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Systematic position and taxonomy of *Pipistrellus deserti* (Chiroptera: Vespertilionidae)

Abstract: *Pipistrellus deserti* is a small, pale-coloured bat occurring in the most arid parts of the Sahara, in Morocco, Algeria, Libya, Egypt, and the Sudan, and marginally also in sub-Saharan Africa. Although most authors consider *P. deserti* as a full species, others regard it as a subspecies, or even as a junior synonym of *Pipistrellus kuhlii*. We analysed the topotype material of *P. deserti* from Libya using both morphologic and molecular characters, and compared them with samples from other Saharan countries and with *P. kuhlii* from around the Mediterranean. The Libyan samples of *deserti* are morphologically very similar to other populations from arid parts of North Africa (Morocco, Algeria, Egypt, Sudan), but differ markedly in the size of most skull dimensions when compared to *P. kuhlii* sampled in more mesic areas. However, phylogenetic reconstructions indicate that mitochondrial haplotypes of typical *P. deserti* from Libya and those from Morocco do not form a monophyletic group but are fully embedded within the larger radiation of *P. kuhlii* from Africa and Europe, rendering this species paraphyletic. Limited nuclear information (five microsatellite loci) also failed to provide evidence of significant differences between the two morphotypes, as pipistrelles are instead grouped by geographic origin. Altogether, these genetic data suggest that the morphological uniqueness of *P. deserti* may result from recent adaptations to arid habitats, rather than reflect a long independent evolutionary history. In the absence of more compelling evidence of barriers to gene flow, we therefore suggest *Pipistrellus deserti* to be considered a junior synonym of *Vespertilio kuhlii* (= *P. kuhlii*).

Keywords: Africa; cytochrome *b*; microsatellites; morphometry; Sahara.

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Introduction

The Desert pipistrelle, *Pipistrellus deserti*, was described by Thomas (1902: 4) as “a small buff-coloured desert ally of *P. kuhlii*” on the basis of a male obtained from Murzuq, Fezzan, south-western Libya. Thomas differentiated his *P. deserti* from *P. kuhlii* practically only on the basis of smaller size (e.g., a forearm length 29.5 mm or greatest skull length 11.6 mm). For a long time, Thomas' (1902) report remained the only authenticated record of *P. deserti* and represented also the only specimen available for this species (Ellerman and Morrison-Scott 1951). Other old records of *P. deserti* from Kenya and Uganda (Allen 1911, Dollman 1914, De Beaux 1923) are now considered as misidentifications (Hollister 1918, Watson 1951, Gaisler et al. 1972, Koopman 1975).

More recent Saharan records of *Pipistrellus deserti* were reported from Djanet, southern Algeria (Heim de Balsac 1934) and from Wadi Halfa, northern Sudan (Kock 1969), but the first larger series unambiguously attributable to *P. deserti* and comprising 16 specimens was collected by Gaisler et al. (1972) in Luxor, Upper Egypt. Using this relatively extensive material, Gaisler et al. (1972) detailed the external, dental, and bacular characteristics of *P. deserti*. Desert pipistrelles now have been reported from various desert regions of Morocco, Algeria, Libya, Egypt, Sudan, and Somalia, and marginally from more mesic habitats of sub-Saharan Africa in Burkina, Ghana, Nigeria, South Sudan, and possibly Senegal (Koopman et al. 1978, Qumsiyeh 1985, Kowalski and Rzebik-Kowalska 1991, Koopman 1993, 1994, Decher et al. 1997, Benda et al. 2004a, Benda et al. 2010, Van Cakenberghe and Benda 2013).

Since Thomas' (1902) description, *Pipistrellus deserti* has been considered as full species by a majority of authors (Klaptocz 1909, Heim de Balsac 1934, 1936, Zavatari 1934, 1937, Allen 1939, Ellerman and Morrison-Scott 1951, Toschi 1954, Setzer 1957, Kock 1969, 1999, Hayman and Hill 1971, Gaisler et al. 1972, Hufnagl 1972, Koopman

1975, 1993, 1994, Anciaux de Faveaux 1976, Madkour 1977, Jones et al. 1982, Hanák and Elgadi 1984, Qumsiyeh 1985, Gaisler and Kowalski 1986, Hill and Harrison 1987, Le Berre 1990, Kowalski and Rzebik-Kowalska 1991, Nowak 1994, Decher et al. 1997, Grubb et al. 1998, Horáček et al. 2000, Benda et al. 2004a, Simmons 2005, Aulagnier et al. 2008, Grimmberger and Rudloff 2009, Van Cakenberghe and Benda 2013), but some others (Rode 1947, Corbet 1978, Pavlinov et al. 1995, Dalhoumi et al. 2011) regard it as conspecific with the more widespread and essentially Mediterranean species *P. kuhlii* (Kuhl 1817).

Nevertheless, Gaisler et al. (1972), Gaisler and Kowalski (1986), and Kowalski and Rzebik-Kowalska (1991) reported both forms, *Pipistrellus deserti* and *P. kuhlii*, to live in sympatry in the oases of northern Algeria (Taghit). Kock (2001) confirmed again the separation of *P. deserti* and considered that *P. kuhlii* is a Mediterranean and Middle Eastern species reaching the African continent only marginally, along a belt fringing the Atlantic and Mediterranean coasts, and that it does not occur in the Sahara and/or in sub-Saharan Africa. The sub-Saharan populations formerly assigned to *P. kuhlii* are currently classified as a separate species, *P. hesperidus* (Temminck, 1840) (Kock 2001, Simmons 2005).

Qumsiyeh (1985) suggested to use an older name for the Desert pipistrelle, *Vespertilio pipistrellus* β . *Aegyptius* Fischer, 1829, as *Pipistrellus aegyptius* (Fischer, 1829), a form described from Thebes in Upper Egypt (see Geoffroy Saint-Hilaire 1818). However, Qumsiyeh's (1985) proposal was accepted only partly (Koopman 1993, 1994, Nowak 1994, Pavlinov et al. 1995, Decher et al. 1997), whereas several other authors did not adopt this opinion (Hill and Harrison 1987, Le Berre 1990, Kowalski and Rzebik-Kowalska 1991, Grubb et al. 1998). Kowalski and Rzebik-Kowalska (1991) and Kock (1999) suggested that the name *Vespertilio pipistrellus aegyptius* is a *nomen dubium* and therefore unavailable as a taxon name. Although Fischer's (1829) description might include the populations later recognised as *P. deserti* Thomas, 1902 (as well as the name *Pipistrella minuta* Loche, 1867 described from Messad, northern Algeria; see Kowalski and Rzebik-Kowalska 1991). Here we follow Kock's (1999) conclusion in considering *aegyptius* as a name unavailable for a certain species.

During field trips to some Saharan countries (Morocco, Libya, Egypt), we obtained several series of *Pipistrellus deserti* and of *P. kuhlii* (Figure 1; for details on the records see Appendix 1) that include the first recent specimens caught at or very close to the type locality of *P. deserti* in Fezzan (Libya). These specimens provide a unique opportunity to compare this form with other Desert pipistrelles from North Africa (59 specimens) and

with samples of typical *P. kuhlii* from around the Mediterranean (368 specimens). We used qualitative and multivariate analyses of skull, dental, and external characters to compare these samples. A fraction of these specimens were also sequenced for a mitochondrial gene and genotyped for five bi-parentally inherited, nuclear markers to estimate phylogenetic relationships between these two taxa. Finally, we combined these approaches to determine the taxonomic status of *P. deserti* and its relations to *P. kuhlii*.

Materials and methods

Morphological analyses

The museum specimens labelled *Pipistrellus deserti* or *P. kuhlii* from Africa, Europe, and the Middle East listed in Appendix 1 were examined and used in the morphological analyses (427 specimens in total). This comprehensive material includes part of the type specimens concerning the respective group (*deserti* Thomas, 1902, *ikhwanius* Cheesman et Hinton, 1924, *marginatus* Cretzschmar, 1830). Morphological variations of these specimens were first explored on a multivariate space using principal component analyses of skull and dental characters. Maximum factor loadings of variables were also calculated to identify the best discriminating variables. According to these analyses, the samples were then assigned to both morphotypes for further comparisons. Descriptive statistics of each group and multivariate analyses were performed with the Statistica 6.0 software (StatSoft, Inc., Tulsa, Oklahoma, USA). For these morphometric analyses, we primarily took skull, teeth (taken including cingula), and forearm measurements: FA – forearm length (incl. wrist); GLS – greatest length of skull; CBL – condylobasal length; ZB – zygomatic breadth; IC – breadth of interorbital constriction; RBFI – rostral breadth between foramina infraorbitalia; BB – neurocranium (braincase) breadth; MB – mastoidal breadth; BH – neurocranium (braincase) height; CC – rostral breadth between canines (incl.); M³M³ – rostral breadth between third upper molars (incl.); CM³ – length of upper tooth-row between canine and third molar (incl.); M¹M³ – length of upper molar-row (incl.); CP⁴ – length of upper tooth-row between canine and second premolar (incl.); LI¹ – mesio-distal length of first upper incisor; LI² – mesio-distal length of second upper incisor; ML – condylar length of mandible; CH – height of coronoid process; CM₃ – length of lower tooth-row between canine and third molar (incl.); M₁M₃ – length of lower

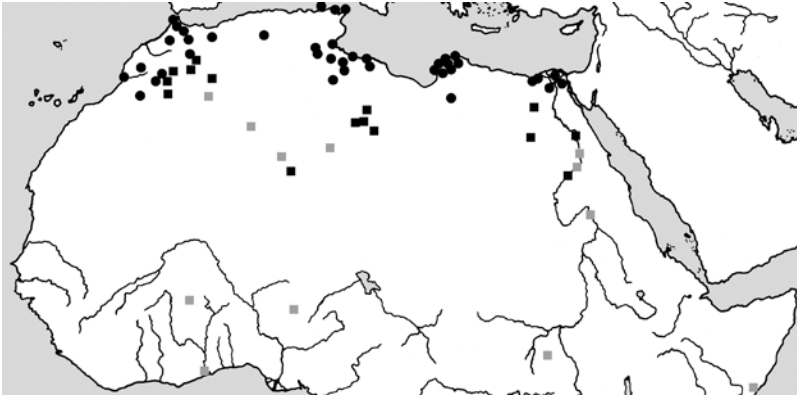


Figure 1 Sites of records of *Pipistrellus deserti* (black squares – origin sites of examined specimens; grey squares – other records; for the records see Appendix 1 and Van Cakenberghe and Benda 2013) and of examined specimens of *Pipistrellus kuhlii* from North Africa (black circles).

molar-row (incl.); CP_4 – length of lower tooth-row between canine and second premolar (incl.). All specimens were measured by the same person (PB) in a standard way using mechanical and optical (for teeth measurements) callipers (see Barlow et al. 1997 and Benda et al. 2004b).

