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# Taxonomy of the genus *Otonycteris* (Chiroptera: Vespertilionidae: Plecotini) as inferred from morphological and mtDNA data

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Two alternative opinions on geographic variation and taxonomy of the genus *Otonycteris* are available in the literature; (1) the genus is rather invariable and includes one monotypic species, or (2) local populations of the genus are rather diverse and create up to five subspecies and/or represent a complex of more species. We analysed a relatively extensive material of *Otonycteris* from all essential parts of its distribution range, using both morphological and molecular genetic approaches to revise taxonomic status of the genus. Results of our analysis suggest rather manifold taxonomic arrangement of the genus. Morphological comparisons of cranial and bacular characters revealed three distinct geographically separated morphotypes in the set of examined bats; (1) in North Africa and in the western part of the Middle East (Levant and Mesopotamia), (2) in the eastern part of the Middle East (E Arabia and Iran) and (3) in Central Asia (incl. NE Iran, Afghanistan and Pakistan). Molecular genetic comparisons of two mitochondrial genes revealed two deeply separated clades differing in uncorrected *p*-distances at > 11.8% (cytochrome *b*) and > 9.3% (ND1), respectively. These clades correspond with two groups of morphotypes, (1+2) and (3), and we therefore regard the respective populations as two separate species, *O. hemprichii* and *O. leucophaea*. Within the species rank of *O. hemprichii* sensu stricto, three sublineages were found, each tentatively considered to be a separate subspecies.

*Key words*: *Otonycteris*, morphology, morphometry, mtDNA, phylogeography, taxonomy

## INTRODUCTION

The plecotine genus *Otonycteris* Peters, 1859 is a Saharo-Sindian faunal element which inhabits arid and semi-arid areas of the central and south-western Palaearctic (Fig. 1 — cf. Gharaibeh and Qumsiyeh, 1995; Simmons, 2005). In Africa, it occurs in Saharan countries from Morocco, southern Algeria and Niger to Egypt and Sudan; the Asian range comprises almost the whole Middle East and Central Asia to Afghanistan and northwestern India (Hayman and Hill, 1971; Corbet, 1978; Nader and Kock, 1983; Horáček, 1991; Bates and Harrison, 1997; Benda *et al*., 2006). *Otonycteris* is a large bat reported to forage in two different ways; very close to the ground or at the height of some 4–8 metres (Horáček, 1991). According to the studies from different parts of its range, its prey includes mainly large ground arthropods, like Coleoptera, Blattodea, Orthoptera, Solpugida, and Scorpionida (Horáček, 1991; Whitaker *et al*., 1994; Arlettaz *et al*., 1995; Fenton *et al*., 1999; Benda *et al*., 2001, 2006).

A single species is currently recognised within the genus, *Otonycteris hemprichii* Peters, 1859 (Koopman, 1993, 1994; Simmons, 2005). However, five subspecies can be found within its rank according to Koopman (1994) and Gharaibeh and Qumsiyeh (1995). The nominotypical form, *O. h. hemprichii*, from the North-African part of the range, was described by Peters (1859) who gave no type locality (TL). Based on the material collected by F. W. Hemprich and C. G. Ehrenberg, Ellerman and Morrison-Scott (1951: 180) suggested "NE Africa" as TL, but Kock (1969: 184) reasonably restricted TL to "the Nile valley between Assuan, Egypt, and Chondek, N-Sudan". *Otonycteris h. leucophaea* (Severcov, 1873) from Turkmenistan to Kirghizstan and India, was described from western Tajikistan; TL: near Djan-Bulak, between Tashkent and Hodjent (= western promontory of the Kuraminskiy Range — see Ognev, 1927; Rossolimo and

Pavlinov, 1979; Pavlinov and Rossolimo, 1987; etc.). *Otonycteris h. petersi* Anderson, 1902 was described from Iraq (TL: Fao, Persian Gulf). Another subspecies *O. h. cinerea* Satunin, 1909 is reported from eastern Iran and Afghanistan, and TL of this form was stated by Satunin (1909: 281) as "Nukendžag, Ge county, Persian Beluchestan". Nevertheless, Ognev (1928: 579) restricted TL of *O. h. cinerea* to "Zirkuh county, near Bamrud, Khorasan" (= Zarakkuh county, near Bamrud, Khorassan, E Iran) and this change was accepted by subsequent authors (Etemad, 1967, 1969; DeBlase, 1980; Baranova *et al*., 1981; Gharaibeh and Qumsiyeh, 1995). Finally, *O. h. jin* Cheesman et Hinton, 1924 from the Levant and Arabia, was described from Hufuf, Hasa, eastern Saudi Arabia.

Besides the above-mentioned forms, which are assigned as subspecies under *O. hemprichii* by recent reviewers (Koopman, 1994; Gharaibeh and Qumsiyeh, 1995), two other names appeared in the *Otonycteris* nomenclature and are currently considered synonyms of the nominotypical form (Kock, 1969). These are *Plecotus ustus* von Heuglin, 1877, which was described from northern Sudan (TL: Batn-el-Hadjar, south of Wadi Halfa — see Fitzinger, 1866; Kock, 1969), and *Plecotus auritus saharae* Laurent, 1936, described from El Golea, northern part of Algerian Sahara. Status of the former description under *Otonycteris* was showed by Anderson (1902), of the latter one by Heim de Balsac (1937).

Most of the forms currently attributed to the species rank of *O. hemprichii* (see Simmons, 2005) were originally described as separate species. *Otonycteris petersi* was regarded by elder authors (Anderson, 1902; Kinnear, 1916; Bianki, 1917; Cheesman and Hinton, 1924; Ognev, 1928) an independent form, smaller than *O. hemprichii*, with shorter ears and tragi, occurring in Lower Mesopotamia. Similarly, most of the older Russian authors (Bobrinskoy, 1925; Ognev, 1928; Kuzyakin, 1950, 1965; Strelkov, 1963; Strelkov *et al*., 1978) regarded the Persian form *O. cinerea* to be separated from Central Asian populations which they assigned to *O. hemprichii*. Cheesman and Hinton (1924) described another species, *O. jin*, on the basis of its larger and denser fur, paler colour, and more inflated auditory bullae. Finally, Ellerman and Morrison-Scott (1951) integrated all described forms of *Otonycteris* into a single species, *O. hemprichii*, with three subspecies (*hemprichii*, *cinerea*, *jin*), however, tagged this opinion with a question mark.

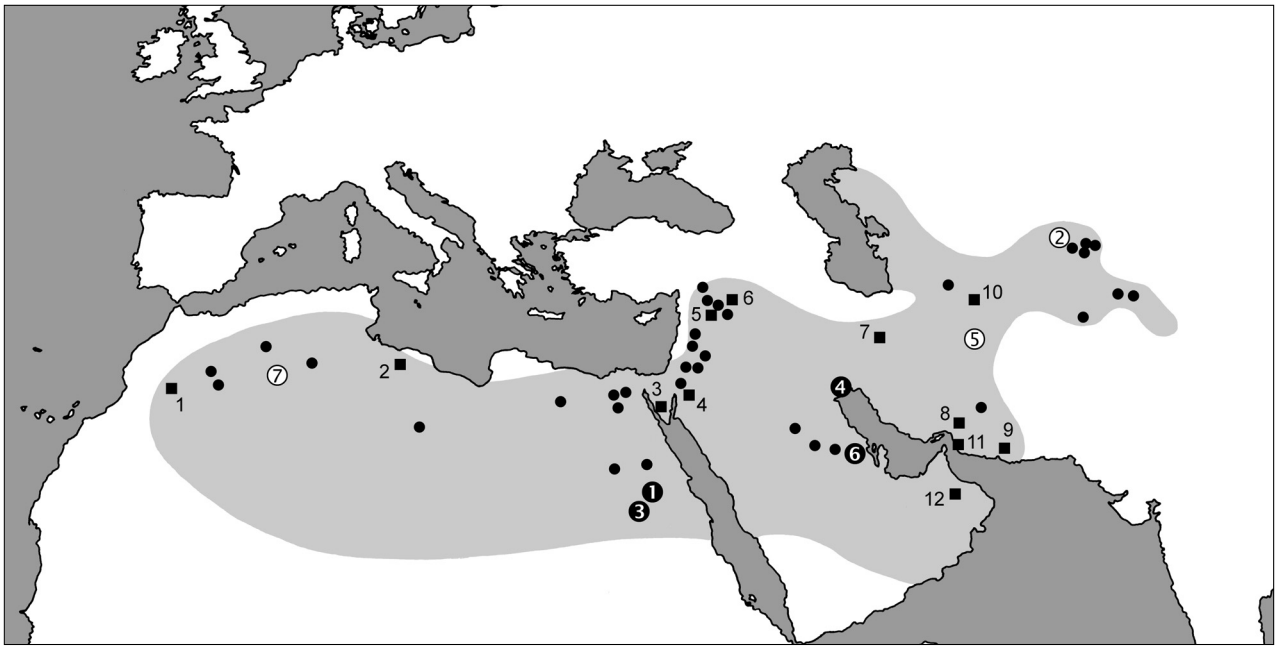


FIG. 1. Map of approximate distribution of the genus *Otonycteris* (after Nader and Kock, 1983; Harrison and Bates, 1991; Horáček, 1991; Bates and Harrison, 1997; and own records) with the sampling sites denoted. Squares indicate morphologic and genetic samples, while dots indicate morphologic samples only. Numbers associated with the squares indicate the sites of origin of the genetically examined material (see Appendix II). Circles with number show type localities of nominal taxa of the genus *Otonycteris*; full circles with white number denote those of type material included in the analysis, open circles with black number those not included. Legend of type localities: 1 — *hemprichii* Peters, 1859; 2 — *leucophaeus* Severcov, 1873; 3 — *ustus* von Heuglin, 1877; 4 — *petersi* Anderson, 1902; 5 — *cinereus* Satunin, 1909; 6 — *jin* Cheesman et Hinton, 1924; 7 — *saharae* Laurent, 1936

On the other hand, Kock (1969) did not detect any subspecies within the whole rank of *O. hemprichii*. Although Corbet (1978: 59) listed five valid subspecies in the species rank (*hemprichii*, *jin*, *petersi*, *leucophaeus*, *cinerea*), he noted: "it seems likely that variation will prove to be continuous throughout the range". According to Nader and Kock (1983), coloration seems inadequate for a subspecies definition and there is no indication that any subspecies could be defined within the rank of *O. hemprichii*. Horáček (1991) carried out a partial analysis of geographic variation in *O. hemprichii*. He found evidence of cline variation in (1) metrical characters: in Arabia the mean dimensions were largest in comparison with both the northwest (smallest in the Maghreb) and the northeast (also smaller in Central Asia); and in (2) pelage coloration (from east to west): the Central Asian specimens were often greyish brown while the Maghrebian specimens were extremely pale. Moreover, he did not find the differences among local populations to be sharp enough to justify their separation into different subspecies. Similarly, Horáček *et al*. (2000) concluded that the geographic variation in *O. hemprichii* is rather clinal and therefore, local populations cannot be considered separate subspecies (see also Simmons, 2005).

To summarise, the following alternative opinions on the geographic variation in *Otonycteris* were available in the literature: (1) the genus is more or less invariable and the differences observed among individual populations are clinal, and the genus includes one monotypic species (Kock, 1969; Horáček, 1991; cf. Corbet, 1978); or (2) local populations of the genus are rather diverse and create up to five subspecies (Harrison, 1956, 1964; Harrison and Bates, 1991; Koopman, 1994; Gharaibeh and Qumsiyeh, 1995) and/or represent a complex of more species (Cheesman and Hinton, 1924; Kuzyakin, 1950; etc.).

Under these assumptions, Benda *et al*. (2006) performed a simple comparison of a set of *Otonycteris* specimens from North Africa and the Middle East. The examined bats fell into two groups: (1) bats with a rather small skull, relatively longer rostrum and a relatively broader braincase, which originated in North Africa and the western part of the Middle East, and (2) specimens with a larger skull but with a relatively shorter rostrum and a relatively narrower braincase coming from Iran. The existence of these clear morphotypes seemed to confirm the categorical variation within the genus (contrary to Horáček, 1991). Hence, Benda *et al*. (2006) suggested two subspecies within the only species of the genus, *O. hemprichii*; in the western part of the range from North Africa to the Syrian Desert *O. h. hemprichii* and in the eastern part of the Middle East *O. h. cinerea*. However, the position of Arabian and Central Asian populations remained unclear. Therefore, the taxonomic status of the whole genus *Otonycteris* appears to be unresolved and poses a challenge for a detailed revision.

Although *Otonycteris* specimens are rather scarce in collections (cf. Gharaibeh and Qumsiyeh, 1995), we conducted a morphological examination of a set of more than a hundred bats from North Africa, Middle East and Central Asia, a portion of these specimens being newly collected during several trips to the Middle East and North Africa (see e.g., Benda *et al*., 2001, 2004*a*, 2006, 2008). Geographically representative subsets of these newly collected bats were also subjected to molecular genetic comparisons. A synthesis of the results from these two approaches is presented here and we propose a new perspective on the intrageneric relations within *Otonycteris*, an enigmatic component of bat taxonomy (cf. Horáček, 1991).

## Material and Methods

### *Analyses*

In the morphological analysis, museum material of *Otonycteris* bats from all parts of the distribution range was used. Primarily cranial data were used for the analyses (see the Abbreviations and Terminology for the dimensions taken), the examined specimens are listed in Appendix I. The skull data on the type specimen of *Plecotus ustus* von Heuglin, 1877 as well as on three additional specimens from North Africa were taken and kindly provided by Prof. Ivan Horáček (CUP, Praha). In the comparison, the type material of the taxa *hemprichii* Peters, 1859, *ustus* von Heuglin, 1877, *petersi* Anderson, 1902, and *jin* Cheesman et Hinton, 1924 was evaluated.

The specimens were measured in a standard way using a mechanical caliper, according to Benda *et al*. (2004*b*). Bacula were extracted in 6% solution of KOH and coloured with alizarin red. Statistical analyses were performed using the Statistica 6.0 software. We performed stepwise discriminant function analysis as a test of importance of particular dimensions for the intrageneric and intraspecific variation. Statistically significant parameters most affecting morphological variation were selected and employed in a subsequent canonical analysis, which was used to test grouping or separation of population samples of similar or different morphotypes, respectively.

