5.66±0.185 5.33–5.89 6	5.67±0.196 4.85–6.22 165	5.67±0.226 4.83–6.13 129	5.94±0.203 5.43–6.43 78
M^3M^3	8.63±0.299 7.75–9.7 217	9.01±0.238 8.73–9.48 7	8.84±0.292 7.54–9.92 174	8.88±0.309 8.08–9.98 130	9.22±0.247 8.43–9.88 81

Table 3. Results of the overall comparisons (ANOVA, Welch Test and Kruskal-Wallis Test) and the post-hoc tests between the samples from Crete and the sample sets of *M. b. oxygnathus*, *M. b. blythii*, *M. b. omari*, and the Lesvos samples. For explanations see text

dimension	overall comparison: test statistic	overall comparison: significance	Crete vs. Lesvos	Crete vs. *M. b. oxygnathus*	Crete vs. *M. b. blythii*	Crete vs. *M. b. omari*
LAt	$F(3, 330) = 11.557$	***	–	ns	ns	***
LCr	$F_w(4, 43.78) = 115.700$	***	ns	***	***	***
LaZ	$F(4, 455) = 99.079$	***	ns	***	***	ns
LaI	$H(4) = 58.567$	***	ns	ns	***	***
LaN	$F(4, 557) = 27.255$	***	ns	***	***	***
LaM	$F(4, 525) = 71.546$	***	ns	***	***	ns
ANc	$H(4) = 182.321$	***	ns	***	***	ns
CM^3	$H(4) = 244.256$	***	***	***	***	***
CC	$H(4) =117.114$	***	ns	***	***	***
M^3M^3	$H(4) =186.040$	***	***	***	***	***

*** = p<0.001; ns = not significant

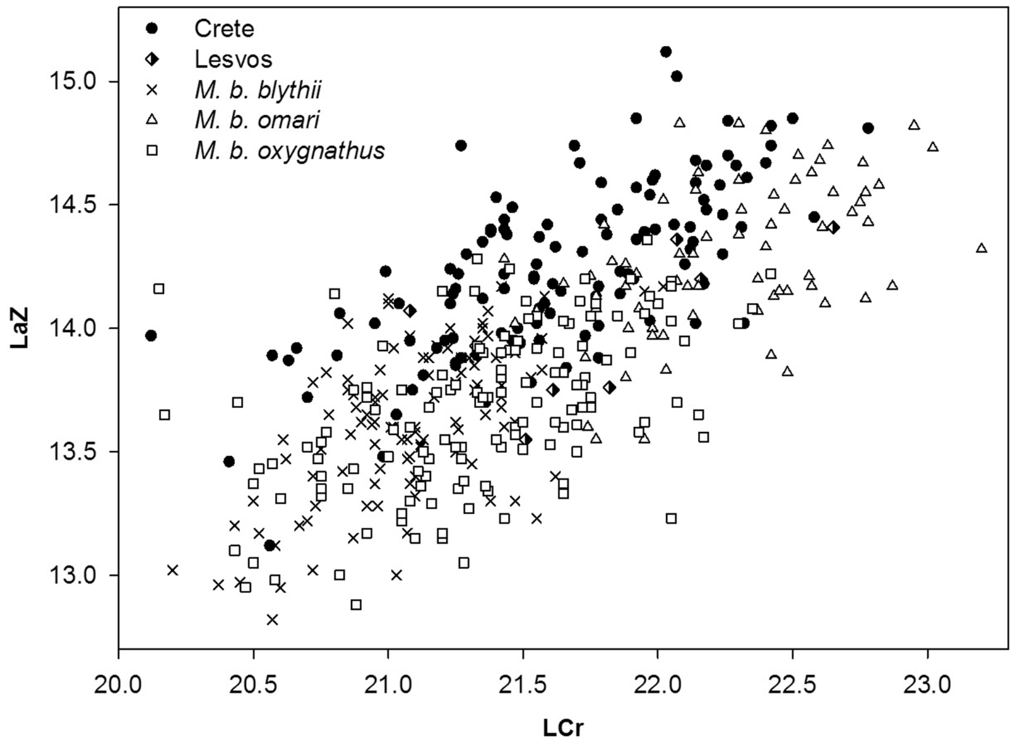

Fig. 1. Bivariate plot of examined Cretan and comparative samples of *Myotis blythii*: greatest length of skull (LCr) against zygomatic breadth (LaZ).