Acronyms of collections housing the specimens examined

BMNH – Natural History Museum, London, United Kingdom; IVB – Institute of Vertebrate Biology, Brno, Czech Republic; MHNG – Natural History Museum, Geneva, Switzerland; MNHN – National Museum of Natural History, Paris, France; MUB – Institute of Botany and Zoology, Masaryk University, Brno, Czech Republic; NMP – National Museum (Natural History), Prague, Czech Republic; NMW – Natural History Museum, Vienna, Austria; SMF – Senckenberg Institute and Museum, Frankfurt am Main, Germany; ZFMK – Zoological Institute and Museum Alexander Koenig, Bonn, Germany.

Genetic analyses

Ethanol-preserved tissue samples of Libyan, Moroccan, Middle Eastern, and European specimens of *Pipistrellus kuhlii*, as well as Libyan and Moroccan specimens of *P. deserti*, were used for the genetic analyses (see Appendix 2). Total genomic DNA was extracted with a standard salting-out protocol as described by Miller et al. (1988) and re-diluted into 100 μ l of pure water. The initial part of the cytochrome *b* gene was then amplified in a PCR reaction using the primer pair L14724 (Kocher et al. 1989) and MVZ16 (Smith

and Patton 1993), and sequenced with an automated DNA sequencer (Applied Biosystems, Life Technologies, Foster City, CA, USA) following standard methods (e.g., Ruedi and Mayer 2001). Sequences were aligned and edited visually using Sequencher 3.0 (Gene Codes Corp., Ann Arbor, MI, USA). All different haplotypes were deposited in GenBank under accession numbers KM252756–KM25277. To determine the phylogenetic position of these taxa relative to other members of the genus *Pipistrellus*, we also used homologous sequences of *P. abramus* (Temminck, 1840), *P. hanaki* Hulva et Benda, 2004, *P. hesperidus* (Temminck, 1840), *P. cf. javanicus* (Gray, 1838), *P. maderensis* Dobson, 1878, *P. nathusii* (Keyserling et Blasius, 1839), *P. pipistrellus* (Schreber, 1774), and *P. pygmaeus* (Leach, 1825), as well as other *P. kuhlii* sequences deposited in GenBank (see Appendix 2 for origins and/or references). The two Asian species (*P. abramus*, *P. cf. javanicus*) were used as a composite outgroup. To estimate levels of DNA sequence divergence, we used the K2P model of correction (K2P distance) that is commonly mentioned for comparative purpose in bat systematics (Bradley and Baker 2001, Ibáñez et al. 2006, Vallo et al. 2013).

To provide a nuclear perspective to the genetic analyses, we also genotyped 12 specimens of *deserti* and 10 specimens of *kuhlii* (see details in Appendix 2) at the following five polymorphic microsatellite loci: EF6 (Vonhof et al. 2002), NN8 (Petri et al. 1997), Paur05 (Burland et al. 1998), L45 (Wei et al. 2009), and Ppip05 (Racey et al. 2007). These loci were amplified in three multiplexed reactions containing a forward primer labelled with fluorescent dyes (see Appendix 3). The amplification was achieved in 10 μ l reaction volume, with 1.2 μ l H_2O , 5 μ l 2 \times Qiagen Multiplex PCR Master Mix[®] (Qiagen, Hilden, Germany), 1 μ l of primer mix (10 μ M of each primer), 2 μ l 5 \times Q-Solution, and 0.8 μ l extracted DNA. The thermal cycling consisted in a

15 min initial denaturation at 95°C, followed by 32 cycles with 40 s denaturation at 94°C, 90 s annealing with a temperature from 55 to 50°C for reaction 1, and 65–60°C for reactions 2 and 3 (the first five cycles consisted in a touch-down with a pitch of 1°C) and 1 min extension at 72°C, followed by a final extension for 30 min at 60°C. Resulting PCR products were run on a Beckman Coulter GeXP Genetic Analysis System and allele callings analysed with the associate software GenomeLab™ (Beckman Coulter, Inc., Brea, CA, USA). Given that the sample size for each locality was too small, no test for Hardy-Weinberg equilibrium was done, but a larger-scale survey of genotypes indicated that no significant deviations or ghost alleles affected these microsatellite loci in *Pipistrellus kuhlii* s.l. (Andriollo and Ruedi, unpublished data). The individual, multilocus genotypes of the essayed pipistrelles were then submitted to a principal component analysis with the program PCA-GEN v1.2 (Goudet 1999). Given that we had low sample sizes, we opted to use this program because it is better suited for exploring individual relationships than the other programs, e.g., methods based on Bayesian clustering that rely on equilibrium models in population genetics. Number of significant components and overall *Fst* values were tested with 15,000 randomisations.

Phylogenetic reconstructions

We used Bayesian (BA) inference and maximum likelihood (ML) methods to reconstruct phylogenetic relationships of mitochondrial sequences. For the BA inference and ML method, the appropriate model of nucleotide substitutions was determined with the program MrModeltest version 2.2 (Nylander 2004). The HKY+I+G model best fitted to the cytochrome *b* data set ($I=0.5488$, gamma distribution with shape parameter $\alpha=2.448$). Bayesian posterior probabilities were calculated using four simultaneous Markov chains run for 1 million generations and trees sampled every 1000 generations, as implemented in the software MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001). After the log-likelihoods of trees reached stationarity, the initial 10% of trees were discarded as burn-in and posterior probabilities were computed from the consensus of the remaining trees. Adequate sampling ($ESS>200$) and stationarity of values were checked with TRACER v1.5 (Rambaut and Drummond 2009). ML analyses were conducted with the program RAxML (Stamatakis 2006) and were done on a fully partitioned model, where each codon partition was allowed to have partition-specific model parameters. Reliability of nodes in the ML analyses was assessed by 1000 bootstraps with RAxML.

Results and discussion

Morphological characters and identification

Bivariate comparison (Figure 2) and the multivariate factor analysis of all skull and dental measurements (Figure 3; 1st PC 64.86%; 2nd PC 5.49%) confirmed that the two morphotypes identified by the collectors segregate in two non-overlapping groups among African samples. The general high factor loadings of most morphological variables on the first principal component indicate that this is a size factor. One of these morphogroups represents all smaller desert forms of pipistrelles, including the type specimen of *Pipistrellus deserti* Thomas, 1902 from Libya (Table 1), whereas most of the larger bats correspond to the *P. kuhlii* sampled elsewhere in the more mesic parts of North Africa. The latter group also includes the type specimen of *Vespertilio marginatus* Cretzschmar, 1830 from Egypt. These North African *P. kuhlii* specimens show a similar morphology and comparable skull and dental variation as the samples of *P. kuhlii* from Europe and the Middle East (Table 2). In particular, most external and cranial measurements of the type specimen of *P. deserti* from Murzuq, Fezzan, Libya (male, BMNH 2.11.4.1.) fit well into the size variation of our recent sample of 16 specimens of *P. deserti* collected from four localities in the same region (Table 1). Exceptions include the mandible length (which is slightly smaller) and length of the second upper incisor, I^2 (which is slightly larger). In comparison with samples of typical *P. kuhlii* from the Mediterranean (North Africa, Europe, Middle East), skull dimensions of all south Libyan samples form a separate group without overlap in the larger skull dimensions (GLS, CBL, ZB, MB, ML; Table 2, Figure 2). Other samples from the Sahara, identified as *P. deserti* by their collectors (Kock 1969, Gaisler et al. 1972, Kowalski and Rzebik-Kowalska 1991, Benda et al. 2004a; cf. Appendix 1), also fit well into the variation range of dimensions reported here for the Libyan Desert pipistrelles, which confirms their original morphotype assignation (Figures 2 and 3). The examined samples from northern Sudan (Wadi Halfa) lies on the lower margin of a cluster composed of *P. deserti* from Libya, Egypt, Algeria, and Morocco. As a general observation, most skull and dental dimensions illustrate discrete size differences between the smaller *P. deserti* and the larger *P. kuhlii* from the Mediterranean (Figures 2 and 3, and Table 3).

Qumsiyeh (1985) proposed the greatest length of skull (GLS) as a discriminant criterion for Egyptian populations, where GLS is longer than 12.0 mm in *Pipistrellus kuhlii* and shorter than 12.0 mm in *P. deserti*. Our extensive

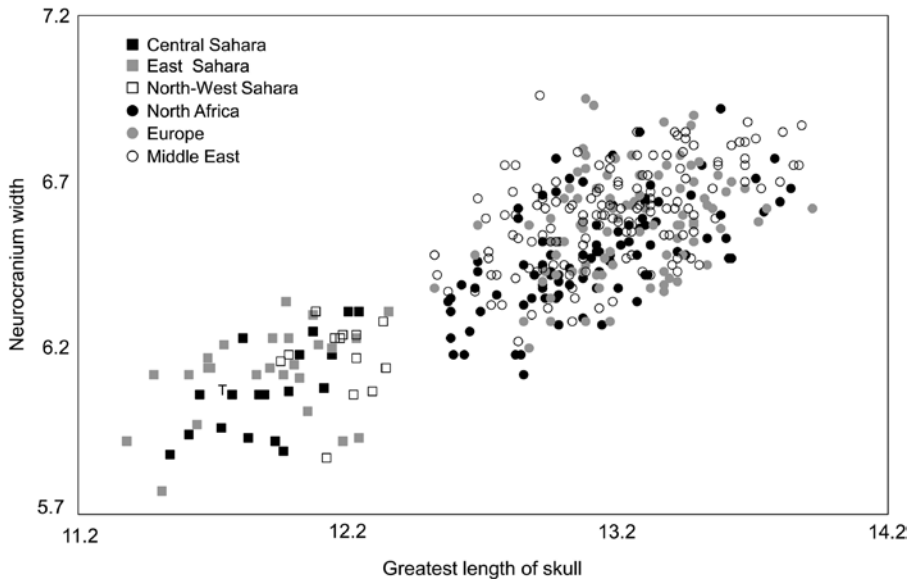


Figure 2 Bivariate plot of *Pipistrellus kuhlii* from the Sahara, North Africa, and the Mediterranean: the greatest length of skull against the neurocranium breadth (both in millimetres). Squares denote the *deserti* morphotype, circles the *kuhlii* morphotype. Legend: Central Sahara=south-western Libya (Fezzan) and south-eastern Algeria (Hoggar Mountains.); East Sahara=Upper Egypt and northern Sudan; North-West Sahara=north-western Algeria and south-eastern Morocco; North Africa=Tunisia and the Mediterranean parts of Morocco, Algeria, Libya, and Egypt; T=holotype specimen of *Pipistrellus deserti* Thomas, 1902.

material (including the Egyptian samples) suggests that this discriminant limit lies rather around 12.4–12.5 mm. According to this single criterion, bats with GLS smaller than 12.4 mm would all come from the drier parts of the Sahara and group with the topotype material of the Desert pipistrelles from Libya, whereas bats with GLS larger than 12.5 mm group with the Mediterranean *P. kuhlii* (see