For the molecular genetic analysis, total genomic DNA was extracted from tissue samples using the Genomed JetQuick Tissue DNA Spin Kit (Löhne, Germany) and following the manufacturer's protocol. Two mitochondrial (mtDNA) genes, the complete (1,140 bp) cytochrome *b* gene (*Cytb*) and the complete (957 bp) NADH dehydrogenase subunit 1 gene (*ND1*), were amplified, however only a 1,127 bp fragment of *Cytb* was

successfully sequenced in all samples. PCR primers for amplification of *Cytb* (L14724, H15915R) were taken from Irwin *et al*. (1991), and PCR primers and protocol for amplification of *ND1* (ER65, ER66) were taken from Mayer and von Helversen (2001). The thermal profile for amplification of *Cytb* was as follows: initial cycle of denaturation at 94°C for 4 min, 39 subsequent cycles of 94°C for 1 min, 36°C for 30 s and 72°C for 2 min, and a final extension step of 72°C for 10 min. Sequencing was carried out by Macrogen Inc. (Seoul, Korea, http://www.macrogen.com) using a combination of PCR primers and newly developed specific internal primers Locb (5'-AATGAATCTGAGGTGGRTT-3') and Hocb (5'-TTGGRTTRTTAGATCCTGT-3') for *Cytb* and OLinND1 (5'-GAGCATCCAACTCAAAA-3') and OHinND1 (5'-CTC TTGGGTTGTGATTA-3') for *ND1*. Specimens examined in the genetic analysis are listed in Appendix II and the sequences were deposited in GenBank (HM030826–HM030863).

*Pipistrellus abramus* (Temminck, 1838) (AB061528; Nikaido *et al*., 2001) and *Plecotus auritus* (Linnaeus, 1758) sensu lato (AY665169; Tsytsulina *et al*., unpublished data; AB079817, Kawai *et al*., 2002) were used as outgroup species. Four additional sequences of the ND1 gene of *O. hemprichii* from Morocco and Israel (DQ915082–DQ915085; Mayer *et al*., 2007) were taken from GenBank. DNA sequence alignments were performed using BioEdit 7.0 (Hall, 1999) and sequences were examined by translation with the vertebrate mitochondrial genetic code into amino acids using DnaSP 5.00 (Librado and Rozas, 2009). No stop codons were detected. Genetic uncorrected *p*-distances (*p*-dist) and maximum likelihood-corrected distances (*ML*-dist) were estimated using PAUP* 4.0b10 (Swofford, 2003). For the calculation of genetic distances, the alignment of the ND1 gene was shortened (900 bp) according to the length of the four *Otonycteris* sequences from GenBank and two of these sequences were deleted from the alignment, as they were incomplete in their middle section.

Phylogenetic trees were constructed using the maximum likelihood (ML), Bayesian inference (BI) and maximum parsimony (MP) methods. For ML analyses, PhyML 3.0 (Guindon and Gascuel, 2003) was employed using the best-fit model according to the Akaike information criterion (Akaike, 1974) as inferred by jModelTest 0.1.1 (Posada, 2008) (*Cytb*: the transitional model TIM2 + G (Posada, 2003); A = 0.31, C = 0.28, G = 0.12, T = 0.29; AC = AT = 4.89, AG = 38.97, CG = GT = 1.00, CT = 59.77, $\alpha = 0.272$ // and *ND1*: the 3-parameter model TPM2uf+I (Kimura, 1981); A = 0.34, C = 0.27, G = 0.10, T=0.29; AC = AT = 66.69, AG = CT = 1146.80, CG = GT = 1.00, $P_{inv} = 0.567$). A BioNJ tree was used as a starting tree and the following tree-topology search settings were applied: branch swapping = the best of the nearest neighbour interchange and the new subtree pruning and regrafting algorithms (Hordijk and Gascuel, 2005); and optimalisation of the topology and branch lengths. The bootstrap branch support was computed based on 1,000 resampled data sets (Felsenstein, 1985). Bayesian analyses were carried out with MrBayes 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The likelihood settings corresponded to the general time-reversible model (GTR + G and GTR + I + G, respectively; Tavaré, 1986), which is the closest approximation of the TIM and TPM models available in MrBayes. Bayesian analyses were performed with two runs and four chains for each run for six million generations, and sampling every 100th tree. A majority-rule consensus tree was produced from the remaining trees after discarding 20,000 trees as burn-in, and the posterior probabilities were calculated as the frequency of samples recovering any particular clade (Huelsenbeck and Ronquist, 2001). The BI analysis was run three more times in both data sets with random starting trees and the results were compared to assess the convergence by looking at likelihood trends (log-likelihood scores of sampled trees plotted against the generation time). The MP analyses were performed in PAUP* 4.0b10 (Swofford, 2003). All characters were equally weighted and a heuristic search was conducted with 100 random taxon stepwise addition replicates using tree bisection and reconnection branch swapping. The topology was reconstructed as the 50% majority-rule consensus of the equally most-parsimonious trees, and support values were assessed using 1,000 bootstrap pseudoreplicates (Felsenstein, 1985).

## *Abbreviations and Terminology*

**Dimensions** (in mm): LAt = forearm length (incl. wrist); LCr = greatest length of skull; LCb = condylobasal length; LaZ = zygomatic width; LaI = width of interorbital constriction; LaInf = rostral width between infraorbital foramens; LaN = neurocranium width; LaM = mastoidal width; ANc = neurocranium height; ACr = skull height (incl. tympanic bullae); LBT = largest horizontal length of tympanic bulla; CC = rostral width between upper canines (incl.); PP = rostral width between upper premolars (incl.); $M^3M^3$ = rostral width between 3rd upper molars (incl.); $IM^3$ = length of upper tooth-row between incisor and 3rd molar (incl.); $CM^3$ = length of upper tooth-row between canine and 3rd molar (incl.); $PM^3$ = length of upper tooth-row between premolar and 3rd molar (incl.); $M^1M^3$ = length of upper molar-row (incl.); LMd = condylar length of mandible; ACo = height of coronoid process; $I_1M_3$ = length of lower tooth-row between 1st incisor and 3rd molar (incl.); $CM_3$ = length of lower tooth-row between canine and 3rd molar (incl.); $P_4M_3$ = length of lower tooth-row between second (large) premolar ($P_4$) and 3rd molar (incl.); $M_1M_3$ = length of lower molar-row (incl.); $CP_4$ = length of lower tooth-row between canine and 2nd premolar (incl.).

**Collections**: BMNH = Natural History Museum, London, United Kingdom; HZM = Harrison Zoological Museum, Sevenoaks, United Kingdom; ISEA = Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland; IVB = Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Brno, Czech Republic; JOC = Ján Obuch Private Collection, Blatnica, Slovakia; JUST = Department of Biology, Jordan University for Science and Technology, Irbid, Jordan; CUP = Department of Zoology, Charles University, Prague, Czech Repubic; MNHN = National Museum of Natural History, Paris, France; MSNG = Civil Museum of Natural History Giacomo Doria, Genoa, Italy; NMP = National Museum (Natural History), Prague, Czech Republic; SMF = Research Institute and Museum Senckenberg, Frankfurt am Main, Germany; ZFMK = Zoological Institute and Museum Alexander Koenig, Bonn, Germany; ZMB = Zoological Museum, Humboldt University, Berlin, Germany.

**Other abbreviations**: A = alcoholic preparation; B = skin (balg); f = female; m = male; $\bar{x}$ = mean; max, min = range margins; S = skull; SD = standard deviation, Sk = skeleton.

**Geographic terms used** (considering origin of the examined material — see Fig. 1): Arabia = northeastern part of Saudi Arabia and Oman; Central Asia = northeastern Iran (Iranian part of the Karakum Desert), Hindukush and Kirghizstan; Hindukush = Afghanistan, Pakistan and Kashmir; Iran = central, southern and eastern Iran; Levant = the arid parts of southeastern

Turkey, Syria, and Jordan; Maghreb = Morocco, Algeria and western Libya; Middle East = Levant, Mesopotamia, Iran and Arabia; North Africa = Maghreb, Libya and Egypt; Western Middle East = Levant and Mesopotamia; Eastern Middle East = Arabia and Iran.

## Results

Simple comparison of biometric data showed considerable differences among geographic groups of the samples examined (Table 1). On average the largest bats originated in Iran and Arabia, while the smallest ones in the Levant and North Africa (Fig. 2A). Bats from Central Asia were medium in size, however, this group of samples largely differed in skull shape from other compared samples. These bats possessed the relatively and (particularly) absolutely longest rostra (see $CM^3$ and $CM^3$/LCb in Table 1), smallest tympanic bullae (LBT; LBT/LCb), and very low coronoid processes of the mandible (ACo; ACo/LMd). In these dimensions, the group of Central Asian samples mostly did not (absolutely did not in LBT) overlap with other compared sample sets (Figs. 2–4). Central Asian bats were also characterised by relatively narrow neurocrania. However, for this character they broadly overlapped with other samples (Fig. 2C and Table 1).

Among the remaining samples (i.e., from North Africa and the Middle East), the most distinct samples originated in Iran and Arabia. These bats were not only the largest, but also possessed the relatively highest coronoid processes of the mandible and narrowest neurocrania and on average the shortest rostra which were also relatively very narrow (Fig. 2B–C and Table 1). The sets of bats from North Africa and the Levant were similar to each other in most respects, mainly in their skull size and most skull shape characters. From these sets, only that from Egypt slightly differed in zygomatic width, showing relatively similar values to the Iranian bats. On the other hand, in several respects, e.g. in the size of molars and molar-rows as well as rostral widths across molars, the geographic sample sets showed almost no remarkable differences.

Results of multivariate statistic analyses of the skull dimensions and their ratios showed similar relations among the compared geographic sets as shown above. The stepwise discriminant analysis of all skull dimensions selected eight dimensions affecting the interpopulation variation most significantly ($p < 0.05$), viz. LCr, LaZ, LaI, LaN, CC, $IM^3$, $I_1M_3$, and LBT; i.e. the dimensions best describing skull size, length and width of the braincase and rostrum and size of the tympanic bulla. The subsequent canonical analysis (CA) of these eight dimensions divided the geographic sample sets (defined as shown in Fig. 5) into three main groups, corresponding to their geographic origin; (1) bats from North Africa and the Levant, (2) bats from Iran and Arabia, and (3) bats from Central Asia (Fig. 5). The CA absolutely isolated (1st CV 79.06% of variance; 2nd CV 14.34%) the Central Asian bats (1st CV < -3.0) from the Iranian and Arabian samples (1st CV > -0.5; 2nd CV < -1.25) and North African and Levantine bats (1st CV > -1.2; 2nd CV > -1.3). These results divided the samples in a very similar way to that shown in Fig. 2C, which is based on real skull dimensions and their ratios, respectively.

The examined bacula of *Otonycteris* from different parts of the distribution range are very similar in shape (Fig. 6). The bones are simple, dorso-ventrally flattened, crescent-shaped sticks. In the distal direction (baculum length), the bacula were 2.47–3.31 mm long. Slightly differing specimens, originating in northeastern Iran and Kirghizstan, possessed bacula which were absolutely larger (baculum length 3.02–3.31 mm), relatively narrower and in most cases also slightly less curved than bacula from other parts of the range (baculum length 2.47–2.96 mm).

In summary, morphological comparison of *Otonycteris* specimens coming from almost the entire genus range supports existence of three morphotypes which correspond to their geographic origin: (1) the small and medium-sized bats from North Africa and the Levant with relatively wide and short rostra, wide braincases, large tympanic bullae and high coronoid processes of the mandible (Figs. 3A and 4A) and rather small and robust bacula (Fig. 6A–D) (hereafter morphotype 1, M1); (2) the large bats from Iran and Saudi Arabia with relatively narrow and short rostra, narrow braincases, large tympanic bullae and high coronoid processes of the mandible (Figs. 3B–C and 4B–C) and rather small, robust bacula (Fig. 6E and 6J) (M2); and (3) the medium-sized bats from Central Asia with relatively wide and long rostra, medium-wide braincase, small tympanic bullae, and low coronoid processes of the mandible (Figs. 3D and 4D) and rather large and narrow bacula (Fig. 6F–I) (M3). While bats of the M1 and M2 morphotypes differed mainly in the skull size and in the relative width of the skull (i.e., in one common character: elongated skull → relatively narrower braincase and rostrum), the bats of the M3 morphotype differed from the remaining two groups substantially in their skull shape, including size of tympanic bulla, shape of mandible body, and

TABLE 1. Forearm and skull dimensions (in mm) of the examined sample sets of the genus *Otonycteris*. See abbreviations and terminology for explanation of dimension abbreviations