Cretan samples showed significantly higher mean values than *M. b. oxygnathus* (except LaI) and *M. b. blythii*, but significantly lower than *M. b. omari* (except LaZ, LaM and ANc). No significant differences were found between values of the Cretan and Lesvos samples. Finally, the mean forearm length (LAt) of the Cretan samples was significantly lower than that of *M. b. omari*.

Although our data do not conform to the assumptions of the correlation analysis, the Correlation Matrix that resulted from the PCA showed that all correlation coefficients are below 0.9 and most (except one) correlations are significant. Additionally, the KMO statistic exceeded 0.8 and the Bartlett's Test of Sphericity was highly significant (p>0.001). The first factor (component), containing LCr, LaZ, LaI, LaN, LaM, ANc accounted for 39.03% of variation, while the second factor (containing CM^3, CC and M^3M^3) accounted for 27.34% of variation. The Cretan samples were clearly separated, with little overlap, from the compared samples from Europe, Lesvos, Middle East and central Asia (Fig. 2).

Discussion

Iliopoulou-Georgudaki (1977) examined 33 specimens of *M. blythii*, collected from a single locality in central Crete and compared several measurements with those provided by Strelkov (1972) from northern Iran (22 individuals) and a wide part of the *M. b. omari* range (100 individuals). Although she did not perform a proper statistical analysis, comparison of descriptive statistics (mean values, ranges, etc) did not reveal any important differences between the Cretan and the comparative data sets. Our analysis, based on a considerably larger sample series, showed that in many aspects (including dimensions of the maxillae) the Cretan representatives of *M. blythii* are significantly smaller than those of *M. b. omari* (Tables 2, 3). Interestingly, our measurements from Cretan bats and *M. b. omari* also had similar values of the descriptive statistics with those given by Iliopoulou-Georgudaki (1977) and Strelkov (1972) from northern Iran and the Caucasus, respectively. Under the light of these results, the assignment of the Cretan populations of *M. blythii* to *M. b. omari* (Strelkov 1972, Iliopoulou-Georgudaki 1977, 1979) seems to be rather uncertain.

Following Arlettaz et al. (1997) and Castella et al. (2000), Güttinger et al. (2001) suggested possible occurrence of *M. myotis* or *M. punicus* in Crete instead of *M. blythii*, but this opinion is quite speculative and is not justified by our results (see also Benda et al. 2009), since the Cretan samples fall well within the dimensional range of *M. blythii* and several specimens have a white tuff of hair between ears, a typical characteristic of this species (Arlettaz et al. 1991).