Figure 2). Qumsiyeh (1985) and Kowalski and Rzebik-Kowalska (1991) mentioned also the length of the upper tooth-row (CM^3) as another discriminant character, where specimens with CM^3 shorter than 4.5 mm were regarded as typical *P. deserti*, whereas larger bats were recognised as *P. kuhlii*. In the material examined here, the largest *P. deserti* identified in the multivariate analysis showed a CM^3 of

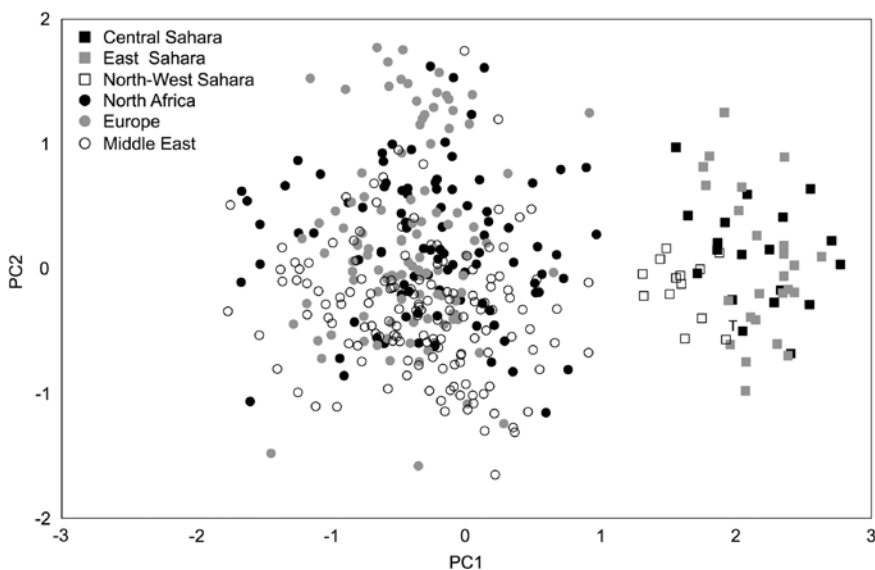


Figure 3 Bivariate plot of *Pipistrellus kuhlii* from the Sahara, North Africa, and Mediterranean on the first two principal components of all cranial and dental measurements. Squares denote the *deserti* morphotype, circles the *kuhlii* morphotype. For legend see Figure 2.

Table 1 Dimensions of populations of the *deserti* morphotype, including the holotype of *Pipistrellus deserti* Thomas, 1902 (BMNH 2.11.4.1.).

	Holotype				Central Sahara				East Sahara				North-West Sahara					
	n	M	min	max	n	M	min	max	n	M	min	max	n	M	min	max	SD	
FA	17	31.59	29.7	33.3	27	31.27	29.5	33.3	27	31.27	29.5	33.3	13	32.87	29.4	34.4	0.815	1.402
GLS	18	11.91	11.54	12.24	25	11.90	11.38	12.35	25	11.90	11.38	12.35	13	12.17	11.95	12.34	0.259	0.120
CBL	18	11.43	11.08	11.75	25	11.45	10.75	11.93	25	11.45	10.75	11.93	13	11.76	11.47	12.02	0.304	0.150
ZB	18	7.83	7.49	8.18	12	7.86	7.52	8.22	12	7.86	7.52	8.22	11	7.95	7.67	8.13	0.218	0.168
IC	19	2.99	2.74	3.17	25	3.07	2.84	3.33	25	3.07	2.84	3.33	13	2.99	2.88	3.13	0.119	0.086
RBF1	19	3.55	3.31	3.75	25	3.52	3.35	3.73	25	3.52	3.35	3.73	13	3.71	3.48	3.88	0.091	0.143
BB	18	6.08	5.88	6.31	25	6.12	5.77	6.34	25	6.12	5.77	6.34	13	6.17	5.87	6.31	0.137	0.116
MB	18	7.01	6.62	7.19	25	6.93	6.43	7.22	25	6.93	6.43	7.22	13	7.00	6.87	7.16	0.193	0.100
BH	18	4.32	4.05	4.61	25	4.34	3.96	4.59	25	4.34	3.96	4.59	13	4.39	4.18	4.53	0.141	0.088
CC	19	3.73	3.58	3.83	24	3.66	3.32	3.89	24	3.66	3.32	3.89	13	3.82	3.58	4.02	0.143	0.102
M ³ M ³	19	5.07	4.81	5.35	24	5.04	4.62	5.27	24	5.04	4.62	5.27	13	5.24	5.08	5.39	0.162	0.098
CM ³	19	4.33	4.17	4.56	25	4.33	3.98	4.49	25	4.33	3.98	4.49	13	4.51	4.37	4.68	0.167	0.093
M ¹ M ³	19	2.98	2.87	3.05	18	2.89	2.42	3.08	18	2.89	2.42	3.08	13	3.10	3.05	3.13	0.174	0.031
CP ⁴	19	3.20	3.05	3.37	18	3.20	2.76	3.37	18	3.20	2.76	3.37	13	3.36	3.05	3.53	0.157	0.167
LI ¹	19	0.46	0.41	0.51	18	0.47	0.39	0.52	18	0.47	0.39	0.52	13	0.49	0.47	0.52	0.037	0.021
LI ²	19	0.30	0.25	0.38	18	0.31	0.21	0.38	18	0.31	0.21	0.38	13	0.32	0.28	0.36	0.039	0.026
ML	17	8.55	8.22	8.87	24	8.50	8.03	8.83	24	8.50	8.03	8.83	13	8.78	8.54	8.87	0.174	0.095
CH	18	2.76	2.56	3.01	24	2.61	2.33	2.88	24	2.61	2.33	2.88	13	2.78	2.62	2.94	0.131	0.084
CM ₃	19	4.65	4.47	4.78	25	4.60	4.24	4.83	25	4.60	4.24	4.83	13	4.80	4.63	4.95	0.147	0.093
M ₁ M ₃	19	3.20	3.08	3.34	18	3.12	2.58	3.29	18	3.12	2.58	3.29	13	3.38	3.29	3.53	0.201	0.086
CP ₄	19	2.84	2.58	3.24	18	2.74	2.39	2.92	18	2.74	2.39	2.92	13	2.92	2.79	3.05	0.146	0.111
RI	19	0.654	0.553	0.810	18	0.671	0.541	0.810	18	0.671	0.541	0.810	13	0.668	0.540	0.756	0.067	0.076
RR1	18	0.313	0.300	0.323	24	0.308	0.288	0.334	24	0.308	0.288	0.334	13	0.313	0.300	0.329	0.010	0.007
RR2	18	0.299	0.280	0.318	25	0.296	0.280	0.312	25	0.296	0.280	0.312	13	0.306	0.291	0.321	0.007	0.011
RR3	19	0.860	0.787	0.893	24	0.842	0.712	0.910	24	0.842	0.712	0.910	13	0.847	0.819	0.863	0.036	0.012
RR4	18	0.269	0.261	0.279	18	0.271	0.243	0.288	18	0.271	0.243	0.288	13	0.277	0.255	0.292	0.010	0.012
PC1	19	2.15	1.55	2.77	25	2.17	1.75	2.63	25	2.17	1.75	2.63	13	1.59	1.30	1.92	0.234	0.191

Central Sahara, south-western Libya (Fezzan) and south-eastern Algeria (Hoggar Mountains.); East Sahara, Upper Egypt and northern Sudan; North-West Sahara, north-western Algeria and south-eastern Morocco; n, number of case; M, mean; SD, Standard deviation. For dimension abbreviations, see Materials and methods; indices: RI=LI¹/LI¹; RR1=CC/GLS; RR2=RBF1/GLS; RR3=CC/CM³; RR4=CP⁴/GLS; PC1=first principal component (see text and Figure 3 for details).

Table 2 Dimensions of particular morphotypes in the *Pipistrellus kuhlii* group.

	<i>deserti</i> morphotype (Sahara)					<i>kuhlii</i> morphotype (North Africa)					<i>kuhlii</i> morphotype (Europe and Middle East)				
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
FA	57	31.73	29.4	34.4	1.178	96	33.81	30.5	36.7	1.282	250	34.41	31.10	36.80	1.058
GLS	56	11.96	11.38	12.35	0.242	95	13.10	12.52	13.84	0.312	240	13.21	12.45	13.92	0.287
CBL	56	11.51	10.75	12.02	0.280	94	12.68	12.13	13.43	0.315	241	12.76	11.87	13.55	0.318
ZB	41	7.87	7.49	8.22	0.204	72	8.58	8.18	9.27	0.252	178	8.58	7.88	9.24	0.230
IC	57	3.02	2.74	3.33	0.119	95	3.26	2.92	3.55	0.132	250	3.29	2.98	3.60	0.120
RBF1	50	3.55	3.31	3.88	0.123	84	4.02	3.66	4.41	0.167	223	3.99	3.48	4.97	0.170
BB	56	6.12	5.77	6.34	0.136	95	6.48	6.12	6.92	0.158	250	6.58	5.93	6.96	0.160
MB	49	6.97	6.43	7.22	0.175	60	7.62	7.23	8.07	0.190	116	7.68	7.09	8.20	0.195
BH	56	4.35	3.96	4.61	0.127	93	4.70	4.32	6.19	0.223	239	4.70	4.18	5.16	0.163
CC	56	3.72	3.32	4.02	0.129	93	4.22	3.87	4.65	0.170	246	4.20	3.64	4.61	0.167
M ³ M ³	56	5.10	4.62	5.39	0.161	96	5.65	4.95	6.18	0.192	246	5.60	4.98	5.99	0.179
CM ³	57	4.39	3.98	5.46	0.199	96	4.88	4.51	5.27	0.164	250	4.93	4.48	5.23	0.144
M ¹ M ³	43	2.96	2.42	3.13	0.139	82	3.31	3.00	3.63	0.135	223	3.29	2.89	3.55	0.113
CP ^a	43	3.22	2.76	3.53	0.140	82	3.58	3.21	4.00	0.170	222	3.64	3.13	4.05	0.153
LI ¹	43	0.47	0.39	0.52	0.032	82	0.56	0.48	0.64	0.035	221	0.58	0.44	1.66	0.092
LI ²	43	0.31	0.21	0.38	0.036	80	0.37	0.29	0.48	0.035	221	0.38	0.29	0.51	0.039
ML	54	8.58	8.03	8.87	0.194	94	9.48	8.87	10.13	0.289	247	9.56	8.54	10.27	0.257
CH	55	2.70	2.33	3.01	0.140	94	3.03	2.67	3.39	0.147	247	2.99	2.67	3.37	0.143
CM ₃	57	4.66	4.24	4.95	0.137	95	5.24	4.91	5.63	0.151	249	5.29	2.93	5.72	0.206
M ₁ M ₃	43	3.19	2.58	3.53	0.165	81	3.59	3.32	3.87	0.126	221	3.59	3.18	3.92	0.122
CP _a	43	2.81	2.39	3.24	0.145	81	3.16	2.79	3.53	0.150	221	3.22	2.82	3.53	0.137
RI	43	0.663	0.540	0.810	0.071	80	0.666	0.526	0.792	0.065	221	0.667	0.308	0.880	0.073
RR1	55	0.311	0.288	0.334	0.008	92	0.322	0.303	0.342	0.009	236	0.318	0.276	0.342	0.010
RR2	49	0.298	0.280	0.321	0.009	83	0.307	0.287	0.331	0.010	217	0.302	0.275	0.368	0.011
RR3	56	0.849	0.712	0.910	0.028	93	0.865	0.818	0.933	0.023	246	0.851	0.770	0.916	0.026
RR4	42	0.271	0.243	0.292	0.009	81	0.273	0.251	0.292	0.010	215	0.275	0.241	0.301	0.011
PC1	57	2.03	1.30	2.77	0.361	96	-0.26	-1.67	0.96	0.596	251	-0.38	-1.77	0.91	0.490

For legend, see Table 1.