| Variable | Egypt | | | | Maghreb | | | | Western Middle East | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | $\bar{x}$ | min–max | SD | *n* | $\bar{x}$ | min–max | SD | *n* | $\bar{x}$ | min–max | SD |
| LAt | 15 | 61.37 | 58.5–64.0 | 1.489 | 13 | 61.28 | 57.8–66.6 | 2.342 | 27 | 59.15 | 55.1–64.4 | 2.506 |
| LCr | 15 | 22.67 | 21.58–23.59 | 0.557 | 15 | 22.55 | 21.85–23.19 | 0.472 | 27 | 22.27 | 21.07–23.22 | 0.572 |
| LCb | 14 | 21.40 | 20.43–22.22 | 0.492 | 15 | 21.18 | 20.34–22.01 | 0.546 | 27 | 21.19 | 20.16–22.43 | 0.566 |
| LaZ | 15 | 13.95 | 12.95–15.04 | 0.558 | 15 | 14.22 | 13.66–14.74 | 0.385 | 27 | 14.45 | 13.87–15.38 | 0.385 |
| LaI | 15 | 4.01 | 3.76–4.34 | 0.179 | 15 | 4.15 | 3.97–4.32 | 0.109 | 26 | 4.30 | 4.01–4.61 | 0.172 |
| LaInf | 15 | 5.84 | 5.50–6.21 | 0.206 | 15 | 5.85 | 5.57–6.40 | 0.260 | 26 | 5.95 | 5.43–6.62 | 0.284 |
| LaN | 15 | 9.99 | 9.27–10.56 | 0.369 | 15 | 10.32 | 9.88–11.37 | 0.412 | 27 | 10.25 | 9.81–10.76 | 0.253 |
| LaM | 14 | 11.12 | 10.05–11.99 | 0.550 | 14 | 11.46 | 10.98–12.02 | 0.347 | 26 | 11.48 | 10.82–12.14 | 0.342 |
| ANc | 15 | 7.17 | 6.66–7.47 | 0.229 | 15 | 7.12 | 6.76–7.68 | 0.278 | 25 | 7.24 | 6.75–7.91 | 0.242 |
| ACr | 13 | 9.65 | 9.09–10.15 | 0.318 | 15 | 9.62 | 9.05–10.27 | 0.365 | 26 | 9.53 | 8.55–10.37 | 0.389 |
| LBT | 10 | 5.73 | 5.62–5.88 | 0.101 | 13 | 5.81 | 5.41–6.06 | 0.162 | 26 | 5.77 | 5.42–6.11 | 0.168 |
| CC | 15 | 5.84 | 5.33–6.34 | 0.253 | 15 | 5.90 | 5.59–6.30 | 0.203 | 27 | 6.09 | 5.74–6.62 | 0.232 |
| $M^3M^3$ | 15 | 9.34 | 8.30–9.74 | 0.367 | 15 | 9.49 | 9.08–10.02 | 0.222 | 27 | 9.59 | 9.08–10.44 | 0.300 |
| $CM^3$ | 15 | 8.26 | 7.89–8.49 | 0.162 | 15 | 8.12 | 7.76–8.41 | 0.170 | 27 | 8.11 | 7.72–8.65 | 0.241 |
| $M^1M^3$ | 15 | 5.13 | 4.88–5.37 | 0.148 | 15 | 5.18 | 5.00–5.36 | 0.101 | 26 | 5.14 | 4.89–5.41 | 0.151 |
| LMd | 14 | 16.04 | 15.47–16.57 | 0.330 | 15 | 15.94 | 15.21–16.62 | 0.463 | 32 | 15.86 | 14.95–16.71 | 0.443 |
| ACo | 14 | 7.05 | 6.52–7.89 | 0.320 | 15 | 7.07 | 6.48–7.64 | 0.340 | 30 | 6.92 | 6.27–7.45 | 0.313 |
| $CM_3$ | 15 | 9.14 | 8.89–9.31 | 0.136 | 15 | 9.02 | 8.73–9.25 | 0.157 | 26 | 9.08 | 8.67–9.74 | 0.281 |
| $M_1M_3$ | 15 | 6.00 | 5.74–6.23 | 0.137 | 15 | 5.94 | 5.70–6.11 | 0.094 | 25 | 5.95 | 5.61–6.38 | 0.203 |
| LaN/LCb | 14 | 0.469 | 0.452–0.497 | 0.012 | 15 | 0.487 | 0.462–0.544 | 0.023 | 27 | 0.484 | 0.467–0.505 | 0.011 |
| LBT/LCb | 10 | 0.265 | 0.258–0.277 | 0.006 | 13 | 0.273 | 0.266–0.285 | 0.006 | 26 | 0.273 | 0.257–0.293 | 0.009 |
| $CM^3$/LCb | 14 | 0.386 | 0.371–0.400 | 0.009 | 15 | 0.384 | 0.370–0.394 | 0.008 | 27 | 0.383 | 0.368–0.403 | 0.007 |
| LaM/LCr | 14 | 0.490 | 0.456–0.529 | 0.019 | 14 | 0.508 | 0.487–0.522 | 0.010 | 26 | 0.516 | 0.489–0.533 | 0.011 |
| ACo/LMd | 13 | 0.439 | 0.418–0.478 | 0.017 | 15 | 0.443 | 0.422–0.462 | 0.013 | 26 | 0.436 | 0.410–0.463 | 0.013 |

the general shapes of neurocranium and rostrum and their mutual massiveness in the skull forming. Concerning the limited available preparations of bacula, the M1 and M2 morphotypes showed similar baculum shapes and sizes, differing from those of the M3 morphotype.

From 19 specimens of *Otonycteris* which were processed in the molecular phylogenetic analysis, we obtained 19 sequences of *Cytb* as well as of *ND1*. After the acquired *Cytb* sequences were trimmed to 1,127 bp, the resulting partial sequences corresponded to 14 haplotypes. Twenty-three sequences of *ND1* (including four GenBank sequences) produced 18 haplotypes. Within the examined part of *Cytb* gene and including the outgroup, 400 characters were variable and 256 characters were parsimony-informative; while 222 characters were variable and 210 characters were parsimony-informative without the outgroup. Within the complete *ND1* gene, 353 characters were variable and 219 characters were parsimony-informative including the outgroup; while 186 characters were variable and 163 characters were parsimony-informative without the outgroup. The ML phylogeny (see Fig. 7) and all independent BI runs produced essentially identical topologies and similar likelihood estimates in the respective gene (*Cytb*: ML tree with log likelihood (ln*L*) = -4154.7; BI mean ln*L* = -4184.8; *ND1*: ML ln*L* = -3588.3; BI mean ln*L* = -3626.8). The MP analyses yielded most-parsimonious trees with identical topologies of the main clades, and also with respect to the results of ML and BI (*Cytb*: three most-parsimonious trees, length = 609 steps, consistency index, CI = 0.764; retention index, RI = 0.823; *ND1*: 12 most-parsimonious trees, length = 535 steps, CI = 0.764; RI = 0.824). Topologies of the main lineages according to the *Cytb* and *ND1* phylogenies were identical in all independent analyses.

Genetic divergences among the *Otonycteris* haplotypes ranged between 0.3–13.2% (*p*-dist) and 0.3–26.0% (*ML*-dist) in *Cytb* and 0.2–11.7% (*p*-dist) and 0.2–20.0% (*ML*-dist) in *ND1*, respectively (Table 2). The most divergent *Otonycteris* lineage contained a pair of haplotypes from NE Iran (corresponding with the above-defined Central Asian morphotype, M3), which differed from the remaining samples by 11.9–13.2% (*p*-dist) and 21.7–26.0% (*ML*-dist) in *Cytb* and 9.4–11.7% (*p*-dist) and 14.7–20.0% (*ML*-dist) in *ND1*, respectively (Table 2). Within the remaining haplotypes forming a highly statistically supported clade, originating in North Africa and the Middle East, three well separated

TABLE 1. Extended

| Variable | Eastern Middle East | | | | Kirghizstan | | | | NE Iran, Afghanistan and Pakistan | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | x̄ | min–max | SD | *n* | x̄ | min–max | SD | *n* | x̄ | min–max | SD |
| LAt | 17 | 65.29 | 63.5–67.1 | 1.215 | 26 | 61.85 | 58.3–65.5 | 1.937 | 6 | 61.00 | 56.8–65.1 | 2.650 |
| LCr | 16 | 23.61 | 22.87–24.55 | 0.511 | 19 | 22.85 | 21.88–23.59 | 0.446 | 7 | 22.84 | 22.03–23.75 | 0.564 |
| LCb | 17 | 22.16 | 21.36–22.97 | 0.499 | 19 | 21.50 | 20.48–22.10 | 0.445 | 7 | 21.33 | 20.65–22.08 | 0.523 |
| LaZ | 20 | 14.74 | 14.15–15.25 | 0.339 | 19 | 14.81 | 14.45–15.41 | 0.285 | 6 | 15.07 | 14.61–15.56 | 0.364 |
| LaI | 21 | 4.19 | 3.78–4.72 | 0.260 | 19 | 4.43 | 4.17–4.82 | 0.154 | 8 | 4.43 | 4.16–4.61 | 0.175 |
| LaInf | 17 | 6.00 | 5.52–6.48 | 0.305 | 19 | 5.86 | 5.57–6.44 | 0.201 | 7 | 5.98 | 5.63–6.37 | 0.230 |
| LaN | 20 | 10.02 | 9.32–10.42 | 0.276 | 19 | 10.00 | 9.48–10.41 | 0.261 | 7 | 10.08 | 9.48–10.74 | 0.393 |
| LaM | 16 | 11.57 | 11.20–12.02 | 0.264 | 19 | 11.25 | 10.82–11.76 | 0.249 | 6 | 11.30 | 10.62–11.65 | 0.359 |
| ANc | 16 | 7.49 | 7.18–7.86 | 0.192 | 19 | 7.26 | 6.87–7.58 | 0.218 | 7 | 7.18 | 6.27–7.59 | 0.445 |
| ACr | 13 | 9.98 | 9.66–10.35 | 0.235 | 19 | 9.42 | 8.83–9.81 | 0.285 | 6 | 9.44 | 9.20–9.73 | 0.189 |
| LBT | 16 | 5.86 | 5.50–6.35 | 0.246 | 19 | 5.00 | 4.77–5.28 | 0.130 | 7 | 5.12 | 4.82–5.40 | 0.193 |
| CC | 17 | 6.18 | 5.68–6.62 | 0.288 | 19 | 6.31 | 5.92–6.81 | 0.229 | 7 | 6.25 | 6.04–6.38 | 0.128 |
| $M^3M^3$ | 15 | 9.72 | 9.09–10.08 | 0.273 | 19 | 9.62 | 9.22–10.02 | 0.193 | 7 | 9.71 | 9.42–10.14 | 0.249 |
| $CM^3$ | 22 | 8.40 | 8.11–8.82 | 0.199 | 19 | 8.51 | 8.14–8.81 | 0.174 | 8 | 8.50 | 8.29–8.81 | 0.153 |
| $M^1M^3$ | 17 | 5.29 | 5.02–5.56 | 0.157 | 19 | 5.30 | 5.08–5.46 | 0.104 | 7 | 5.41 | 5.27–5.61 | 0.123 |
| LMd | 17 | 16.49 | 15.71–17.08 | 0.331 | 19 | 16.41 | 15.82–16.82 | 0.281 | 8 | 16.37 | 15.79–17.16 | 0.507 |
| ACo | 17 | 7.43 | 6.90–7.83 | 0.227 | 19 | 6.78 | 6.42–7.34 | 0.250 | 7 | 6.73 | 6.48–7.65 | 0.417 |
| $CM_3$ | 16 | 9.49 | 8.92–9.69 | 0.194 | 19 | 9.56 | 9.26–9.88 | 0.184 | 8 | 9.51 | 9.13–9.64 | 0.174 |
| $M^1M_3$ | 16 | 6.20 | 5.67–6.34 | 0.161 | 19 | 6.17 | 5.93–6.34 | 0.128 | 7 | 6.26 | 6.11–6.35 | 0.096 |
| LaN/LCb | 17 | 0.452 | 0.423–0.473 | 0.014 | 19 | 0.466 | 0.433–0.485 | 0.014 | 7 | 0.472 | 0.454–0.488 | 0.012 |
| LBT/LCb | 15 | 0.264 | 0.250–0.279 | 0.009 | 19 | 0.233 | 0.219–0.244 | 0.007 | 7 | 0.240 | 0.230–0.248 | 0.007 |
| $CM^3$/LCb | 17 | 0.379 | 0.366–0.390 | 0.007 | 19 | 0.396 | 0.374–0.411 | 0.008 | 7 | 0.399 | 0.383–0.412 | 0.010 |
| LaM/LCr | 15 | 0.490 | 0.469–0.510 | 0.012 | 19 | 0.492 | 0.480–0.506 | 0.008 | 6 | 0.494 | 0.482–0.504 | 0.009 |
| ACo/LMd | 17 | 0.451 | 0.429–0.464 | 0.011 | 19 | 0.413 | 0.396–0.442 | 0.012 | 7 | 0.413 | 0.400–0.446 | 0.015 |

sublineages were found. The first sublineage from SE Iran was the most distant, differed around 6.3–7.2% (*p*-dist) and 8.5–10.2% (*ML*-dist) in *Cytb* and 6.1–8.1% (*p*-dist) and 8.1–11.7% (*ML*-dist) in *ND1* from the remaining two sublineages from central and southern Iran (second sublineage) and from numerous samples from the Levant and North Africa (third sublineage, corresponding with the above-defined North African/Levantine M1 morphotype). The latter two sublineages differed from each other at 4.3–5.7% (*p*-dist) and 5.5–7.5% (*ML*-dist) in *Cytb* and 4.1–5.7% (*p*-dist) and 4.9–7.3% (*ML*-dist) in *ND1*, respectively (Table 2). Within the Levantine/North African sublineage, a further subdivision to two geographically distinct groups, Maghrebian (Morocco, Libya) and Levantine (Syria, Jordan, Israel and Sinai), may also be detected. All main lineages and sublineages of *Otonycteris* bats were found to be highly statistically supported by ML bootstrap values (≥ 82%), Bayesian posterior probabilities (≥ 0.99) and MP bootstrap values (≥ 83%) (Fig. 7).

## DISCUSSION

### *Phylogeny*

Our analyses uncovered the existence of several phylogroups within the genus *Otonycteris*, challenging the existing taxonomic arrangement of the genus as reported by Horáček *et al*. (2000) and Simmons (2005). Morphological examination of representative set of specimens showed three main, geographically exclusive skull morphotypes in the genus *Otonycteris*; Levantine/North African (M1), Iranian/Arabian (M2), and Central Asian (M3). Molecular genetic analysis revealed two main lineages within *Otonycteris*, Central Asian (based on bats from NE Iran) and North African/Middle Eastern, being deeply separated from each other by genetic distances (*p*-dist) of > 11.9% (*Cytb*) and > 9.4% (*ND1*). Within the North African/Middle Eastern lineage, where relatively good sampling was available, further sublineages were found. The sublineage from SE Iran was the most distant, differing in *p*-dist at 6.3–7.2% (*Cytb*) and 6.1–8.1% (*ND1*) from the remaining two sublineages, central and southern (mountain) Iranian/Omani and Levantine/North African. The latter two sublineages again differed from each other at > 4.0% of *p*-dist in both compared genes.