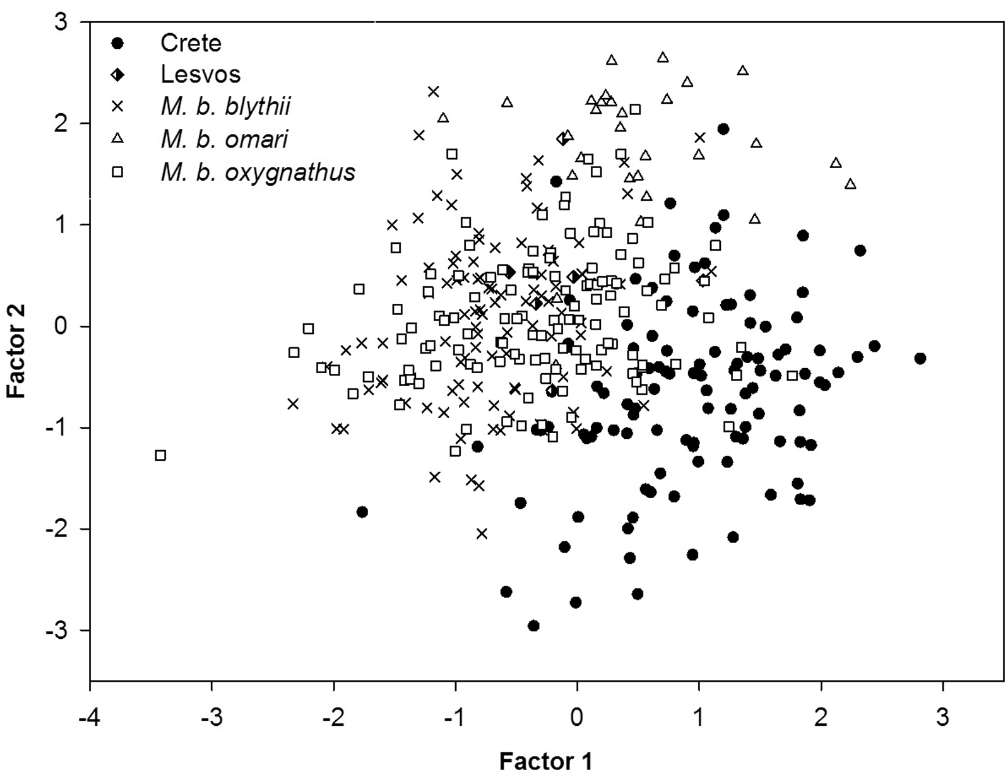

Fig. 2. Bivariate plot based on PCA of examined Cretan and comparative samples of *Myotis blythii*. Factor 1 corresponds to measures of LCr, LaZ, Lal, LaN, LaM and ANc (39.03% of variance) and Factor 2 corresponds to measures of CM^3, CC and M^3M^3 (27.34% of variance).

The statistical comparison with bats of the two smaller-sized subspecies *M. b. oxygnathus* and *M. b. blythii* showed that the Cretan populations have significantly smaller maxillae, but all other skull measurements are larger on Crete (excluding LaI which is not significantly different from *M. b. oxygnathus*; Tables 2, 3). No statistically significant differences were found between the Cretan samples and *M. b. oxygnathus* nor *M. b. blythii*, regarding the forearm length (LAt).

Regarding the comparison of the Cretan and Lesvos samples, only CM^3 and M^3M^3 were found to be significantly smaller on Crete (comparison of forearm lengths was not performed due to the small number of the Lesvos samples). These results contradict the findings by Iliopoulou-Georgudaki (1984) and Benda et al. (2009), a fact that may be due to the small number of individuals examined by the latter authors.

In conclusion, regarding forearm length and several cranial measurements, the Cretan populations of *M. blythii* seem to be intermediate in size between the smaller-sized *M. b. oxygnathus* (and *M. b. blythii*) and the larger-sized *M. b. omari*, and are clearly separated from the comparative samples by the PCA. This position, already stated by Benda et al. (2009) perfectly agrees with the clinal increase of size in *M. blythii* from the western part of the species range (*M. b. oxygnathus* in western Mediterranean) to the east of Iran where *M. b. omari* is replaced by *M. b. blythii* reported by many authors (Harrison & Lewis 1961, Strelkov 1972, Felten et al. 1977, Benda & Horáček 1995b). A similar cline has been also reported in Turkey (Spitzenberger 1996, Aşan & Albayrak 2011), which together with Crete seems to fall in a dimensional transition zone between Europe and the Middle East (Benda et al. 2009).

On the other hand, the significantly smaller maxillary dimensions found in the Cretan populations, compared to the three mainland western Palaearctic subspecies, rises questions regarding the effect of insularity on the feeding ecology of the mouse-eared bats on Crete. Skull shape in bats is associated with feeding behaviour and diet (Van Cakenberghe et al. 2002, Dumont 2007) and many endemic mammal species (including artiodactyls and carnivores) have muzzles specialized to harder food compared to phylogenetically related taxa from the mainland (van der Geer et al. 2010). Unfortunately, no such studies on island bats are available and it is unknown whether the Cretan lesser mouse-eared bats have different diet than those of the mainland. Feeding ecology, geometric morphometric, as well as molecular investigations of the Cretan population are needed in order to fully resolve its taxonomic status.

Acknowledgements

Fieldwork on Crete was supported by the 03ED375 research project, implemented within the framework of the “Reinforcement Programme of Human Research Manpower” (PENED) and co-financed by National and Community Funds (25% from the Greek Ministry of Development – General Secretariat of Research and Technology and 75% from E. E. – European Social Fund). The preparation of the study was also supported by the NAKI project of the Ministry of Culture of the Czech Republic (# DF12P01OVV021). The authors are thankful to many colleagues and friends for joining them in the field. We are also thankful to two anonymous reviewvers for having helped us to improve this article.

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received on 24 November 2012