Table 3 Results of analyses of variance comparing the *deserti* and *kuhlii* morphotypes.

	<i>deserti</i> vs. <i>kuhlii</i> (North Africa)			<i>deserti</i> vs. <i>kuhlii</i> (Mediterranean)		
	F	p	df	F	p	df
FA	99.5	a	151	230.4	a	400
GLS	543.6	a	149	844.4	a	388
CBL	516.0	a	148	739.6	a	388
ZB	240.0	a	111	343.2	a	288
IC	120.4	a	150	207.7	a	399
RBF1	301.2	a	132	328.6	a	354
BB	208.0	a	149	359.1	a	398
MB	341.0	a	107	525.7	a	222
BH	115.4	a	147	198.8	a	385
CC	359.5	a	147	432.5	a	392
M ³ M ³	329.8	a	150	404.2	a	395
CM ³	272.8	a	151	541.5	a	400
M ¹ M ³	192.9	a	123	294.5	a	345
CP ⁴	143.0	a	123	246.3	a	344
LI ¹	215.4	a	123	73.1	a	343
LI ²	89.0	a	121	131.2	a	341
ML	411.8	a	146	641.7	a	392
CH	180.1	a	147	202.5	a	393
CM ₃	551.7	a	150	527.5	a	398
M ₁ M ₃	227.0	a	122	359.2	a	342
CP ₄	160.3	a	122	294.8	a	342
RI	0.1		121	0.1		341
RR1	60.0	a	145	35.7	a	380
RR2	27.7	a	130	11.4	a	346
RR3	3.8		147	2.6		392
RR4	1.5		121	5.2	a	335
PC1	690.2	a	151	1086.3	a	402

For legend, see Table 1.

4.6 mm (NMP 48302, adult female from Gabrun, Libya, GSL 12.0 mm) and 4.7 mm (NMP 90072, adult female from Gorges du Todra, Morocco, GSL 12.2 mm), whereas the smallest specimens of Mediterranean *P. kuhlii* could have an upper tooth row length as small as 4.4 mm (SMF 34362, adult male from Sush, Iran, GSL 12.7 mm; see also Table 2). Owing to this large overlap of values, the length of tooth-row alone is not useful to discriminate these morphotypes, unlike the greatest length of skull (Figure 2).

Descriptive statistics of skull and dental dimensions are given in Tables 1 and 2, and univariate analyses indicate that almost all comparisons show highly significant size differences between the two morphotypes (Table 3). However, none of the qualitative characters examined differed in a consistent way. For instance, the skull outline of both morphotypes is almost identical, except for absolute size (Figure 4). The second upper incisor (I²) is very tiny in both forms, with the height of crown about 35%–45% of the height of the crown of the first incisor (I¹); the tip of

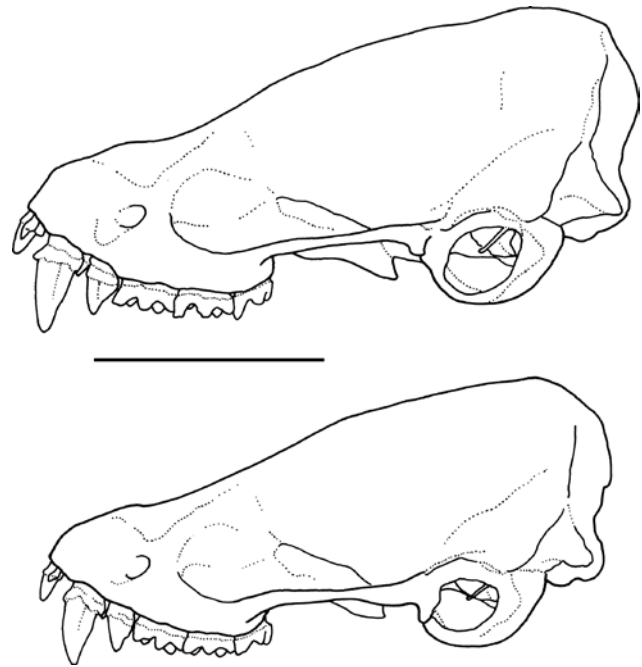


Figure 4 Outline comparison of skulls of *Pipistrellus kuhlii*: (above) the *kuhlii* morphotype (♀, Ain Sharshara, Tripolitania, Libya, NMP 49953), (below) the *deserti* morphotype (♀, Gabrun, Fezzan, Libya, NMP 48310). Scale bar=5 mm.

I² is slightly overlapping the cingulum of I¹ in both forms (Figure 5). The ratio between the mesio-distal length of crown of I² and that of I¹ in *Pipistrellus deserti* is almost identical as that in *P. kuhlii* (Tables 2 and 3). The first and second upper incisors thus differ essentially in the same way in both morphotypes, which is in accordance with observations described by Qumsiyeh (1985): Figure 20). Gaisler et al. (1972) found difference between *P. deserti* and *P. kuhlii* in terms of the degree of reduction of the first upper premolar (P³), with the former species having a more reduced premolar. The degree of reduction of this premolar in a larger material examined here show that this character is variable, but comparable in both morphotypes (Figure 6).

Qumsiyeh (1985) observed that Egyptian *Pipistrellus deserti* had more slender rostrum compared to *P. kuhlii*. This observation is supported in our results (Tables 1–3) as the ratios between breadths of rostrum (RBF1, CC) and greatest length of skull (GLS) differ significantly (Table 3). However, another relative dimension of the breadth of the rostrum (CC/CM³) did not show significant differences between *P. deserti* and *P. kuhlii* (Table 3).

The baculum of *P. deserti* was described by Gaisler et al. (1972) from two specimens from Egypt and by Hill and Harrison (1987) from a specimen from Algeria. This bone has the typical habitus known in members of the

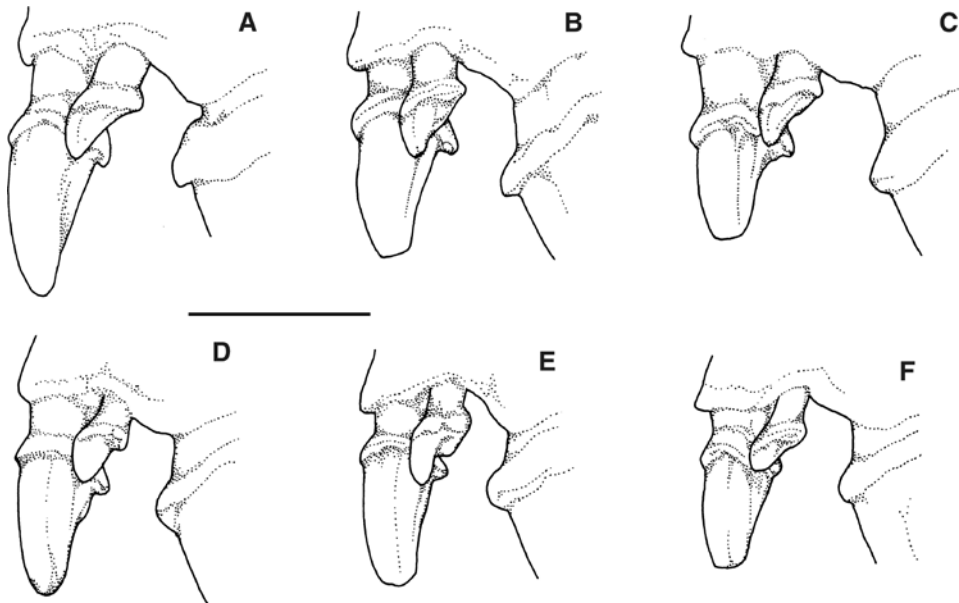


Figure 5 Fronto-lateral view on the upper incisors of *Pipistrellus kuhlii* from North Africa. Legend: a – *kuhlii* morphotype (Tabouda, Morocco, NMP 90030); b – *kuhlii* morphotype (Ain Sharshara, Tripolitania, Libya, NMP 49953); c – *kuhlii* morphotype (Tolmeita, N Cyrenaica, Libya, NMP 49930); d – *kuhlii* morphotype (Jalu, S Cyrenaica, Libya, NMP 49939); e – *deserti* morphotype (Oued Drâa, Morocco, NMP 90058); f – *deserti* morphotype (Gabrun, Fezzan, Libya, NMP 48310). Scale bar=1 mm.

genus *Pipistrellus* (Lanza 1959, Hill and Harrison 1987) with a thin stick arched dorsally and a bifurcation on both epiphyses. As in other morphological characters, the baculum of *P. deserti* differs from that of *P. kuhlii* only in absolute size, but we found no difference in the shape of the published preparations (Lanza 1959, Gaisler et al. 1972, Wassif and Madkour 1972, Hill and Harrison 1987).

Most previous authors (e.g., Gaisler et al. 1972, Qumsiyeh 1985, Kowalski and Rzebik-Kowalska 1991) mentioned substantial differences in colouration between *Pipistrellus deserti* and *P. kuhlii*, the former being generally paler than the latter for both wing and pelage characteristics. Indeed, as the *deserti* morphotype lives in the more arid parts of the Sahara, its colouration is very pale (pale olive brown in dorsal pelage, pale brown skin on face, ears and wing membranes), and the very pale (creamish, whitish, or translucent) posterior wing margin is up to 4.5–5.0 mm wide on plagiopatagium with indistinct transition to darker colour of the wing membrane. However, the same pattern of colouration was observed in bats classified by multivariate analyses as *P. kuhlii* and caught in the Libyan oases of Sinawan and Jalu (situated in the Sahara, ca. 250 km from the sea coast). This very pale colouration pattern was also found in some populations of the arid regions of the Middle East (Syrian Mesopotamia, Iranian Baluchistan), all of which were classified in our multivariate analyses as typical *kuhlii* (Figures 2 and 3). The darkest individuals representing the typical pelage colouration

of *P. kuhlii* were observed in Iberia and Morocco (Rif Mts.) specimens. These bats had dark chestnut brown dorsal pelage and very narrow (<0.5 mm) and sharply delimited pale (not white) strip on the posterior wing margins, the remaining wing membrane being dark brown. However, in the same region of northern Morocco we found also relatively pale individuals, resembling in colouration the desert forms.