The Central Asian lineage of *Otonycteris* corresponds with the Central Asian morphotype (M3) and represents a well-defined phylogenetic unit, genetically and morphologically distinct and substantially separated from the remaining populations of the

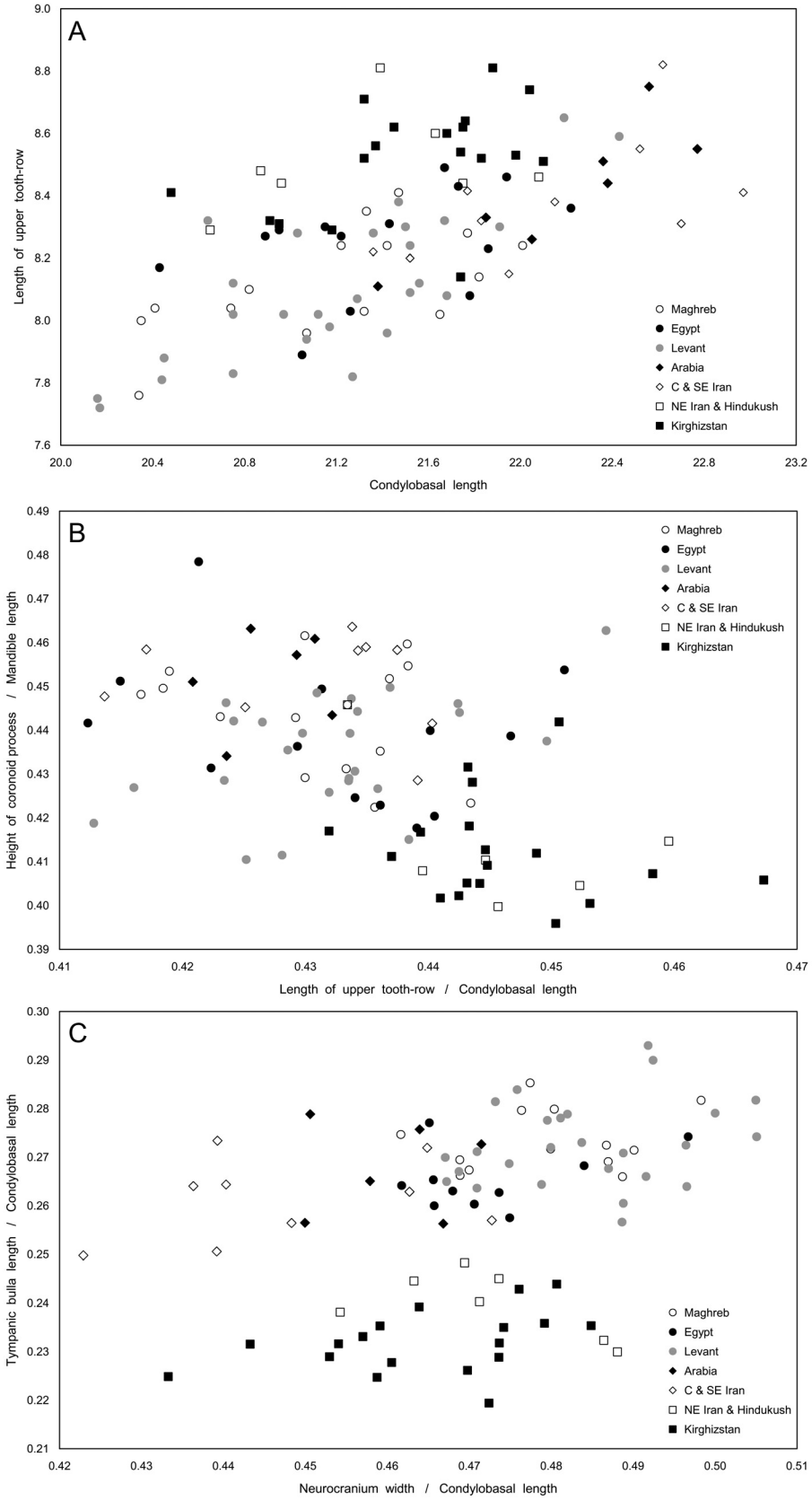


FIG. 2. Bivariate plots of compared *Otonycteris* samples: A — condylobasal length against upper tooth-row ($CM^3$); B — relative length of rostrum (upper tooth-row [$IM^3$] versus condylobasal length) against relative height of the coronoid process (height of the coronoid process versus mandible length); C — relative width of braincase (neurocranium width versus condylobasal length) against relative length of tympanic bulla (length of tympanic bulla versus condylobasal length)

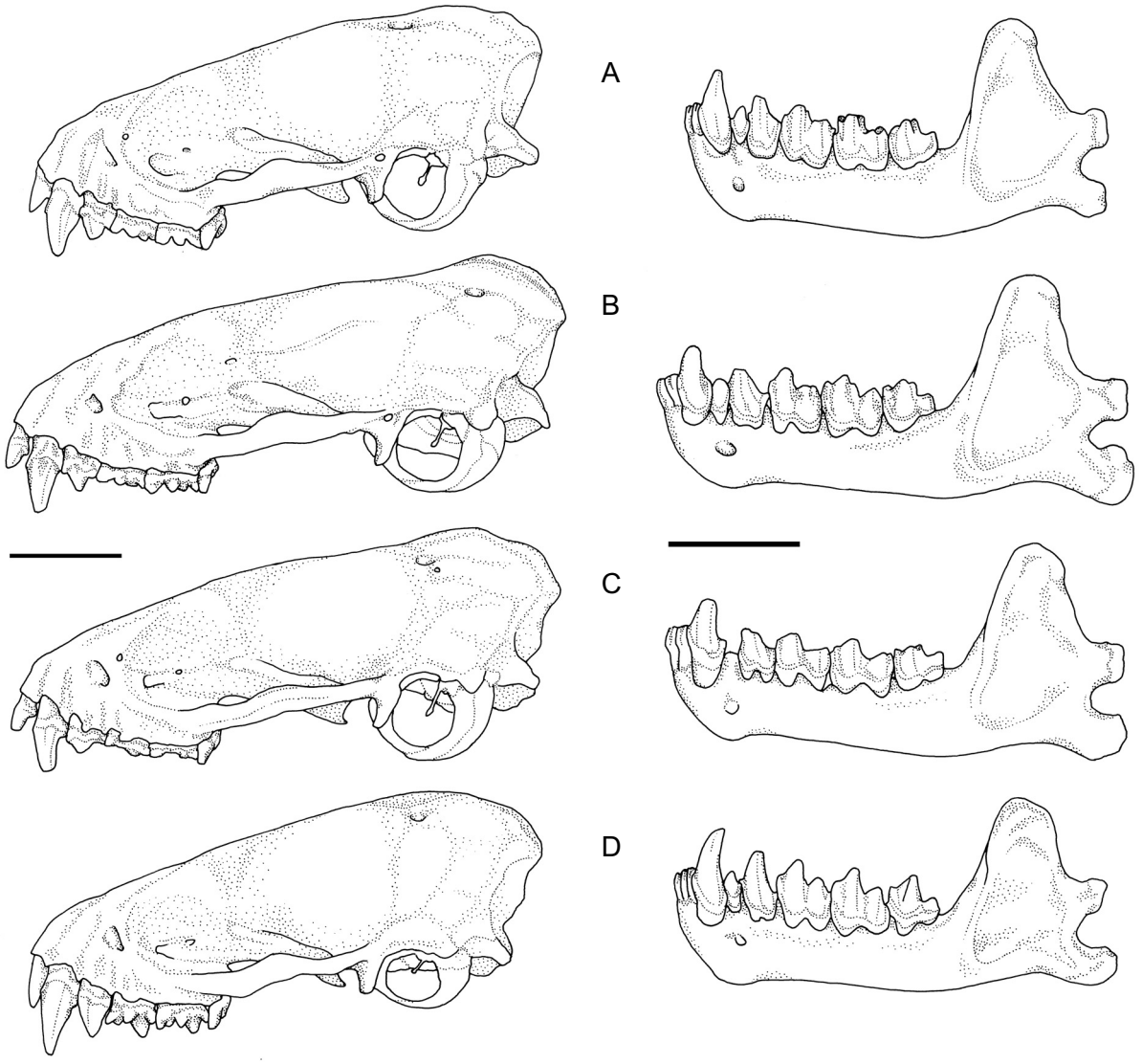


FIG. 3. Skulls and mandibles of the *Otonycteris* bats: A — NMP 91985, El Faiyum, Egypt; B — NMP 48111, Espidan, C Iran; C — NMP 48398, Pir Sohrab, SE Iran; D — NMP 90796, Shurlaq, NE Iran. Note the sizes (both absolute and relative) of the tympanic bulla and the coronoid process of mandible. Scale bars = 5 mm

genus. A similar position was shown for the Levantine/North African sublineage which corresponds to the Levantine/North African morphotype (M1), and thus, also this phylogenetic unit is well defined. However, the positions of the Iranian/Arabian morphotype and both Iranian/Arabian mitochondrial sublineages (central and southern Iranian/Omani and SE Iranian) are rather difficult to interpret. The only morphotype found in these populations (M2) corresponds to two genetically distant sublineages (differing from each other in *p*-dist at around 7% in both examined genes), and therefore cannot be considered as a single phylogenetic unit, but as two divergent units showing similar morphological features.

Within the particular morphotypes/lineages, relatively deep divergences were found. Some of the described distances could be explained by isolation by distance. We speculate that this might apply for the Levantine/North African morphotype/sublineage, where the geographic distance of ca. 1,000–1,500 km seems to correspond to the genetic distance (*p*) of ca. 1%. On the other hand, among bats coming from one site or even from one catch (i.e., from Morocco, Syria and/or Iran) the *p*-distances of up to 0.3% (*Cytb*) and 0.7% (*ND1*), respectively, were observed. This may suggest an ancestral polymorphisms maintained within particular populations which probably survived in isolation in restricted desert regions for a long time and presently co-exist again in relatively restricted subregions. Alternatively, it could suggest an existence of relatively separated populations widespread over severe

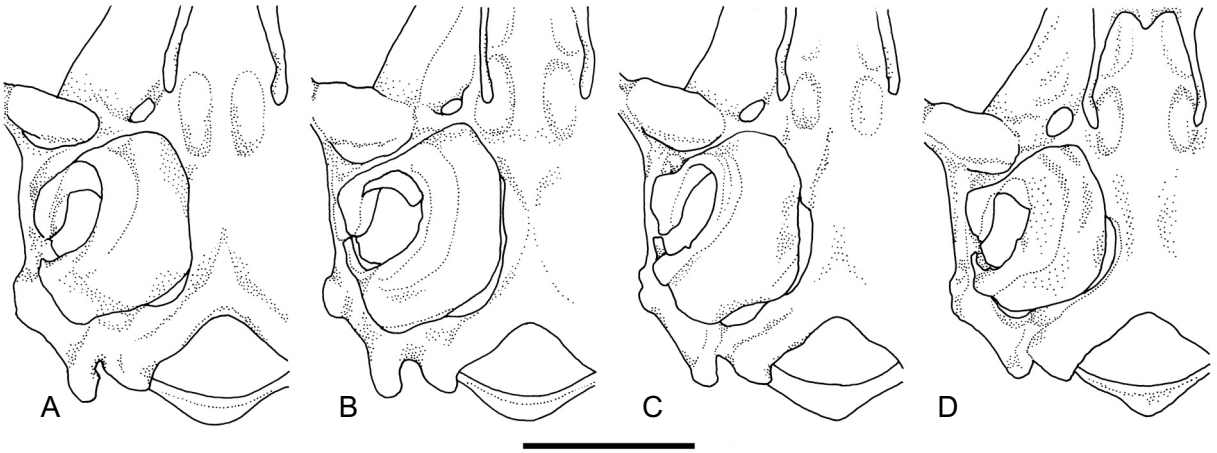


FIG. 4. Right posterior skull bases of the *Otonycteris* bats. For legend see Fig. 5. Note the sizes of tympanic bulla and the sizes and positions of the basioccipital pits. Scale bar = 5 mm

deserts, which meet (rather exceptionally?) at sites with limited sources (water).

A combination of such phenomena (isolation by distance and temporal isolation of maternal lineages) in the desert-dwelling bat genus *Otonycteris* suggests that the interspecific divergences detected in its mtDNA data are much deeper than they were expected e.g., for the Mediterranean arboreal zone bat fauna, where satisfactory distance for interspecific divergence was suggested to be ca. 5% in the ND1 gene by Mayer *et al*. (2007). This arbitrary threshold most probably cannot be applied in the taxonomic assessment of the genus *Otonycteris*, as the evaluation of the available genetic data indicates rather exceptional genetic variation in this genus.

Since all main clades were highly supported and indicated a graduality of splitting events, we suggest a most probable phylogenetic scenario of the genus *Otonycteris* as follows. In the deserts at the border of Central Asia and the Middle East, bats of this genus diverged into two main lineages; populations of the former one occupied deserts and steppes of Central Asia, and populations of the latter one similar habitats of the Middle East. The Central Asian bats retained or evolved small bullae, long rostra and lower mandibular rami, and larger, narrower and slightly less curved bacula, while the Middle

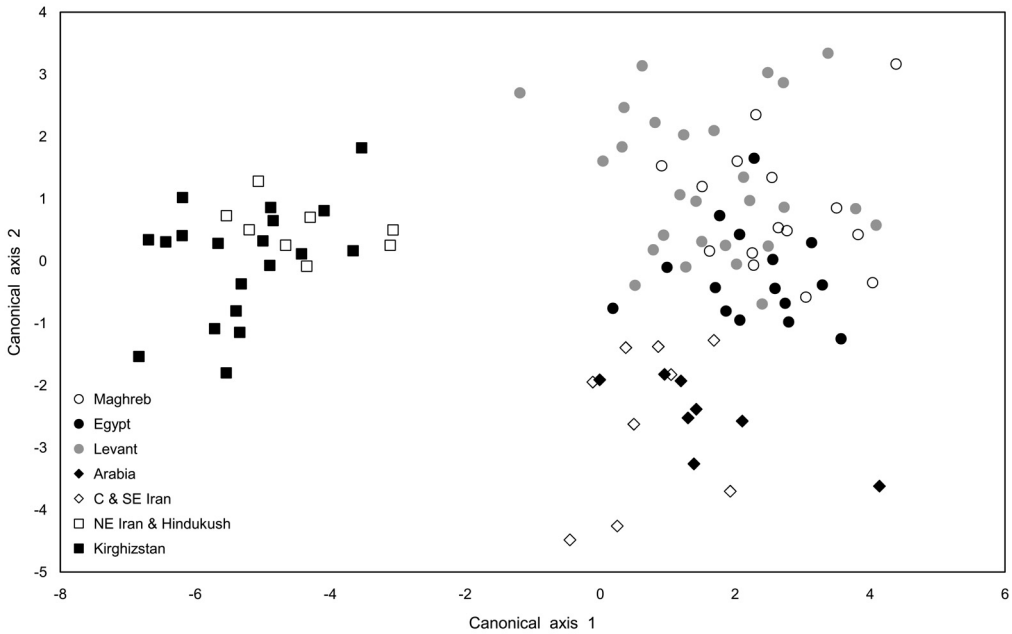


FIG. 5. Bivariate plot of compared *Otonycteris* samples: results of canonical discriminant analysis of selected eight skull dimensions (see the text for details)

Eastern bats larger bullae, short rostra and large mandibular rami, and smaller, broader and more curved bacula. Very similar baculum morphotypes were described also by Fairon (1980) from Niger and Hill and Harrison (1987) and Bates and Harrison (1997) from Saudi Arabia (see Fig. 6). Both of these populations are recently separated in their genetic and morphological characters and could be considered to represent two species. Populations of the Middle Eastern clade (species) were further divided into two groups. One of these consists of the extant populations inhabiting extremely severe lowland deserts of southeastern Iran and possibly also of eastern Arabia. Bat faunas of these two regions share several identical elements which indicate their common history, like *Hypsugo arabicus* (Harrison, 1979), *Rhinopoma muscatellum* Thomas, 1913 and *Triaenops persicus* Dobson, 1871 which are all endemics of southern Iran/Baluchestan and eastern and/or southern Arabia (e.g., Hulva *et al*., 2007; Benda *et al*., 2008; Benda and Vallo, 2009). Two other extant subgroups of *Otonycteris* populations originated in the second Middle Eastern group, which was probably originally situated somewhere north or west of the Persian Gulf. One subgroup recently inhabits bare continental mountainous areas of Iran and Oman. These bats retained the basic morphological characters from the original *Otonycteris* division. The second subgroup spread into an extensive area covering the western part of the Middle East, including Mesopotamia, desert Levant, Sinai, and the whole Sahara from Egypt and Sudan to Niger, southern Algeria and Morocco. Bats of this latter group adapted their skull shape, being small with a relatively broad rostrum and braincase.

However, such phylogeographic pattern as revealed in the genus *Otonycteris* (more structured populations from the Middle Eastern portion and less structured from the African portion of the Saharo-Sindian zone) is present also in other representatives of the desert vertebrate fauna and suggests more common source of this diversity arrangement. Clearly distinct diversity patterns in the above-mentioned two portions of the Palaearctic desert region were indicated also within, e.g., the lizard genera *Trapelus* and *Uromastyx* (see Sindaco and Jeremčenko, 2008 and Wilms *et al*., 2009).

*Taxonomy*

As already discussed, the opinion concerning a single monotypic species within the genus *Otonycteris*, suggested by Kock (1969), Horáček

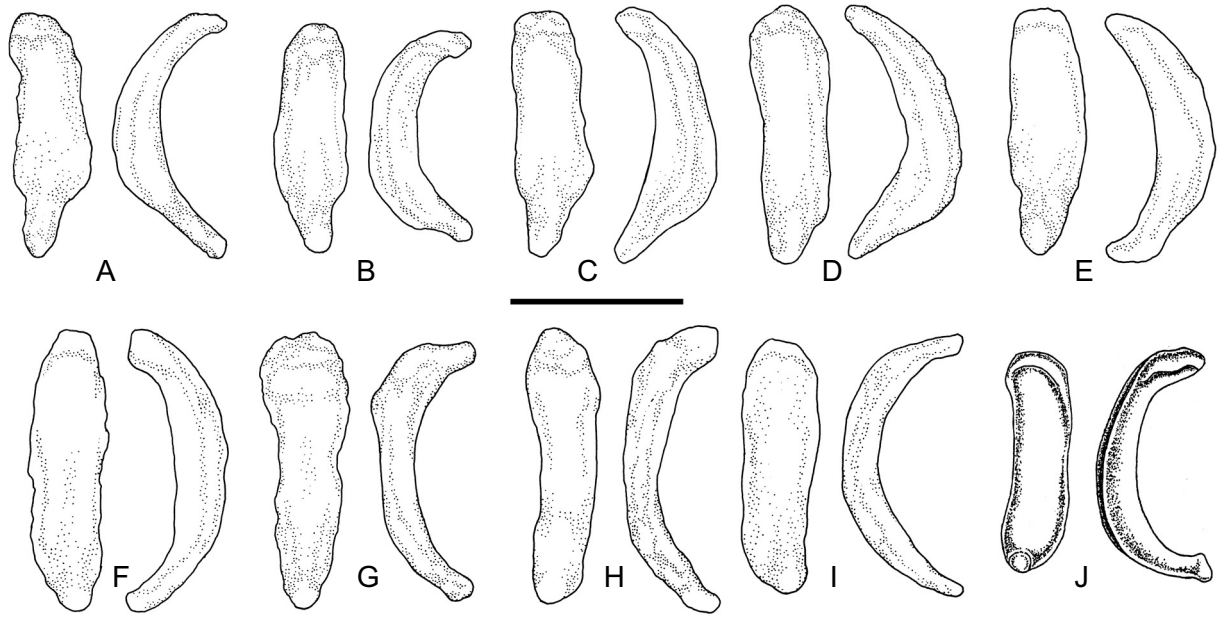


FIG. 6. Baculum views of the *Otonycteris* samples from various parts of the distribution range; A–I — original preparations, J — after Bates and Harrison (1997). Legend: A — NMP 90064, Anagam, Morocco; B — NMP 49964, Nanatalah, Libya; C — NMP 90500, Wadi Feiran, Egypt; D — NMP 48014, Rasafah, Syria; E — NMP 48399, Pir Sohrab, SE Iran; F — NMP 90796, Shurlaq, NE Iran; G — CUP CT84/321, Sasyk Ungur, Kirghizstan; H — CUP CT84/315, Sasyk Ungur, Kirghizstan; I — CUP CT84/264, Aravan, Kirghizstan; J — HZM 6.8174, Saudi Arabia. Left — dorsal views, right lateral views; proximal epiphyses above, distal epiphyses below; scale bar = 2 mm

TABLE 2. Uncorrected *p*-distances (above) and maximum likelihood-corrected distances (below) in percentage among and within the geographic groups of haplotypes found in the genus *Otonycteris*. Results from the *ND1* gene above diagonals, from the *Cytb* gene below diagonals (*Plecotus* = *Plecotus auritus* s.l., outgroup)

| *Cytb**ND1* | Morocco | Libya | Egypt | Israel | Jordan | Syria | C/S Iran and Oman | SE Iran | NE Iran | *Plecotus* |
|---|---|---|---|---|---|---|---|---|---|---|
| *p*-distances (%) | | | | | | | | | | |
| Morocco | 0.3\0.2–0.7 | 1.7–1.9 | 3.5–3.8 | 3.4–3.7 | 3.2–3.6 | 4.0–4.8 | 4.3–5.1 | 6.8–7.6 | 10.9–11.7 | 22.0–22.6 |
| Libya | 1.3–1.4 | – \ – | 3.7 | 3.8 | 3.7 | 4.2–4.7 | 4.2–5.0 | 7.1–7.7 | 10.9–11.1 | 22.4 |
| Egypt | 4.1–4.2 | 3.8 | 0.0\0.0 | 1.5 | 1.3 | 1.9–2.1 | 4.1–4.9 | 7.0–7.6 | 10.1–10.3 | 23.0 |
| Israel | – | – | – | – \ – | 0.3 | 2.0–2.2 | 4.5–5.2 | 6.5–7.0 | 10.3–10.5 | 22.4 |
| Jordan | 4.0–4.1 | 3.7 | 1.9 | – | – \ – | 1.9–2.1 | 4.3–5.1 | 6.6–7.1 | 10.1–10.3 | 22.8 |
| Syria | 4.1–4.2 | 3.8 | 2.0 | – | 1.9 | 0.0\0.0–0.7 | 4.4–5.7 | 7.1–8.1 | 11.0–11.6 | 23.2–23.3 |
| C/S Iran and Oman | 4.3–5.1 | 4.5–5.2 | 5.1–5.7 | – | 5.1–5.2 | 5.3–5.7 | 0.0–0.9\0.0–1.4 | 6.1–6.8 | 9.4–10.1 | 22.9–23.6 |
| SE Iran | 6.7 | 6.3 | 6.6–6.7 | – | 6.3 | 6.5 | 6.7–7.2 | 0.1–0.3\0.3–0.7 | 9.9–10.6 | 21.4–21.8 |
| NE Iran | 12.7–12.9 | 13.1–13.2 | 12.2–12.3 | – | 12.3 | 12.3–12.4 | 12.1–12.6 | 11.9–12.3 | 0.3\0.2 | 21.1–21.3 |
| *Plecotus* | 19.7–20.0 | 19.6 | 19.2 | – | 19.6 | 19.4 | 18.8–19.1 | 19.3–19.5 | 19.3–19.4 | – \ – |
| *ML*-distances (%) | | | | | | | | | | |
| Morocco | 0.3\0.2–0.7 | 1.8–2.1 | 4.1–4.6 | 4.0–4.4 | 3.8–4.2 | 4.8–6.0 | 5.3–6.5 | 9.3–10.7 | 18.3–20.0 | 85.1–88.2 |
| Libya | 1.4–1.5 | – \ – | 4.4 | 4.6 | 4.4 | 5.1–5.8 | 5.2–6.3 | 9.9–10.9 | 18.2–18.7 | 88.1 |
| Egypt | 5.0–5.1 | 4.6 | 0.0\0.0 | 1.6 | 1.4 | 2.1–2.3 | 4.9–6.1 | 9.6–10.6 | 16.3–16.9 | 92.4 |
| Israel | – | – | – | – \ – | 0.3 | 2.2–2.5 | 5.5–6.7 | 8.7–9.7 | 16.7–17.2 | 86.9 |
| Jordan | 4.8–5.0 | 4.5 | 2.0 | – | – \ – | 2.1–2.3 | 5.3–6.4 | 8.8–9.8 | 16.2–16.7 | 89.6 |
| Syria | 5.0–5.1 | 4.7 | 2.2 | – | 2.0 | 0.0\0.0–0.7 | 5.4–7.3 | 9.8–11.7 | 18.2–19.7 | 92.6–94.3 |
| C/S Iran and Oman | 5.5–6.7 | 5.7–6.8 | 6.6–7.5 | – | 6.5–6.7 | 7.0–7.5 | 0.0–0.9\0.0–1.5 | 8.1–9.2 | 14.7–16.2 | 89.8–93.9 |
| SE Iran | 9.2–9.4 | 8.6–8.7 | 9.0–9.3 | – | 8.5–8.6 | 8.9–9.0 | 9.2–10.2 | 0.1–0.3 \ 0.3–0.7 | 15.8–17.5 | 80.5–83.1 |
| NE Iran | 24.0–24.7 | 25.5–26.0 | 22.7 | – | 22.9–23.0 | 23.4–23.5 | 22.4–24.2 | 21.7–23.2 | 0.3\0.2 | 81.1–82.4 |
| *Plecotus* | 62.3–63.7 | 62.6 | 59.3 | – | 61.3 | 61.1 | 58.5–59.8 | 60.2–61.1 | 60.0–61.1 | – \ – |

(1991), and Simmons (2005) is not supported by the results of our analyses. The morphological and genetic analyses clearly separated two groups of populations, which markedly differ in their morphological characters (shape of skull and baculum), and have substantially diverged in the mitochondrial DNA. Since these groups represent two well-separated evolutionary units, we suggest each of these units to represent a separate species. Populations inhabiting North Africa and the Middle East obviously belong to *O. hemprichii* Peters, 1859 sensu stricto (s. str.) described from the Egyptian-Sudanese border area, a geographic centre of that distribution range in the longitudinal sense.

Populations occurring in Central Asia, including southern parts of the Karakum Desert of Turkmenistan and northeastern Iran and severe mountainous parts of Kirghizstan, Afghanistan and Pakistan (presumably also Tajikistan, Kashmir and NW India) belong to a species for which *Plecotus leucophaeus* Severcov, 1873 (Corbet, 1978; Koopman, 1994) is the prior name. Although Severcov (1873: 79) himself doubted his new description, considering it a synomym of *Plecotus auritus* var. *brevimana* Bonaparte, 1837 [= *Plecotus austriacus* (Fischer, 1829)], the name remains available. According to Bobrinskoy (1925), who revised the type specimen, this name comes under synonymy of *Otonycteris* and could be thus applicable to the respective populations; this opinion was broadly accepted by subsequent authors (Ognev, 1927, 1928; Kuzyakin, 1950; Ellerman and Morrison-Scott, 1951; Corbet, 1978; Rossolimo and Pavlinov, 1979; Strelkov *et al*., 1981; Pavlinov and Rossolimo, 1987; Koopman, 1993, 1994; Borisenko and Pavlinov, 1995; Gharaibeh and Qumsiyeh, 1995; Simmons, 2005). Hence, we suggest to apply the name *Otonycteris leucophaea* (Severcov, 1873) for the Central Asian species. The peculiar position of this form was indirectly indicated already by Kuzyakin (1950) who noted tympanic bullae of Central Asian populations to be smaller than those of populations from Iran, a character which we showed to be one of the most remarkable among morphological traits of *O. leucophaea*.

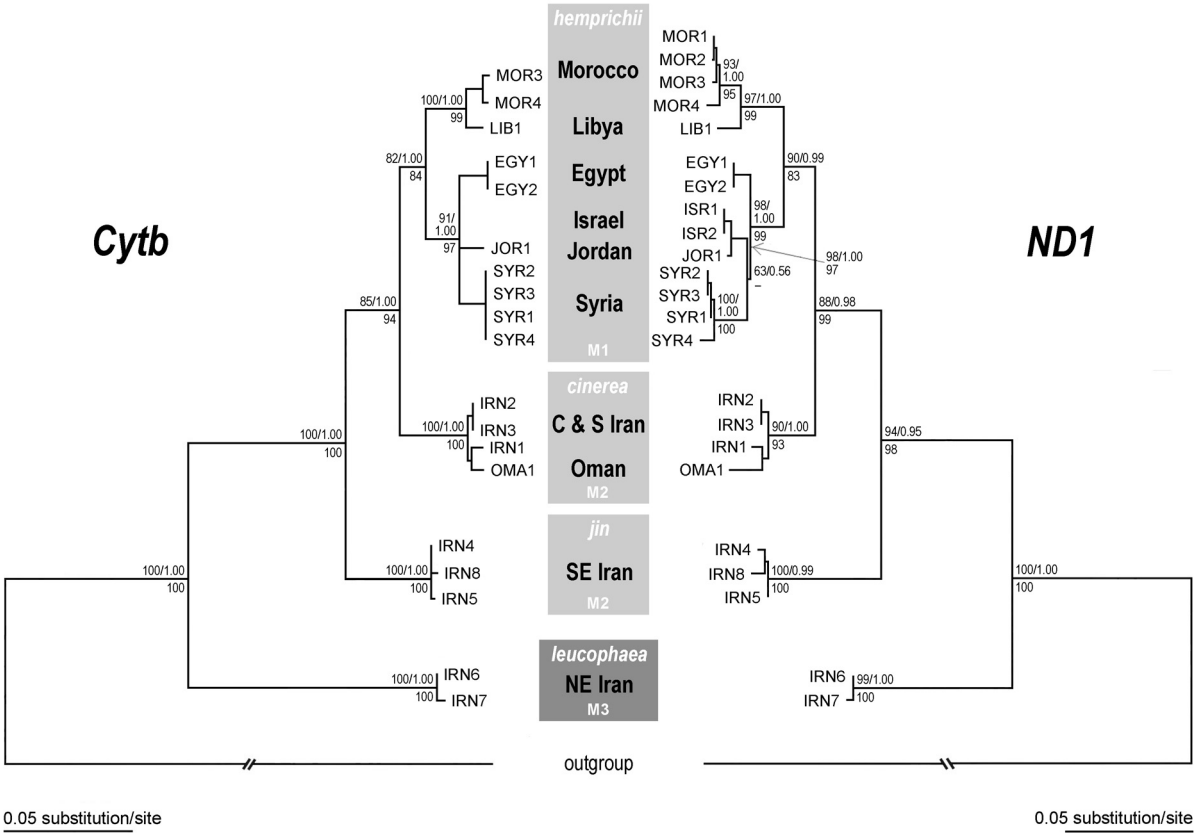


FIG. 7. Maximum likelihood trees of the examined *Otonycteris* samples based on *Cytb* and *ND1* genes. Numbers above the branches are the ML bootstrap support values and Bayesian posterior probabilities, numbers below the branches are the MP bootstrap values. For explanation of the specimen codes see Appendix II. M1, M2, M3 refer to the respective morphotypes as defined in the text

However, Kuzyakin (1950) considered small tympanic bullae to be typical for *O. hemprichii* from North Africa, contra our findings, which showed similar relative LBT in the African (typical) and the Middle Eastern populations.