Thus, *P. kuhlii* specimens identified as such by their skull and dental dimensions (Figures 2 and 3) can have very variable colouration. As a general trend, we found that the colouration intensity of pipistrelles varied clinally from uniformly paler bats in more arid habitats to darker and more variable colours in populations inhabiting more mesic regions (i.e., in the Mediterranean zone). This trend was described in *P. kuhlii* from Algeria already by Kowalski and Rzebik-Kowalska (1991) and in populations from the eastern Mediterranean by Lewis and Harrison (1962). Nevertheless, without a proper GIS analysis of these colouration trends along dedicated transects, it is difficult to determine if such local variation is significant and valid across the entire distribution of this species complex. Pelage colouration and width of the pale posterior margin of wing membrane are highly variable characters that bear little taxonomic importance (in agreement with Corbet 1984, contra Panouse 1951, Deleuil and Labbé 1955a,b, Gaisler et al. 1972, Hanák and Elgadi 1984, Qumsiyeh 1985, etc.).

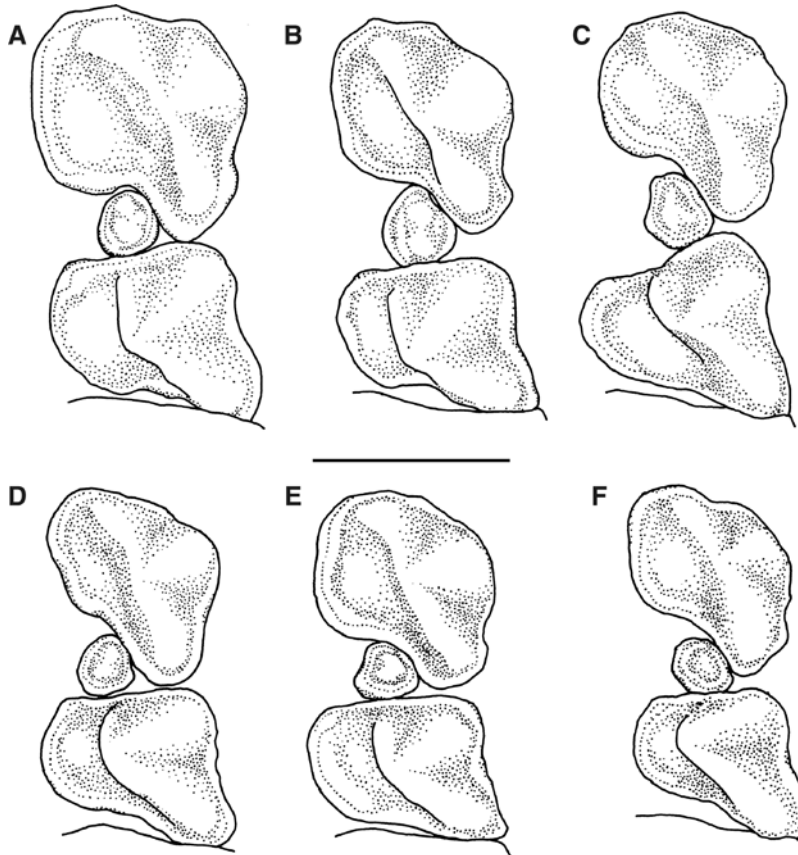


Figure 6 Occlusal view on the rostral part of the upper tooth-row (C–P⁴) of *Pipistrellus kuhlii* from North Africa. For legend, see Figure 5. Scale bar=1 mm.

Genetic comparison

We sequenced the initial 620 bases pairs of the cytochrome *b* gene of 22 individuals identified in the multivariate morphological analyses as typical *Pipistrellus kuhlii* and 12 individuals from Morocco and Libya identified as *P. deserti* (Appendix 2). The alignment of these cytochrome *b* sequences with six further homologous sequences of *P. kuhlii* taken from the GenBank resulted in 12 distinct haplotypes (C1, C4, D1 to D3, K1 to K5, K8, and PK03; Appendix 2). Two haplotypes (K2 and K5) were found in all specimens from the Middle East (Iran and Syria), three others (K8, C1 and C4) were confined to West European bats, whereas the remaining ones originated from a vast area comprising North Africa and Europe and included both typical *P. kuhlii* and typical *P. deserti* individuals (Figure 7). Within the *kuhlii* complex, haplotypes differed by one (D2 vs. D3 or K2 vs. K5) to 36 mutations (K2 vs. C1), which correspond to a K2P divergence of <1% to up to 6% (Table 4). Outside this group, interspecific divergences were much larger, exceeding 12%, except between *P. pygmaeus* and *P. hanaki* (7.5%); the latter species is, however, represented only by a partial

sequence of 402 bp, which does not include the more variable, central portion of the cytochrome *b* gene, and thus is not directly comparable to other distances.

All phylogenetic reconstructions (ML and BA) identified a strongly supported (>95% bootstrap or posterior probability; Figure 7) monophyletic group comprising all haplotypes of *Pipistrellus kuhlii*, *P. deserti*, and *P. maderensis*, to the exclusion of any other species (including a Southern African *P. hesperidus*). As already documented in all reconstructions based on distinct mitochondrial genes (e.g., Ibáñez et al. 2006, Mayer et al. 2007, Evin et al. 2011, Veith et al. 2011, Çoraman et al. 2013), sequences issued from this species complex form more or less well-separated clades, but relationships among them lack resolution, which is fully consistent with the reconstructions presented in Figure 7.

Representatives of Clade 1 are widespread across most of Europe, North Africa, the Canary Islands, the Balkans, and the Levant (see Çoraman et al. 2013 for a larger geographic sampling). This clade is well supported and also includes typical *Pipistrellus kuhlii*, as well as all sequences of *P. deserti* from Morocco and Libya

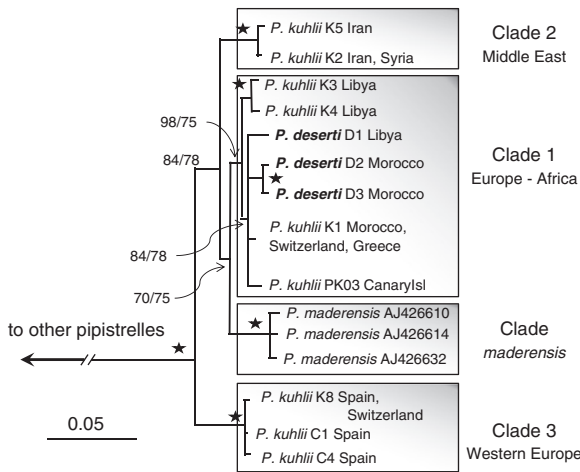


Figure 7 Bayesian consensus tree representing the phylogenetic relationships of haplotypes of the *Pipistrellus kuhlii* group based on sequences (620 bp) of the mitochondrial cytochrome *b* gene. A star associated to a node denotes that it is supported by at least 95% posterior probability (BA reconstructions) and 95% bootstrap (ML reconstructions). Other support values are given as percentages. We named the clades according to the recent review of Çoraman et al. (2013) and pruned the tree from all outgroup species (i.e., *P. abramus*, *P. hanaki*, *P. hesperidus*, *P. nathusii*, *P. pipistrellus*, *P. cf. javanicus*, and *P. pygmaeus*; see Appendix 2) to simplify this representation. Scale bar=5% divergence.

(Figure 7). More specifically, all nine pipistrelles sampled near the type locality of *P. deserti* in Fezzan (Libya) shared a single haplotype (D1), which is most closely related (1.1% K2P divergence) to the widespread haplotype K1 in Clade 1 (Table 4). Haplotypes from Clade 3 are restricted to Western European *P. kuhlii*, whereas those of Clade 2 include all sequences from the Middle East (Figure 7 and Çoraman et al. 2013). Partial cytochrome *b* haplotypes from the desert region of Arabia reported in Bray et al. (2013) also pertain to this Clade 2 and differs only by two

point mutations from the haplotype K5 (result not shown). The haplotypes of *P. maderensis* form a sister group close to the widespread Clade 1, albeit with moderate support (Figure 7), rendering this taxon paraphyletic, as shown by Pestano et al. (2003). Thus, according to all molecular reconstructions based on mitochondrial DNA, *P. deserti* and *P. kuhlii* do not appear in distinct units (Figure 7; Mayer et al. 2007).

However, these conclusions on phylogenetic relationships are based on mitochondrial markers, which retain the history of the females only. As such, female lineages may underlie a different history than the organisms themselves (Ballard and Whitlock 2004). For instance, at least two pairs of biological species of bats (*Myotis myotis* vs. *M. blythii* and/or *Eptesicus serotinus* vs. *E. nilssonii*; Berthier et al. 2006, Artyushin et al. 2009) show striking cytonuclear discordance, supposedly due to ancient but massive episodes of mtDNA introgression. In these introgressed species the unusually low divergence measured at mtDNA genes thus does not reflect their true organismal relationships, as shown by their divergent external morphology or nuclear genes (Berthier et al. 2006, Juste et al. 2013).

To exclude the possibility that the strong similarities in mtDNA genes of both morphotypes are due to introgression, we also report the nuclear genetic relationships of a subsample of 22 pipistrelles (mostly collected in Libya, Morocco, and Switzerland; see Appendix 2) in Figure 8. This subsample represents both typical *kuhlii* and *deserti* identified in the previous multivariate, morphological analysis. The PCA-GEN output of these multilocus, nuclear genotypes suggests that samples are grouped according to their geographic origin rather than morphotypes (Figure 8). Most of the inertia of the first (and only significant) component is indeed due to the separation of the African versus European samples, regardless of the morphotype tested. If *deserti*

Table 4 Absolute number of substitutions (above the diagonal) and Kimura-two parameter (K2P) distance matrix (below the diagonal) between cytochrome *b* haplotypes of the *kuhlii-deserti* species complex (620 aligned base pairs).

	D1	D2	D3	K1	K2	K3	K4	K5	K8	C1	C4	PK03
D1	–	11	10	7	25	13	12	24	30	30	29	8
D2	0.018	–	1	6	23	13	12	22	34	34	33	5
D3	0.016	0.002	–	5	24	12	11	23	33	33	32	6
K1	0.011	0.010	0.008	–	21	7	6	20	30	30	29	3
K2	0.042	0.038	0.040	0.035	–	21	22	1	36	36	35	18
K3	0.021	0.021	0.020	0.011	0.035	–	3	20	32	32	31	8
K4	0.020	0.020	0.018	0.010	0.037	0.005	–	21	31	31	30	8
K5	0.040	0.037	0.038	0.033	0.002	0.033	0.035	–	35	35	34	17
K8	0.051	0.058	0.056	0.051	0.062	0.054	0.052	0.060	–	2	1	24
C1	0.051	0.058	0.056	0.051	0.062	0.054	0.052	0.060	0.003	–	1	25
C4	0.049	0.056	0.054	0.049	0.060	0.053	0.051	0.058	0.002	0.002	–	24
PK03	0.017	0.011	0.013	0.006	0.039	0.017	0.017	0.037	0.053	0.055	0.053	–

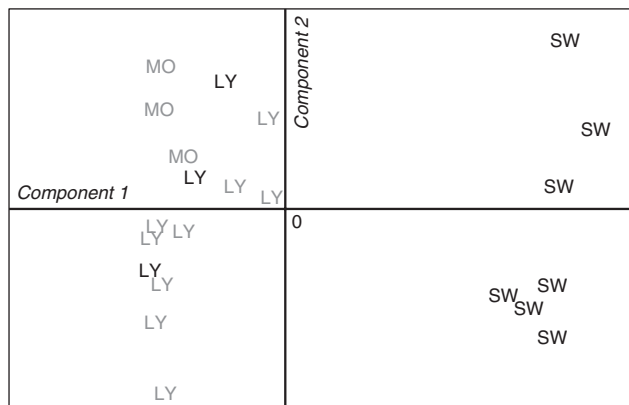


Figure 8 Projection on the first two principal components (each representing 28% and 12% of total inertia, respectively) of the multilocus genotypes of 10 *kuhlii* morphotypes (in bold face) and 12 *deserti* morphotypes (greyed) analysed with PCA-GEN (Goudet 1999). Samples come from Morocco (MO), Libya (LY), and Switzerland (SW). Only the first axis is significant according to the broken-stick distribution.

would represent a distinct species, *kuhlii* genotypes from both sides of the Mediterranean should be more closely related to each other than either is to desert genotypes. If the same analyses are repeated without the European pipistrelles, the results are similar (not shown), with all Moroccan and all Libyan samples being grouped together, regardless of morphotypes. This data set, albeit limited, therefore clearly confirms that pipistrelles of the two morphotypes in North Africa not only share very similar mitochondrial cytochrome *b* genes (Figure 7), but also share similar allelic composition at five independent, nuclear loci (Figure 8). The hypothesis that the morphologically identified *Pipistrellus deserti* samples from Morocco and Libya (and by extension all those from the Sahara) would share a single common ancestor that is distinct from other *kuhlii* morphotypes is thus falsified by all current genetic evidence.

Taxonomic and biogeographical conclusions

Our phylogenetic reconstructions clearly suggest that the mitochondrial DNA of bats representing the *deserti* morphotype are very closely related and are imbedded within the broader radiation of other mitochondrial DNA lineages belonging to the *kuhlii* morphotype sampled around the Mediterranean (Figure 7). The same conclusion can be drawn from a limited number of samples genotyped at five nuclear loci (Figure 8), which excludes the possibility that the results revealed from the mtDNA analysis could be biased by recent or past events of introgression. These genetic results rather suggest that the bats of the *deserti*

morphotype are issued from multiple, independent *kuhlii* ancestors, but evolved a convergent, desert-adapted morphology in different parts of the Sahara. According to the genetic or biological species concepts (de Queiroz 2007) and despite the clear morphologic differences observed between the *deserti* and *kuhlii* populations in North Africa (Figures 2 and 3), the small-sized and pale-coloured Saharan populations of the *deserti* morphotype do not seem to represent a distinct biological species. Hence, we suggest to consider the name *Pipistrellus deserti* Thomas, 1902 a junior synonym of *Vespertilio kuhlii* Kuhl, 1817=*Pipistrellus kuhlii* (Kuhl, 1817).

The significant meristic differences between the two morphotypes of *Pipistrellus kuhlii* in North Africa, which is not reflected in their genetic characters, may be due to the contrasting environments found in this region. The *deserti* morphotype is clearly a desert inhabitant of the Sahara, which is composed of a complex of relatively young habitats – the current state being approximately 5500 years old (Foley et al. 2003, Bray et al. 2013). Thus, the form *deserti* is living in this harsh environment of the Sahara since a short period on an evolutionary time scale. This short period did not lead to major genetic differences but was sufficient for morphologic (and supposedly physiologic) adaptations to evolve in response to such harsh desert habitats.

The two morphotypes of *P. kuhlii* coincident with mesic and arid habitats is a general phenomenon that is found also in other organisms living in such contrasted environments (Heim de Balsac 1936, Lewis and Harrison 1962, Guillaumet et al. 2008). Indeed, several bat species are represented by two distinct morphotypes in North Africa, in which a larger form (and often also darker morph) inhabits coastal regions of the Mediterranean Sea and a smaller (and paler) form occurs in a belt of the central Sahara. Examples include *Rhinopoma cystops* Thomas, 1903, *Rhinolophus clivosus* Cretzschmar, 1828 and/or *Asellia tridens* (Geoffroy, 1818). Similarly as in the *kuhlii* complex, these pairs of morphotypes were originally described and, for a long time, treated as pairs of separate taxa (see Gaisler et al. 1972, Hill 1977, Qumsiyeh 1985, Owen and Qumsiyeh 1987, Van Cakenberghe and De Vree 1994). All are now considered as morphologically distinct populations of a single species or even subspecies because of close similarities in genetic traits found between morphotypes (Hulva et al. 2007, Benda et al. 2011, Benda and Vallo 2012).

Small and pale individuals of *Pipistrellus kuhlii* were also found in other desert regions of the western Palaearctic, e.g., in Arabia (Gaisler et al. 1972, Bray et al. 2013) or in the Iranian Baluchistan (Benda et al. 2012). Whereas in

Arabia the degree of size reduction in Desert pipistrelles does not exceed the variation extremes of Mediterranean *P. kuhlii*, the Baluchistani bats differ significantly in size and represent a dimensional transition between the African *kuhlii* and *deserti* morphotypes (see Benda et al. 2012 for details).

Most records of the *deserti* morphotype come from the belt of the central Sahara from southern Algeria via southern Libya and southern Egypt to northern Sudan, from 28°N to the south (see Figure 1), i.e., an area with the lowest annual precipitation in the Sahara (≤ 20 mm). In this region, this species was captured in oases, where it uses petrophilous or synanthropic shelters (rocky fissures and fissures between beams in abandoned houses) or was netted among palm trees (Gaisler et al. 1972, Kowalski and Rzebik-Kowalska 1991; our records). However, some records came also from the north-Saharan region of north-western Algeria and south-eastern Morocco (Qumsiyeh 1985, Gaisler and Kowalski 1986, Kowalski and Rzebik-Kowalska 1991, Benda et al. 2004a, 2010), where these bats were netted in oases. In the latter region, the distribution range of the *deserti* morphotype was found to be in close parapatry to connect with the *kuhlii* morphotype in the High Atlas and Anti-Atlas Mountains in Morocco (Benda et al. 2004a) and probably also in the Saharan Atlas Mountains in Algeria (Kowalski and Rzebik-Kowalska 1991, our own observations).

In general, we observed that the border between the ranges of both morphotypes extends to a distance of ca. 250–350 km from the sea coast throughout North Africa

(Figure 9). However, in the region of the north-western Sahara in Morocco, the distribution of both morphotypes is more mosaic-like and the exact limits probably depend on the mesic/arid character of each site of occurrence. Thus, the reported sympatric occurrence of both forms in nearby Algeria (Gaisler et al. 1972, Kowalski and Rzebik-Kowalska 1991) may probably result from sparse sampling in such mosaics, where annual precipitation (50–100 mm) could represent a transition zone for intermediate populations.

The *deserti* morphotype is a desert form of *Pipistrellus kuhlii*, which most probably developed in the most arid habitats of the northern and/or central Sahara after several independent invasions from the Mediterranean or, perhaps less probably, from relic populations that persisted in oasis islets in the Sahara. Therefore, we consider as highly unlikely the possibility that these desert forms may have a sub-Saharan origin, i.e., in the Afro-tropic region. Thus, we hypothesise that the published records assigned to *P. deserti* from sub-Saharan Africa (see Van Cakenberghe and Benda 2013 actually belong to another species. One such candidate is *P. aero* Heller, 1912 a bat described from central Kenya and distributed in the north-western part of this country (Aggundey and Schlitter 1984, Van Cakenberghe and Happold 2013). Koopman (1975) differentiated this species from *P. deserti* only on the basis of its slightly larger size. However, new sampling coupled with proper phylogeographic analyses are needed to validate this taxonomic and biogeographic hypothesis.

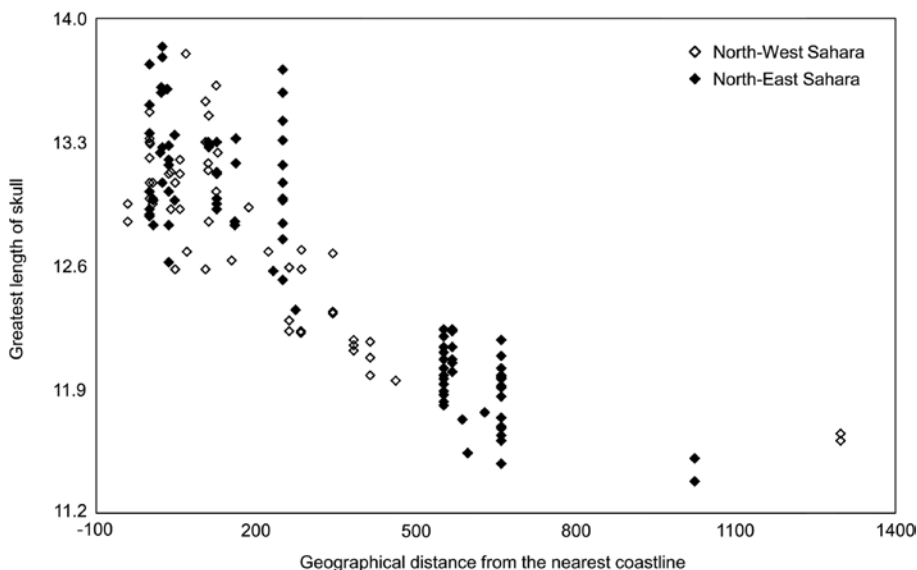


Figure 9 Greatest length of skull (GLS, in millimetres) against relative aridity of a record (expressed as a geographical distance of the respective site from the Mediterranean Sea and/or Atlantic Ocean coasts; in kilometres) in North African samples of *Pipistrellus kuhlii* group. Legend: North-West Sahara=Morocco, Algeria and Tunisia; North-East Sahara=Libya, Egypt and the Sudan.