Within the distribution range of *O. hemprichii* s. str., four species were originally recognised: *O. hemprichii*, *O. petersi*, *O. cinereus* and *O. jin* (Bianki, 1917; Cheesman and Hinton, 1924; Ognev, 1928; Tate, 1942), though their mutual distinctness was mainly due to the geographic separation of their insufficiently known ranges. Mainly because of this ambiguity, all of these forms were integrated into a single species by Ellerman and Morrison-Scott (1951). Although differences among particular forms of this species were not stated accurately, a majority of authors considered the body size and pelage coloration as the most distinct characters (see reviews by Kock, 1969; Horáček, 1991; and Benda *et al*., 2006). A number of taxonomic opinions considering the populations of *O. hemprichii* are thus available from the Middle East, where our comparison revealed considerable variation.

Harrison (1956) mentioned two forms to occur in Arabia, the smaller and darker *O. h. hemprichii* (LAt 57–61 mm) and the larger and paler *O. h. jin* (LAt 64–66 mm). However, Harrison (1964) and Harrison and Bates (1991) regarded most populations from Arabia as belonging to *O. h. jin* (paler pelage coloration and large size; LAt 60.3–69.8 mm; LCr 23.4–26.9 mm) and the northernmost Arabian populations (Syrian Desert, Iraq) to *O. h. petersi* (smaller; LAt 57–60.7 mm; LCr 21.9–23.2 mm). Qumsiyeh (1985) determined the population from continental Egypt to belong to the nominotypic subspecies, but those from Sinai possibly to the larger *O. h. jin*, living also in Arabia and Israel. Corbet and Hill (1992) and Bates and Harrison (1997) considered *O. h. cinerea* to occur in northwestern India and Afghanistan due to the darker colour, longer ears and larger size of the local representatives. On the other hand, in North Africa only one subspecies has been recognised, *O. h. hemprichii* (Kock, 1969; Hayman and Hill, 1971; Corbet, 1978; Qumsiyeh, 1985; Kowalski and Rzebik-Kowalska, 1991; Koopman, 1994). In summary, the *Otonycteris* populations from North Africa and the Middle East, i.e., here revised as *O. hemprichii* s. str., have been divided by various authors up to four subspecies, which all meet in the Middle East.

However, our evidence suggests a rather different view on the intraspecific variance within *O. hemprichii* s. str. The North African and Levantine populations were shown to belong to one morphologically rather uniform type and pertain to one monophyletic clade, while bats from the eastern parts of the Middle East (Iran, Arabia) differ morphologically and belong to two phylogenetically distant forms. Hence, three evolutionary units were found within the species rank of *O. hemprichii* s. str. The most reliable taxonomic arrangement of these units, as a consensus between genetics and morphology, is to regard them as three separate subspecies.

The form occurring in the belt of arid areas along the southern and eastern shore of the Mediterranean Sea from Morocco to Mesopotamia is morphologically most restricted and geographically most widespread and therefore most abundant among our samples. These bats were found to be small throughout their range, having relatively wide braincases and rostra compared to bats from Iran and Arabia. Genetic distances (*p*-dist) in the two examined mitochondrial genes among different geographic sample subsets within this form were found to be between 1.3–4.2% (*Cytb*) and 1.7–4.8% (*ND1*), respectively. Higher values were then found between two distant geographic subsets, Maghrebian and Levantine, suggesting a possible further subdivison of this form. However, since the shortest geographic distance between the regions of origin of the genetic samples is ca. 2,300 km (Tripolitania to Sinai), this genetic divergence may rather indicate the isolation by distance type of differentiation, which does not necessarily affect their close phylogenetic relationships evidenced by a monophyly of the whole North-African/Levantine clade and by its very similar morphology (M1 morphotype).

The Afro-Levantine populations differ by > 4.2% (*Cytb*) and > 4.0% (*ND1*) from the sublineages from the eastern parts of the Middle East. Such a difference well conforms with the subspecies differentiation level recognised in bats (see e.g., Juste *et al*., 2004 for the genus *Plecotus*, considered as closely related, see Simmons, 2005). Because the prior name from the range of the Afro-Levantine form is *Otonycteris Hemprichii* Peters, 1859, the respective population thus belongs to the nominotypical subspecies, *O. h. hemprichii*. The revised populations from Mesopotamia (Turkey, Syria and Iraq) also belong to this form. Since this morphotype was described from Iraqi Mesopotamia as *O. petersi* Anderson, 1902 (see Anderson, 1902; Harrison, 1964; Harrison and Bates, 1991; Benda *et al*., 2006; and this analysis), we regard the latter name a subjective junior synonym of *O. h. hemprichii*. There are two other forms which fall into synonymy of

the nominotypical form, *ustus* von Heuglin, 1877 and *saharae* Laurent, 1936, both described from North Africa. This conforms with the previous opinions (Anderson, 1902; Ellerman and Morrison-Scott, 1951; Corbet, 1978; Qumsiyeh, 1985; Kowalski and Rzebik-Kowalska, 1991; Koopman, 1994; Gharaibeh and Qumsiyeh, 1995).

The large *Otonycteris* forms with relatively narrow braincases and rostra living in Iran and Arabia pertain to two sublineages of *O. hemprichii* s. str. These sublineages (C and S Iranian/Omani and SE Iranian) are genetically substantially distant from the nominotypical form as well as from each other (Table 2) and represent clearly separated evolutionary units as demonstrated by well-supported results of the phylogenetic analyses. However, additional features other than the genetic ones still remain to be found — the available material is too scarce to define any distinctive set of morphological characters. Nevertheless, two names are available from the presumptive range of these two sublineages.

One sublineage was discovered in the mountains of central and southern Iran, provinces of Esfahan and Kerman, in isolated bare areas of blind drainage basins, and rather surprisingly also in the Jabal Akhdar Mts. in NE Oman. Besides the geographic appendix of the Omani mountain range, this range covers two extensive upland deserts (Dasht-e Kavir and Dasht-e Lut) surrounded by the high ranges of the Iranian Plateau, the Zagros Mts. in the south and southwest, the Elborz Mts. and Kopetdag Mts. in the north and the chain of the Khorassan mountains (Kuh-e-Eshger, Kuh-e-Palangan, etc.) in the east. *Otonycteris cinereus* Satunin, 1909 was described from the latter area of eastern Iran (see Ognev, 1928) and, thus, this name as *O. hemprichii cinerea* Satunin, 1909 is applicable for this genetically well defined mountain form. As already noted above, some authors (Corbet and Hill, 1992; Bates and Harrison, 1997) regarded *Otonycteris* populations of northwestern India, Pakistan and Afghanistan to belong to *O. h. cinerea*. However, according to our results of examination of limited available specimens from Afghanistan and Pakistan, these countries are inhabited by *O. leucophaea* rather than by any other form of the genus, in line with the occurrence of other Central Asian forms in this region; e.g., *Myotis blythii blythii* (Tomes, 1857) or *Eptesicus bottae ognevi* Bobrinskoj, 1918 (see Bates and Harrison, 1997). Both latter forms occupy Central Asia from Turkmenistan to Kashmir and are considered taxonomically different from their conspecifics in the Middle East. Thus, *O. h. cinerea* seems to be an endemic of mountainous areas of the Iranian Highlands and eastern Oman.

The set of examined specimens from Saudi Arabia is composed also of the type series of *O. jin* Cheesman et Hinton, 1924. The Saudi Arabian samples showed a close relationship to the Iranian morphotypes and, thus, these two populations from both sides of the Persian Gulf could belong to the same taxon. Hence, we tentatively consider the lowland populations from southeastern Iran and eastern Arabia to represent a subspecies, *O. hemprichii jin*. Since this presumably lowland desert form was found in close parapatry (distance of ca. 150 km in southeastern Iran — Fig. 1) with the mountain subspecies *O. h. cinerea*, from which it substantially differs in genetic traits (see Table 2), the separate species status of *O. h. jin* cannot be rejected.

More extensive sampling in the eastern parts of the *Otonycteris* distribution range is necessary to definitely elucidate the phylogenetic relationships and their taxonomic expressions. However, the position of the taxa, which occur out of the Middle Eastern distribution centre, i.e. *O. h. hemprichii* and *O. leucophaea*, seems to be well founded considering our revision.

## *Conclusion*

In respect to the relations found among the examined populations of *Otonycteris* presented above, we suggest the following revised arrangement of the genus:

*Otonycteris* Peters, 1859

***Otonycteris hemprichii* Peters, 1859**
(North Africa and the Middle East)

*Otonycteris hemprichii hemprichii* Peters, 1859
(North Africa, Levant and Mesopotamia)
Syn. *Otonycteris Hemprichii* Peters, 1859: 223.
Syn. *Plecotus ustus* von Heuglin, 1877: 30.
Syn. *Otonycteris petersi* Anderson, 1902: 120.
Syn. *Plecotus auritus saharae* Laurent, 1936: 409.

*Otonycteris hemprichii cinerea* Satunin, 1909
(mountainous areas of eastern Arabia and Iran)
Syn. *Otonycteris cinereus* Satunin, 1909: 281.

*Otonycteris* (*hemprichii*) *jin*
Cheesman et Hinton, 1924
(lowland deserts of eastern Arabia and southeasternmost Iran)
Syn. *Otonycteris jin* Cheesman et Hinton, 1924: 549.

***Otonycteris leucophaea* (Severcov, 1873)**
(Central Asia)
Syn. *Plecotus leucophaeus* Severcov, 1873: 18, 61.

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## Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19: 716–723.

Anderson, J. 1902. Zoology of Egypt: Mammalia. Revised and completed by W. E. de Winton, F.Z.S. Hugh Rees, Ltd., London, 374 pp.

Arlettaz, R., G. Dändliker, E. Kasybekov, J.-M. Pillet, S. Rybin, and J. Zima. 1995. Feeding habits of the long-eared desert bat, *Otonycteris hemprichi* (Chiroptera: Vespertilionidae). Journal of Mammalogy, 76: 873–876.

Baranova, G. I., A. A. Gureev, and P. P. Strelkov. 1981. Katalog tipovykh ekzemplyarov kollektsiy Zoologicheskogo Instituta AN SSSR. Mlekopitayushchiye (Mammalia). Vypusk 1. Nasekomoyadnyye (Insectivora), rukokrylyye (Chiroptera), zajtseobraznyye (Lagomorpha) [Catalogue of the type specimens in the Collection of the Zoological Institute AS USSR. Mammals (Mammalia). Volume 1. Insectivores (Insectivora), bats (Chiroptera), lagomorphs (Lagomorpha)]. Nauka, Leningrad, 24 pp. [in Russian].

Bates, P. J. J., and D. L. Harrison. 1997. Bats of the Indian Subcontinent. Harrison Zoological Museum, Sevenoaks, 258 pp.

Benda, P., and P. Vallo. 2009. Taxonomic revision of the genus *Triaenops* (Chiroptera) with description of a new species from southern Arabia and definitions of a new genus and tribe. Folia Zoologica, 58 (Monograph 1): 1–45.

Benda, P., J. Obuch, M. Andreas, A. Reiter, and M. Uhrin. 2001. New records of bats from Iran. P. 208, *in* Proceedings of the VIIIth European Bat Research Symposium. Volume II. Distribution, ecology, paleontology and systematics of bats (B. W. Wołoszyn, ed.). Chiropterological Information Center, Institute of Systematics and Evolution of Animals PAS, Kraków, 315 pp.

Benda, P., M. Ruedi, and S. Aulagnier. 2004*a*. New data on the distribution of bats (Chiroptera) in Morocco. Vespertilio, 8: 13–44.

Benda, P., A. Kiefer, V. Hanák, and M. Veith. 2004*b*. Systematic status of African populations of long-eared bats, genus *Plecotus* (Mammalia: Chiroptera). Folia Zoologica, 53 (Monograph 1): 1–47.

Benda, P., M. Andreas, D. Kock, R. K. Lučan, P. Munclinger, P. Nová, J. Obuch, K. Ochman, A. Reiter, M. Uhrin, and D. Weinfurtová. 2006. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 4. Bat fauna of Syria: distribution, systematics, ecology. Acta Societatis Zoologicae Bohemicae, 70: 1–329.

Benda, P., C. Dietz, M. Andreas, J. Hotový, R. K. Lučan, A. Maltby, K. Meakin, J. Truscott, and P. Vallo. 2008. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 6. Bats of Sinai (Egypt) with some taxonomic, ecological and echolocation data on that fauna. Acta Societatis Zoologicae Bohemicae, 72: 1–103.

Bianki [Bianchi], V. 1917. Predvaritel'nyye zametki o letuchikh myshakh (Chiroptera) Rossii [Notes préliminaires sur les chauve-souries ou Chiroptères de la Russie]. Ezhegodnik Zoologicheskogo Muzyeya Akademii Nauk, 21[1916]: 73–82. [in Russian].

Bobrinskoj, N. A. 1918. Zametki o letuchikh myshakh dobytykh v predelakh Bukharskogo khanstva letom 1914 g. [Notes on the bats collected on the territory of the Kingdom of Bukhara in the summer 1914]. Materialy k Poznaniyu Fauny i Flory Rossii, Otdyel Zoologicheskiy, 15: 12. [in Russian].

Bobrinskoy, N. A. 1925. Materialy dlya fauny letuchih myshey Turkestanskogo kraya. (Zapadnyy Turkestan s Semirechenskoy i Zakaspiyskoy oblastyami, Khiva i Bukhara) [Materials on the fauna of bats of Turkestan. (Eastern [sic!] Turkestan with the Regions of Semiretchie and of Transcaspia, Khiva and Bouchara)]. Byulletin Moskovskogo Obshestva Izpytateley Prirody, Otdyel Biologii, N.S., 34: 330–374. [in Russian, with a summary in English].

Bonaparte, C. L. Principe. 1837. Iconografia della fauna italica per le quattro classi degli animali vertebrati. Tomo I. Mammiferi e ucceli. Salviucci, Roma [sine pag.].

Borisenko, A. V., and I. Ya. Pavlinov. 1995. Podotryad Microchiroptera [Sub-Order Microchiroptera]. Pp. 72–120, *in* Mlekopitayushchiye Evrazii. II. Non-Rodentia. Sistematiko-geograficheskiy spravochnik [Mammals of Eurasia. II. Non-Rodentia. Systematical-geographic review] (I. Ya. Pavlinov, A. V. Borisenko, S. V. Kruskop, and E. L. Yakhontov, eds.). Sbornik Trudov Zoologicheskogo Muzyeya MGU, 23: 1–334. [in Russian].

Cheesman, R. E., and M. A. C. Hinton. 1924. On the mammals collected in the Desert of Central Arabia by Major R. E. Cheesman. The Annals and Magazine of Natural History, Series 9, 14: 548–558.

Corbet, G. B. 1978. The mammals of the Palaearctic Region: a taxonomic review. British Museum (Natural History) and Cornell University Press, London, 314 pp.

Corbet, G. B., and J. E. Hill. 1992. The mammals of the Indomalayan region: a systematic review. Oxford University Press, London, 488 pp.

DeBlase, A. F. 1980. The bats of Iran: systematics, distribution, ecology. Fieldiana: Zoology (N.S.), 4: xvii + 424 pp.

Dobson, G. E. 1871. On a new genus and species of Rhinolophidae, with descriptions of a new species of *Vesperus*, and notes on some other species of insectivorous bats from Persia. Proceedings of the Asiatic Society of Bengal, 40: 455–461.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian Mammals 1758 to 1946. British Museum (Natural History), London, 810 pp.

Etemad, E. 1967. Notes on bats from Iran. Mammalia, 31: 275–280.

Etemad, E. 1969. Psiandaran airan – khafašha. Khafašhai [The bats of Iran, and the keys to identify them]. University of

Tehran, Tehran, 201 pp. [in Farsi, with a summary in English, paginted separately, 25 pp.].

Fairon, J. 1980. Deux nouvelles espèces de chéiroptères pour la faune du Massif de l'Air (Niger): *Otonycteris hemprichi* Peters, 1859 et *Pipistrellus nanus* (Peters, 1852). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, 52: 1–7.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution, 39: 783–791.

Fenton, M. B., B. Shalmon, and D. Makin. 1999. Roost switching, foraging behaviour, and diet of the vespertilionid bat, *Otonycteris hemprichii*. Israel Journal of Zoology, 45: 501–506.

Fischer, J. B. 1829. Synopsis mammalium. J. G. Cotta, Stuttgardt, 527 pp.

Fitzinger, L. J. 1866. Systematische Übersicht der Säugethiere Nordost-Afrika's mit Einschluß der arabischen Küste, des rothen Meeres, der Somáli- und Nilquellen-Länder, südwärts bis zum vierten Grade nördlicher Breite. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, I. Abtheilung, Mathematische-Naturwissenschaftliche Classe, 54: 537–611.

Gharaibeh, B. M., and M. B. Qumsiyeh. 1995. Otonycteris hemprichii. Mammalian Species, 514: 1–4.

Guindon, S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology, 52: 696–704.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series, 41: 95–98.

Harrison, D. L. 1956. A key to the identification of the bats (Chiroptera) of the Arabian peninsula. Proceedings of the Zoological Society of London, 127: 447–452.

Harrison, D. L. 1964. The mammals of Arabia. Volume I. Introduction, Insectivora, Chiroptera, Primates. Ernest Benn Ltd., London, 192 pp.

Harrison, D. L. 1979. A new species of pipistrelle bat (*Pipistrellus*: Vespertilionidae) from Oman, Arabia. Mammalia, 43: 573–576.

Harrison, D. L., and P. J. J. Bates. 1991. The mammals of Arabia, 2nd edition. Harrison Zoological Museum, Sevenoaks, 354 pp.

Hayman, R. W., and J. E. Hill. 1971. Part 2. Order Chiroptera. Pp. 1–73, *in* The mammals of Africa. An identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.

Heim de Balsac, H. 1937. *Plecotus auritus saharae* Laurent, 1936, n'est autre que *Otonycteris hemprichii* Peters, 1859. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord, 29: 321–324.

Hill, J. E., and D. L. Harrison. 1987. The baculum in the Vespertilionidae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus. Bulletin of British Museum (Natural History), Zoology, 52(7): 225–305.

Horáček, I. 1991. Enigma of *Otonycteris*: ecology, relationship, classification. Myotis, 29: 17–30.

Horáček, I., V. Hanák, and J. Gaisler. 2000. Bats of the Palearctic region: a taxonomic and biogeographic review. Pp. 11–157, *in* Proceedings of the VIIIth European Bat Research Symposium. Volume I. Approaches to biogeography and ecology of bats (B. W. Wołoszyn, ed.). Chiropterological Information Center, Institute of Systematics and Evolution of Animals PAS, Kraków, 280 pp.

Hordijk, W., and O. Gascuel. 2005. Improving the efficiency of SPR moves in phylogenetic tree search methods based on maximum likelihood. Bioinformatics, 21: 4338–4347.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics, 17: 754–755.

Hulva P., I. Horáček, and P. Benda. 2007. Molecules, morphometrics and new fossils provide an integrated view of the evolutionary history of Rhinopomatidae (Mammalia: Chiroptera). BioMedCentral Evolutionary Biology, 7: 165.

Irwin, D. M., T. D. Kocher, and A. C. Wilson. 1991. Evolution of the cytochrome *b* gene of mammals. Journal of Molecular Evolution, 32: 128–144.

Juste, J., C. Ibáñez, J. Muñoz, D. Trujillo, P. Benda, A. Karataş, and M. Ruedi. 2004. Mitochondrial phylogeography of the long-eared bats (*Plecotus*) in the Mediterranean Palaearctic and Atlantic Islands. Molecular Phylogenetics and Evolution, 31: 1114–1126.

Kawai, K., M. Nikaido, M. Harada, S. Matsumura, L. K. Lin, Y. Wu, M. Hasegawa, and N. Okada. 2002. Intra- and interfamily relationships of Vespertilionidae inferred by various molecular markers including SINE insertion data. Journal of Molecular Evolution, 55: 284–301.

Kimura, M. 1981. Estimation of evolutionary distances between homologous nucleotide sequences. Proceedings of the National Academy of Sciences of the United States of America, 78: 454–458.

Kinnear, N. B. 1916. Notes on the animals (mammals, birds and reptiles) of Mesopotamia. Journal of the Bombay Natural History Society, Special Publication: 1–32.

Kock, D. 1969. Die Fledermaus-Fauna des Sudan (Mammalia, Chiroptera). Abhandlungen der Senckenbergische Naturforschende Gesellschaft, 521: 1–238.

Koopman, K. F. 1993. Order Chiroptera. Pp. 137–241, *in* Mammal species of the World. A taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., 1206 pp.

Koopman, K. F. 1994. Chiroptera: Systematics. Pp. 1–217, *in* Handbuch der Zoologie. Band VIII. Mammalia. Teilband 60 (J. Niethammer, H. Schliemann, and D. Starck, eds.). Walter de Gruyter, Berlin, vii + 224 pp.

Kowalski, K., and B. Rzebik-Kowalska. 1991. Mammals of Algeria. Zakład Narodowy im. Ossolińskich — Wydawnictwo, Kraków, 370 pp.

Kuzyakin, A. P. 1950. Letuchiye myshi (Sistematika, obraz zhizni i pol'za dla sel'skogo i lesnogo khozyaystva) [Bats (Systematics, life history and utility in agriculture and forestry)]. Sovetskaya Nauka, Moskva, 444 pp. [in Russian].

Kuzyakin, A. P. 1965. Otryad Rukokrylye. Ordo Chiroptera [Order Bats. Ordo Chiroptera]. Pp. 79–116, *in* Opredelitel' mlekopitayushchikh SSSR [Key to Identification of mammals of the USSR] (N. A. Bobrinskij, B. A. Kuznecov, and A. P. Kuzyakin, eds.). Prosveshenie, Moskva, 384 pp. [in Russian].

Laurent, P. 1936. Une forme Saharienne du genre *Plecotus*, *P. auritus saharæ* subsp. nov. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord, 27: 408–412.

Librado, P., and J. Rozas. 2009. DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics, 25: 1451–1452.

Mayer, F., and O. von Helversen. 2001. Cryptic diversity in

European bats. Proceedings of the Royal Society of London, 268B: 1825–1832.

Mayer F., C. Dietz, and A. Kiefer. 2007. Molecular species identification boosts bat diversity. Frontiers in Zoology, 4: 4.

Nader, I. A., and D. Kock. 1983. Notes on some bats from the Near East (Mammalia: Chiroptera). Zeitschrift für Säugetierkunde, 48: 1–9.

Nikaido, M., K. Kawai, Y. Cao, M. Harada, S. Tomita, N. Okada, and M. Hasegawa. 2001. Maximum likelihood analysis of the complete mitochondrial genomes of eutherians and a reevaluation of the phylogeny of bats and insectivores. Journal of Molecular Evolution, 53: 508–516.

Ognev, S. I. 1927. A synopsis of the Russian bats. Journal of Mammalogy, 8: 140–157.

Ognev, S. I. 1928. Zveri vostochnoy Evropy i severnoy Azii. Tom I [The Mammals of eastern Europe and northern Asia. Volume I]. Gosudarstvennoe Izdatel'stvo, Moskva-Leningrad, 631 pp. [in Russian].

Pavlinov, I. Ya., and O. L. Rossolimo. 1987. Sistematika mlekopitayushchikh SSSR [Systematics of the mammals of the USSR]. Sbornik Trudov Zoologicheskogo Muzyeya MGU, 25: 1–285. [in Russian].

Peters, W. 1859. Neue Beiträge zur Kenntnis der Chiropteren. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 1859: 222–225.

Posada, D. 2003. Using Modeltest and PAUP* to select a model of nucleotide substitution. Pp. 6.5.1–6.5.14, *in* Current protocols in bioinformatics (A. D. Baxevanis, D. B. Davison, R. D. M. Page, G. A. Petsko, L. D. Stein, and G. D. Stormo, eds.). John Wiley & Sons, New York [sine pag.].

Posada, D. 2008. jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution, 25: 1253–1256.

Qumsiyeh, M. B. 1985. The bats of Egypt. Special Publications, Museum of Texas Tech University, 23: 7–102.

Ronquist, F., and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics, 19: 1572–1574.

Rossolimo, O. L., and I. Ya. Pavlinov. 1979. Katalog tipovykh ekzemplyarov mlekopitayushchikh, khranyayushikhsya v Zoologicheskom muzee MGU [Catalogue of type specimens kept in the Zoological Museum of the Moscow State University]. Sbornik Trudov Zoologicheskogo Muzyeya MGU, 18: 5–43. [in Russian].

Satunin, K. 1909. Materialy k poznaniyu mlekopitayushchikh Kavkazskago kraya i Zakaspiyskoy oblasti, XII–XVI [Materials on the knowledge of mammals of the Caucasus and Transcaspian Regions, XII–XVI]. Izvestiya Kavkazskago Muzyeya (Tiflis), 4: 269–300. [in Russian, with German summary].

Severcov, N. A. 1873. Vertikal'noye i gorizontal'noye raspryedeleniye turkestanskikh zhivotnykh [Vertical and horizontal distribution of the animals of Turkestan]. Izvestiya Imperatorskago Obshestva Lyubiteley Yestestvoznaniya, Antropologii i Etnografii (Moskva), 8(2): 1–157. [in Russian].

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529, *in* Mammal species of the World: a taxonomic and geographic reference, 3rd edition (D. E. Wilson and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore, xxxviii + 2142 pp.

Sindaco, R. and V. K. Jeremčenko. 2008. The reptiles of the Western Palaearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. Edizioni Belvedere, Latina, 579 pp.

Strelkov, P. P. 1963. II. Otryad Chiroptera — Rukokrylye [II. Order Chiroptera — bats]. Pp. 122–218, *in* Mlekopitayushchiye fauny SSSR. Chast' 1 [Mammals of the fauna of the USSR. Part 1] (I. I. Sokolov, ed.). Izdatel'stvo Akademii Nauk SSSR, Moskva, 640 pp. [in Russian].

Strelkov, P. P. 1981. Otryad Chiroptera Blumenbach, 1779 — Rukokrylye [Order Chiroptera Blumenbach, 1779 — Bats]. Pp. 31–53, *in* Katalog mlekopitayushchikh SSSR. Pliocen-Sovremennost' [Catalogue of mammals of the USSR. Pliocene-Recent] (I. M. Gromov and G. I. Baranova, eds.). Nauka, Leningrad, 456 pp. [in Russian].

Strelkov, P. P., V. P. Sosnovceva, and N. V. Babaev. 1978. Letuchiye myshi (Chiroptera) Turkmenii [The bats of Turkmenia]. Trudy Zoologičeskogo Instituta Akademii Nauk SSSR, 79: 3–71. [in Russian].

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland.

Tate, G. H. H. 1942. Results of the Archbold Expeditions. No. 47. Review of the Vespertilionine bats, with special attention to genera and species of the Archbold Collections. Bulletin of the American Museum of Natural History, 80: 221–297.

Tavaré, S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. Pp. 57–86, *in* Some mathematical questions in biology — DNA sequence analysis (R. M. Miura, ed.). American Mathematical Society, Providence, 124 pp.