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Appendix

Appendix 1 Specimens used in the morphological analysis. Explanations: ind. – specimen of sex undermined; S – skull, A – alcoholic specimen, B – prepared skin (balg); for collection abbreviations, see Material and methods.

deserti morphotype (59 specimens)

Algeria: 2 ♂♂ (BMNH 79.987., 79.988. [S+A]), Hoggar Plateau, 1887 m a.s.l., 27 February 1979, leg. D. James; – 1 ♀ (MUB A-490 [S+B]), Taghit, 18 July 1983, leg. J. Gaisler. – **Egypt:** 1 ♂ (NMP 92571 [S+A]), Bawiti, Bahariya Oasis, 18 January 2010, leg. P. Benda, R. Lučan and I. Horáček; – 6 ♂♂, 1 ♀ (NMP 92572–92575, 92580, 92581 [S+A], 92579 [A]), El Qasr, Dakhla Oasis, 21–23 January 2010, leg. P. Benda, R. Lučan and I. Horáček; – 1 ♂, 15 ♀♀ (IVB 1–16 [S+B]), Luxor, 26–29 April 1969, 1 May 1969, leg. J. Gaisler, G. Madkour and J. Pelikán. – **Libya:** 1 ♂ (NMP 48321 [S+A]), Al Fjayj, 6 October 1999, leg. P. Benda; – 1 ♂, 12 ♀♀ (NMP 48302–48305, 48309–48316, 48318 [S+A]), Gabrun, 2 October 1999, leg. P. Benda; – 1 ♂ (NMP 48320 [S+A]), Germa, 6 October 1999, leg. P. Benda; – 1 ♂ (BMNH 2.11.4.1. [S+B], holotype of *Pipistrellus deserti* Thomas, 1902), Mursuk [=Murzuq], 3 May 1901, leg. J.I.S. Whitaker; – 1 ♂ (NMP 48319 [S+A]), Murzuq, 6 October 1999, leg. P. Benda. – **Morocco:** 1 ♂, 1 ♀ (NMP 90071, 90072 [S+A]), Gorges du Todra, 5 km SW of Tamtattouchte, 3 September 2003, leg. P. Benda; – 2 ♂♂, 1 ♀ (NMP 90058–90060 [S+A]),

Oued Drâa, 5 km NW of Anagam, 31 August 2003, leg. P. Benda; – 3 ♀♀ (NMP 94481, 94477, 94478 [S+A]), Rissani, 25 April 2008, leg. P. Benda, J. Červený, A. Konečný and P. Vallo; – 1 ♂, 1 ♀ (NMP 94516, 94517 [S+A]), Takoumit, 26 April 2008, leg. P. Benda, J. Červený, A. Konečný and P. Vallo; – 2 ♂♂ (NMP 94449, 94450 [S+A]), Tassetift, 22 April 2008, leg. P. Benda, J. Červený, A. Konečný and P. Vallo. – **Sudan:** 1 ♂, 2 ♀♀ (MHNG 1626.4, 1626.5 [S+A], 1626.6 [A]), Wadi Halfa, date unlisted, leg. F. Bona.

kuhlii morphotype

North Africa (104 specimens)

Algeria: 1 ♂ (ZFMK 54.2 [S+B]), Djelfa, 18 July 1950, collector unlisted; – 2 inds. (MNHN 1962-1770a, 1770b [S]), Algeria, date and collector unlisted. – **Egypt:** 2 ♂♂ (IVB 2, 3 [S+B]), Abu Rawash, 19 April 1969, leg. J. Gaisler; – 1 ♂ (SMF 26114 [S+A]), Bahig, Western Desert, 16 August 1965, leg. J. Kiepenhauer and K. Linsenmair; – 1 ind. (SMF 22014 [S+A]), between Cairo and Ismaila, 5 September 1962, leg. R. Rau; – 1 ♂ (IVB 4 [S+B]), Burgh El Arab, 14 May 1969, leg. J. Gaisler; – 2 ♂♂ (NMP 92614, 92615 [S+A]), Cairo, 29 January 2010, leg. P. Benda, R. Lučan and I. Horáček; – 1 ind. (SMF 4307 [S+B], lectotype of *Vespertilio marginatus* Cretzschmar, 1830), Nubia and Petraean Arabia [=Lower Egypt sensu Anderson 1902], 1822, leg. E. Rüppell; – 6 ♂♂, 3 ♀♀ (NMP 90535, 90536 [S+A], 90534, 90537–90542 [A]), San El Hagar El Gibiliya, Nile Delta, 20 September 2005, leg. M. Andreas, P. Benda, J. Hotový and R. Lučan. – **Libya:** 1 ♀ (NMP 48332 [S+A]), Al Abyar, 11 October 1999, leg. P. Benda; – 1 ♂ (NMP 49843 [S+A]), Al Jawsh, 7 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 1 ♀ (NMP 48326 [S+A]), Al Aquriyah, 9 October 1999, leg. P. Benda; – 2 ♂♂, 2 ♀♀ (NMP 49933, 49934, 49936, 49937 [S+A]), Ar Rajmah, 23 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 2 ♂♂, 4 ♀♀ (NMP 49953–49955, 49958–49960 [S+A]), Ain Sharshara, 27 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 1 ♀ (NMP 49939 [S+A]), Jalu, 24 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 1 ♂ (NMP 48322 [S+A]), Karkurah, 8 October 1999, leg. P. Benda; – 3 ♂♂, 3 ♀♀ (NMP 49968–49970, 49972–49974 [S+A]), Nanatalah, 28 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 3 ♂♂ (NMP 49981–49983 [S+A]), Sabratah, 28 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 3 ♂♂, 6 ♀♀ (NMP 49845–49851, 49853, 49859 [S+A]), Sinawan, 8 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 2 ♀♀ (NMP 49930, 49931 [S+A]), Tolmeita, 22 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 1 ♂ (MHNG 987.14

[S]), Tripoli, 1918, leg. Taubert; – 1 ♀ (NMP 49893 [S+A]), Wadi Al Kuf, Al Bayda, 19 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 2 ♂♂ (NMP 49917, 49918 [S+A]), Wadi Jarmah, 20 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin; – 1 ♂, 1 ♀ (NMP 49921, 49923 [S+A]), Wadi An Nazrat, 22 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter and M. Uhrin. – **Morocco**: 1 ♂ (NMP 93603 [S+A]), Ait-Rahhal, 9 October 2010, leg. P. Benda, A. Reiter, M. Ševčík and M. Uhrin; – 2 ♀♀ (NMP 90066, 90067 [S+A]), Ait-Saoun, 1 September 2003, leg. P. Benda; – 1 ♀ (NMP 94539 [S+A]), Bekrite, 27 April 2008, leg. P. Benda, J. Červený, A. Konečný and P. Vallo; – 2 ♀♀ (NMP 93591, 93592 [S+A]), Dar-el-Aroussi, 5 October 2010, leg. P. Benda, A. Reiter, M. Ševčík and M. Uhrin; – 2 ♂♂ (NMP 93580, 93581 [S+A]), Dardara, 6 km SW of Chefchaouen, 2 October 2010, leg. P. Benda, A. Reiter, M. Ševčík and M. Uhrin; – 3 ♂♂, 1 ♀ (SMF 47747–47780 [S+B]), Dekeira, Oued Sous, 31 January 1975, leg. M. Dachsel; – 1 ♂ (NMP 90024 [S+A]), Makhazen River, Souk-Khémis-des-Beni-Arouss, 25 August 2003, leg. P. Benda; – 1 ♂, 1 ♀ (NMP 90096, 90097 [S+A]), Sebt-des-Ait-Serhrouchèn, 9 September 2003, leg. P. Benda; – 1 ♂, 3 ♀♀ (NMP 90082–90085 [S+A]), Sidi Moussa, 7 September 2003, leg. P. Benda; – 1 ♂ (NMP 90030 [S+A]), Tabouda, 26 August 2003, leg. P. Benda; – 2 ♂♂ (NMP 93585, 93586 [S+A]), Tafeer, 3 October 2010, leg. P. Benda, A. Reiter, M. Ševčík and M. Uhrin; – 1 ♀ (NMP 94518 [S+A]), Takoumit, 26 April 2008, leg. P. Benda, J. Červený, A. Konečný and P. Vallo; – 2 ♀♀ (NMP 94452 [S+A], 94451 [A]), Tassetift, 22 April 2008, leg. P. Benda, J. Červený, A. Konečný and P. Vallo; – 1 ♀ (ZFMK 97.177 [S+B]), Tizin-Test Pass, 11 September 1969, leg. G. Rheinwald. – **Tunisia**: 2 ♂♂, 2 ♀♀ (ZFMK 59.269–59.271 [S+B], SMF 19551 [S+B]), Carthago, 14 March 1959, 6 March 1961, leg. H. Roer and K. Walch; – 1 ♂♂, 2 ♀♀ (SMF 83440–83442 [S+B]), Douz, Nefzaoua, 29 and 30 April 1994, leg. D. Kock and C. Winter; – 1 ♀ (ZFMK 97.169 [S+B]), El Haouaria, 19 March 1957, leg. J. Niethammer; – 1 ♂, 1 ind. (MHNG 921.16, ZFMK 97.174 [S]), Gabès, 1922, 1956, leg. Sicard and M. Costan; – 1 ♂ (MHNG 1684.56 [S]), 100 km S of Gabès, 1984, leg. P. Gaucher and A. Brosset; – 1 ♂, 1 ♀ (SMF 41617, 41618 [S+A]), Galita Archipelago, Ile de la Galite, 29 August 1971, leg. K. Schuberth, I. Vesmanis and F. Charousset; – 3 ♂♂ (SMF 41619–41621 [S+A]), Kebili, 18 March 1971, leg. K. Schuberth, I. Vesmanis and P. Nagel; – 1 ind. (MNHN 1995-1702 [S+B]), Tunisia, date and collector unlisted.