Thomas, O. 1913. Some new Feræ from Asia and Africa. The Annals and Magazine of Natural History, Series 8, 12: 88–92.

Tomes, R. F. 1857. Descriptions of four undescribed species of bats. Proceedings of the Zoological Society of London, 1857: 50–54.

von Heuglin, T. 1877. Reise in Nordost-Afrika. Schilderungen aus dem Gebiete der Beni Amer und Habab nebst zoologischer Skizzen und einem Führer für Jagdreisende. George Westermann, Braunschweig, 304 pp.

Whitaker, J. O. Jr, B. Shalmon, and T. Kunz. 1994. Food and feeding habits of in insectivorous bats from Israel. Zeitschrift für Säugetierkunde, 59: 74–81.

Wilms, T., W. Böhme, P. Wagner, N. Lutzmann, and A. Schmitz. 2009. On the phylogeny and taxonomy of the genus *Uromastyx* Merrem, 1820 (Reptilia: Squamata: Agamidae: Uromastycinae) — resurrection of the genus *Saara* Gray, 1845. Bonner zoologische Beiträge, 56: 55–99.

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## Appendix 1

List of specimens examined in the morphological analysis

*Otonycteris hemprichii* Peters, 1859

**Algeria**: 1 m, 3 inds. (MUB A494, A495, ISEA 9594, 9595 [S+B]), Abadla, 20 July 1983, leg. J. Gaisler, K. Kowalski and B. Rzebik-Kowalska; — 2 f (ZMB 74754, 74759 [S+A]), Algier, leg. Spatz; — 1 f (ISEA 9593 [S+B]), Benni Abbes, 19 July 1983, leg. K. Kowalski and B. Rzebik-Kowalska; — 1 m (ISEA 9592 [S+B]), Brezina, 31 October 1981, leg. K. Kowalski and B. Rzebik-Kowalska; — 1 m, 1 f (BMNH 19.7.7.1213 [S], MSNG 46325 [A]), Ouargla, 8 April 1880, leg. F. Lataste; — 1 ind. (ISEA 1122 [S]), Algeria (undef.), leg. K. Kowalski and B. Rzebik-Kowalska.

**Egypt**: 1 f, 2 inds. (NMP 91983 [S+A], 91988, 91989 [S+B]), Abu Rawash, 19 July and 18 October 1971, leg. J. Groschaft and B. Ryšavý; — 2 inds. (ZMB 441, 442 [B, S inside]), Ägypten [= the Nile valley between Aswan, Egypt, and Khondek, Sudan], [between September 1821 and 21 July 1822], leg. F. Hemprich and C. Ehrenberg (syntypes of *Otonycteris hemprichii* Peters, 1859); — 4 f (NMP 91984, 91985, 92109 [S+A], 91986 [S+B]), El Faiyum, 25 July 1971, leg. B. Ryšavý; — 1 m (SMF 25268 [S]), nr. Cairo, 1959, leg. E. Kulzer; — 2 m (IVB E251, E252 (S+B]), Kharga Oasis, City of Deads, 6 May 1969, leg. J. Gaisler; — 1 ind. (NMP 92616 [S]), Luksor, Karnak Temple, 28 January 2010, leg. P. Benda and R. Lučan; — 2 f (BMNH 3.12.8.6., 3.12.8.7. [S]), Siwa Oasis, leg. J. Anderson; — 1 m, 1 f (NMP 90495, 90500 [S+A]), Wadi Feiran, Sinai, 8 and 10 September 2005, leg. M. Andreas, P. Benda, J. Hotový and R. Lučan.

**Iran**: 5 inds. (JOC unnumbered [Sk]), 12 km E of Bazangan, ca. 18 km NNW Mazdavand, Khorasan Razni, 10 May 1997, leg. J. Obuch; — 3 f (NMP 48440–48442 [S+A]), Dehbarez, Hormozgan, 17 April 2000, leg. P. Benda and A. Reiter; — 1 f (NMP 48111 [S+A]), Espidan, Esfahan, 3 May 1997, leg. P. Benda and J. Obuch; — 1 ind. (NMP 48376 [S+Sk]), Gegan, Sistan va Beluchestan, 9 April 2000, leg. J. Obuch; — 2 m, 2 f (NMP 48396–48399 [S+A]), Pir Sohrab, Sistan va Beluchestan, 12 April 2000, leg. P. Benda and A. Reiter; — 1 f (NMP 48424 [S+A]), Tujak, Hormozgan, 15 April 2000, leg. P. Benda and A. Reiter.

**Iraq**: 1 f (BMNH 93.6.25.8. [S]), Fao, Persian Gulf, leg. Cumming (holotype of *Otonycteris petersi* Anderson, 1902).

**Jordan**: 2 m (NMP 92467, 92468 [S+A]), Al Ghal, 17 May 2009, leg. P. Benda and A. Reiter; — 1 m (JUST unnumbered [B]), Az Zarqa Hazim, 15 April 2003, leg. M. Abu Baker; — 2 m, 1 f (NMP 92376, 92377 [S+A], 92375 [A]), Qasr Burqu, 14 October 2008, leg. P. Benda and J. Obuch; — 1 m (NMP 92366 [S+A]), Qasr Kharana, 12 October 2008, leg. P. Benda and J. Obuch; — 1 m (NMP 92428 [S+A]), Wadi Ghuweir, at Khirbet Feynan, 13 May 2009, leg. J. Obuch; — 1 m (BMNH 14.8.17.1. [S]), Syrian Desert (?Jordan), leg. J. Aharoni.

**Libya**: 1 f (NMP LI-24 [B]), Brak, Fezzan, leg. A. Elgadi; — 1 m (NMP 49964 [S+A]), Nanatalah, Tripolitania, 28 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin.

**Morocco**: 1 m, 3 f (NMP 90061–90064 [S+A]), 5 km NW of Anagam, Oued Drâa, 31 August 2003, leg. P. Benda.

**Oman**: 1 f (NMP 92667 [S+A]), Al Nakhar, Wadi Ghul, 22 October 2009, leg. P. Benda, A. Reiter and M. Uhrin.

**Saudi Arabia**: 1 m, 1 f (BMNH 40.161. 40.162. [S+B]), Anaiza (Qasim), 10 June 1938, leg. H. St. J. B. Philby; — 1 m (BMNH 40.163. [S+B]), Ha'il, 31 May 1938, leg. H. St. J. B. Philby; — 1 ind. (ZFMK 97.149 [S]), ca. 100 km NE of Riyad, Thumama NP, March–April 1985, leg. J. Szij; — 5 m (BMNH 24.8.2.2., 25.4.3.9.–12. [S+B]), Hufuf, C. Arabia, 6–11 December 1923, leg. R. E. Cheesman (incl. the holotype of *Otonycteris jin* Cheesman et Hinton, 1924).

**Sudan**: 1 ind. (NMW 8604 [S]), Batn el Hajjar, leg. T. von Heuglin (holotype of *Plecotus ustus* von Heuglin, 1877).

**Syria**: 1 m (NMP 48767 [S+A]), Al Ghazli, 11 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; — 4 m (NMP 48827–48830 [S+A]), Ayyash, 19 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; — 1 m (MNHN 1983-1485 [A]), Djéroud (= Jeiroud), 1908, leg. H. Gadeau de Kerville; — 1 f (ZMB 42373 [S+A]), El Karyatein (= Al Qaryatein), leg. B. Aharoni; — 2 m, 1 f (NMP 48815–48817 [S+A]), Khazneh, Jebel 'Abd al 'Aziz, 17 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; — 1 m, 2 inds. (NMP 48812 [S+A], SMF 74083 [2 right mandibles from owl pellets]), Qala'at ar Rahba, 17 May 1989, leg. D. Kock, 17 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; — 3 inds. (SMF 90489–90493; 2 left and 3 right mandibles), Raqqa, September 2000, ded. C. Becker; — 2 m, 5 f (NMP 48007–48010, 48014, 48783, 90283 [S+A]), Rasafah, 16 June 1998, 13 May 2001, 9 October 2004, leg. M. Andreas, P. Benda, R. Lučan, A. Reiter, M. Uhrin and D. Weinfurtová.

**Turkey**: 1 m (ZFMK 72.140 [S+B]), Birecik, 11 May 1972, leg. U. Hirsch.

*Otonycteris leucophaea* (Severcov, 1873)

**Afghanistan**: 1 m (ZFMK 97.148 [S+B], betw. Doshi and Pul-i-Khurmi, 6 September 1964, leg. J. Niethammer.

**Iran**: 4 m (NMP 90793–90796 [S+A]), Shurlaq, Khorasan Razni, 18 May 2006, leg. P. Benda and A. Reiter.

**Kashmir**: 1 ind. (BMNH 78.3.73.1. [S+B]), Gilgit, 5000', July 1876, leg. Capt. J. Biddulph.

**Kirghizstan**: 9 m, 4 f, 1 ind. (CUP CT84/263–266, 268, 270, 271, 273 [S+A], CT84/267 [S], CT84/260–262, 269, 272 [A]), Aravan, Osh, 22 and 23 August 1984, leg. I. Horáček; — 1 m (CUP CK89/14 [A]), Kasan-Saj, Osh, 31 May 1989, leg. I. Horáček; — 1 m (CUP CT84/72 [S+A]), Pobednaja Cave, Osh, 3 August 1984, leg. I. Horáček; — 6 m, 3 f (CUP CT84/315, 316, 318–321 [S+A], SMF 77781 [S], CT84/282, 322 [A]), Sasyk Ungur, Osh, 24 and 25 August 1984, 30 May 1990, leg. I. Horáček and J. Červený; — 2 m, 1 f (CUP CK89/10, SMF 91141 [S+A], CUP CK89/12 [A]), Saryk-Tash, 29 May 1989, leg. I. Horáček.

**Pakistan**: 1 m (BMNH 78.299 [S]), Hastuj River Valley, 6 mi S of Chitral, North Pakistan, 12 August 1976, leg. J. M. Wilson; — 1 ind. (BMNH unnumbered [S]), Pakistan (undef., originated in Quetta Museum), date and collector unlisted.

## Appendix II

List of specimens examined in the molecular genetic analysis, *ND1* and *Cytb* = GenBank Acc. Nos. for the respective genes, Map = locality number as indicated in Fig. 1

| Code | Voucher | *ND1* | *Cytb* | Date | Country | Site/(source) | Map | Coordinates |
|---|---|---|---|---|---|---|---|---|
| MOR 1 | biopsy | DQ915082 | | | Morocco | (Mayer *et al*., 2007) | | |
| MOR 2 | biopsy | DQ915083 | | | Morocco | (Mayer *et al*., 2007) | | |
| MOR 3 | NMP 90061 | HM030845 | HM030826 | 31.8.2003 | Morocco | Oued Drâa, 5 km NE of Anagam | 1 | 30°11'N, 05°35'W |
| MOR 4 | NMP 90064 | HM030846 | HM030827 | 31.8.2003 | Morocco | Oued Drâa, 5 km NE of Anagam | 1 | 30°11'N, 05°35'W |
| LIB 1 | NMP 49964 | HM030847 | HM030828 | 28.5.2002 | Libya | Nanatalah, 10 km W of Ar Rhaybah | 2 | 31°47'N, 11°47'E |
| EGY 1 | NMP 90500 | HM030848 | HM030829 | 10.9.2005 | Egypt | Sinai, Wadi El Feiran | 3 | 28°42'N, 33°40'E |
| EGY 2 | NMP 90495 | HM030849 | HM030830 | 8.9.2005 | Egypt | Sinai, Wadi El Feiran | 3 | 28°43'N, 33°37'E |
| ISR 1 | biopsy | DQ915084 | | | Israel | (Mayer *et al*., 2007) | | |
| ISR 2 | biopsy | DQ915085 | | | Israel | (Mayer *et al*., 2007) | | |
| JOR 1 | NMP 92467 | HM030850 | HM030831 | 17.5.2009 | Jordan | Al Ghal, 55 km E of Aqaba | 4 | 29°31'N, 35°36'E |
| SYR 1 | NMP 48783 | HM030851 | HM030832 | 13.5.2001 | Syria | Rasafah | 5 | 35°38'N, 38°46'E |
| SYR 2 | NMP 48014 | HM030852 | HM030833 | 16.6.1998 | Syria | Rasafah | 5 | 35°38'N, 38°46'E |
| SYR 3 | NMP 48815 | HM030853 | HM030834 | 17.5.2001 | Syria | Khazneh | 6 | 36°27'N, 40°20'E |
| SYR 4 | NMP 48817 | HM030854 | HM030835 | 17.5.2001 | Syria | Khazneh | 6 | 36°27'N, 40°20'E |
| IRN 1 | NMP 48111 | HM030855 | HM030836 | 3.5.1997 | Iran | Espidan, 15 km SE of Natanz | 7 | 33°27'N, 52°02'E |
| IRN 2 | NMP 48440 | HM030856 | HM030837 | 17.4.2000 | Iran | 15 km ENE Dehbarez, ca. 22 km W of Manujan | 8 | 27°28'N, 57°19'E |
| IRN 3 | NMP 48442 | HM030857 | HM030838 | 17.4.2000 | Iran | 15 km ENE Dehbarez, ca. 22 km W of Manujan | 8 | 27°28'N, 57°19'E |
| IRN 4 | NMP 48399 | HM030858 | HM030839 | 12.4.2000 | Iran | Pir Sohrab, ca. 60 km NE of Chabahar | 9 | 25°45'N, 60°50'E |
| IRN 5 | NMP 48396 | HM030859 | HM030840 | 12.4.2000 | Iran | Pir Sohrab, ca. 60 km NE of Chabahar | 9 | 25°45'N, 60°50'E |
| IRN 6 | NMP 90793 | HM030860 | HM030841 | 18.5.2006 | Iran | Shurlaq, ca. 60 km WSW of Sarakhs | 10 | 36°19'N, 60°38'E |
| IRN 7 | NMP 90795 | HM030861 | HM030842 | 18.5.2006 | Iran | Shurlaq, ca. 60 km WSW of Sarakhs | 10 | 36°19'N, 60°38'E |
| IRN 8 | NMP 48424 | HM030862 | HM030843 | 15.4.2000 | Iran | Tujak, ca. 100 km S of Minab | 11 | 26°04'N, 57°18'E |
| OMA 1 | NMP 92667 | HM030863 | HM030844 | 22.10.2009 | Oman | Al Nakhar, Wadi Ghul | 12 | 23°12'N, 57°13'E |