Europe (93 specimens)

Croatia: 2 ♀♀ (SMF 23402, 23403 [S+B]), Primošten, 27 September 1964, leg. H. Coffler and K. Walch; – 5 ♂♂, 1 ♀ (SMF 23399–23401, 23404, 23405 23407 [S+B]),

Zadar, 26, 29 and 30 September 1964, leg. H. Coffler and K. Walch. – **France**: 1 ♂ (MHNG 1882.050 [S+A]), Ain, Seyssel, 26 August 2003, leg. N. Chardonnes; – 1 ♂ (MNHN 1997-313 [S]), Camarque, leg. H. Heim de Balsac; – 1 ♂, 1 ♀ (MNHN 1980-453, 1980-454 [S]), Digne, 8 September 1908, leg. C. Mottaz; – 1 ind. (MHNG 1255.32 [S+A]), Chambord, June 1943, leg. F. Chanudet; – 1 ♂ (MNHN 1985-1977 [S]), Thaars, July 1951, leg. D. Senes. – **Greece**: 1 ♀ (NMP 49022 [S+A]), Artiki, 25 August 2001, leg. P. Benda; – 1 ♂, 1 ♀ (NMP 48703, 48704 [S+B]), Asproklisi, 1 July 1989, leg. V. Hanák and V. Vohralík; – 1 ♀ (SMF 28220 [S+B]), Kourna Mouri, Crete, 15 April 1958, leg. H. Kahmann; – 4 ♀♀ (ZFMK 62.59–62.62 [S+B]), Mesologgi, 3 April 1962, leg. O. von Helversen; – 2 ♀♀ (NMP 48705, 48706 [S+B]), Mesopotamo, 2 July 1989, leg. V. Hanák and V. Vohralík; – 2 ♂♂ (NMP 48554, 48555 [S+B]), Ormylia, 14 September 1988, leg. V. Hanák and V. Vohralík; – 1 ♂, 1 ♀ (NMP 48561, 48562 [S+B]), Paralia Skotinas, 19 September 1988, leg. V. Hanák and V. Vohralík; – 1 ♂ (ZFMK 59.429 [S+B]), Perivolo, 21 May 1959, leg. Buchholz and Forst; – 3 ♀♀ (NMP 49013–49015 [S+A]), Simopoulo, 23 August 2001, leg. P. Benda; – 1 ♂, 6 ♀♀ (SMF 45213–45219 [S+B]), Skiathos, North Sporades, 16, 18 and 21 October 1973, leg. D. Kock and G. Storch; – 1 ♂, 4 ♀♀ (NMP 48733–48737 [S+A]), Spárti, 16 September 1996, leg. P. Benda and M. Uhrin; – 2 ♂♂, 2 ♀♀ (SMF 26791–26795 [S+B]), Tegea, 16 August 1960, leg. H. Kahmann. – **Italy**: 1 ♂ (SMF 16989 [S+B]), Favignana (Trapani), Aegedic Isls., 17 May 1955, leg. K. Klemmer and H. Krampitz; – 4 ♂♂, 1 ♀ (MHNG 1716.87 [S]), SMF 50430–50433 [S+A]), Florence, 2 May 1911 and 6 May 1976, leg. K. Walch; – 4 ♂♂, 6 ♀♀ (SMF 16992–17000, 17014 [S+A]), Linguaglossa, Sicily, 9 and 11 July 1955, leg. K. Klemmer and H. Krampitz; – 1 ♂ (SMF 35536 [S+A]), Sicily, Palermo, date and collector unlisted. – **Spain**: 3 ♂♂, 3 ♀♀, 1 ind. (ZFMK 34.119–34.125 [S+B]), Langunilla, Bejar Salamanca, 1–4 June 1934, leg. H. Grünng; – 2 ♂♂, 6 ♀♀ (SMF 18689–18705 [S+A]), Nava de San Pedro, Sierra de Cazorla, 14 May 1959, leg. K. Klemmer. – **Switzerland**: 1 ♂ (MHNG 1868.076 [S+A]), Châteauneuf, Sion, 29 June 2001, leg. R. Arlettaz; – 1 ♀ (MHNG 1828.067 [S+A]), Chêne-Bourg, Genève, 12 December 2001, leg. Cordt-Moller; – 1 ♀ (MHNG 898.38 [S]), Genève, 22 September 1951, leg. Mme. Pelletton; – 1 ♂ (MHNG 1826.026 [S+A]), Genève, 1 September 2001, collector unlisted; – 1 ♂ (MHNG 1826.027 [S+A]), Genève, 7 September 2001, collector unlisted; – 1 ♀ (MHNG 1828.068 [S+A]), Genève, 24 May 2002, collector unlisted; – 1 ♂ (MHNG 1869.032 [S+A]), Genève, 1 March 2003, leg. A. de Chambrier; – 1 ♂ (MHNG 1882.052 [S+A]), Genève, 15 July 2003, leg. de Giorgi; – 1 ♂ (MHNG 1813.034 [S+A]), Plan-les-Ouates, 7 September 2000, leg. A. Keller; – 1 ♀ (MHNG 1806.038 [S+A]), Sion, 10 September 1990,

leg. R. Arlettaz & Baumann; – 1 ♂ (MHNG 1868.075 [S+A]), Sion, 7 April 1999, leg. R. Arlettaz; – 1 ♂ (MHNG 1868.073 [S]), Sion, 3 August 1999, leg. R. Arlettaz; – 1 ♀ (MHNG 1807.028 [S+A]), Veyrier, Genève, 21 August 2000, leg. M. Ruedi.

Middle East (171 specimens)

Iran: 1 ♂ (NMP 48121 [S+A]), Bastam, 1 October 1998, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin; – 5 ♂♂, 6 ♀♀ (NMP 48427–48431, 48433 [S+A], 48425, 48426, 48432, 48434, 48435 [A]), Chah Reza, 16 April 2000, leg. P. Benda and A. Reiter; – 1 ♂, 1 ♀ (NMP 48190, 48191 [S+A]), Choqazanbil, 15 October 1998, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin; – 1 ♀ (SMF 46398 [S+A]), Rafsanjan, 21 April 1974, leg. H. Felten and K. Walch; – 1 ♂, 1 ♀ (NMP 48456, 48457 [S+A]), Sarvestan, 20 April 2000, leg. P. Benda and A. Reiter; – 4 ♂♂ (SMF 34355–34357, 34362 [S+A]), Shush, 21 September 1957, leg. K. Al Robbae; – 2 ♂♂ (NMP 48160, 48161 [S+A]), Si Mili, 12 October 1998, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin; – 1 ♂ (SMF 47843 [S+A]), Tabriz, autumn 1970, collector unlisted. – **Iraq:** 1 ♂, 2 ♀♀, 1 ind. (NMW 21941–21944 [S+A]), Babylon, October–November 1841, leg. T. Kotschy; – 2 ♂♂, 3 ♀♀ (NMW 26309–26313 [S+A]), Karbala, 18 April 1910, leg. V. Pietschmann; – 1 ♂, 3 ♀♀ (NMW 26346–26349 [S+A]), Mosul, 18–31 May 1910, leg. V. Pietschmann. – **Saudi Arabia:** 1 ♂ (BMNH 24.8.2.1. [B]; type specimen of *Pipistrellus kuhlii ikhwanianus* Cheesman et Hinton, 1924), Hufuf, Arabia, date unlisted, leg. R. E. Cheesman. – **Syria:** 5 ♀♀ (NMP 48808–48811 [S+A], 48807 [A]), Abu Kemal, 16 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♀♀ (NMP 48824, 48825 [S+A]), Ain Diwar, 18 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 3 ♀♀ (NMP 48844–48847 [S+A], 48848 [A]), Al Tawani, 21 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 11 ♀♀ (NMW 26294–26306 [S+A]), Ar Raqqa, 28 June 1910, leg. V. Pietschmann; – 3 ♂♂, 3 ♀♀ (NMP 48831, 48832, 48834–48836 [S+A], 48833 [A]), Ayyash, 19 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂, 3 ♀♀ (NMP 48903–48908 [S+A]), Baniyas, 31 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (MNHN 1983-1500 [S+B]), Dimashq, date unlisted, leg. H. Gadeau de Kerville; – 8 ♂♂ (NMP 48029, 48029, 48966–48968 [S+A], 48969–48971 [A]),

Halabiyyeh, 17 June 1998 and 15 April 2001, leg. M. Andreas, P. Benda, P. Munclinger, P. Nová and M. Uhrin; – 2 ♂♂ (NMP 48820, 48821 [S+A]), Khazneh, 17 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 49988 [S+A]), Qala'at Al Hosn, 10 May 2001, leg. R. Lučan; – 1 ♂ (SMF 60364 [S+A]), Qala'at Al Moudik (=Apamea), 25 March 1980, leg. R. Kinzelbach; – 1 ♂ (NMP 49988 [S+A]), Qala'at Al Hosn, 10 May 2001, leg. R. Lučan; – 1 ♂ (NMP 48814 [S+A]), Qala'at Ar Rahba, 17 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂ (NMP 48767–48769 [S+A]), Qala'at Ja'abar, 12 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 48758 [S+A]), Qala'at Najm, 10 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♀♀ (NMP 48888–48890 [S+A]), Qantara, 30 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 48891 [S+A]), Qasr Ibn Wardan, 31 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 1 ♀ (NMP 48929–48931 [S+A]), Qatura, 2 June 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂, 1 ♀ (NMP 48947, 49987 [S+A]), Ras Al Bassit, 29 April 2001, 3 June 2001, leg. M. Andreas, P. Benda, R. Lučan, A. Reiter and D. Weinfurtová; – 26 ♂♂, 8 ♀♀ (NMP 47993–48005, 48784–48786, 48789, 48790, 48948, 48949, 48951, 48952 [S+A], 48787, 48788, 48791, 48792, 48950, 48953–48959 [A]), Rasafah, 16 June 1998, 13 April 2001, 13 May 2001, leg. M. Andreas, P. Benda, P. Nová, P. Munclinger, A. Reiter, M. Uhrin and D. Weinfurtová; – 2 ♂♂, 2 ♀♀ (NMP 48884–48887 [S+A]), Safita, 29 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂, 1 ♀ (NMP 48800–48802 [S+A], 48803 [A]), Sbeikhan, 15 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 5 ♀♀ (NMP 48837–48842 [S+A], 48843 [A]), Tadmor (=Palmyra), 20 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♀♀ (NMP 48862–48864 [S+A]), Talsh'hab, 25 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 1 ♀ (NMP 48034–48036 [S+A]), Tell Sheikh Hamad, 19 June 1998, leg. M. Andreas, P. Benda and M. Uhrin. – **Turkey:** 1 ♀ (SMF 36754 [S+A]), Alanya, Incekum, 24 May 1966, leg. H. Felten et al.; – 5 ♂♂, 5 ♀♀ (SMF 42352–42358, 42361–42363 [S+A]), Alişam, 17 and 25–27 September 1971, leg. H. Felten et al.; – 1 ind. (ZFMK 85.87 [S+B]), Birecik, 28 March 1973, leg. U. Hirsch; – 1 ♂, 1 ♀ (ZFMK 68.244, 68.245 [S+B]), Ceylanpinar, 18 May 1968, leg. H. Mittendorf.

Appendix 2

The specimens used in the genetic analysis are listed according to the classical taxonomy (Simmons 2005).

Species	Locality	Haplotype	GenBank accession #	Microsatellite	Voucher
<i>Pipistrellus deserti</i>	Gabrun, Fezzan, Libya	D1	KM252756	(1)	NMP 48316
<i>Pipistrellus deserti</i>	Gabrun, Fezzan, Libya	D1	–	(5)	NMP 48304
<i>Pipistrellus deserti</i>	Gabrun, Fezzan, Libya	D1	–	(5)	NMP 48305
<i>Pipistrellus deserti</i>	Gabrun, Fezzan, Libya	D1	–	(5)	NMP 48313
<i>Pipistrellus deserti</i>	Gabrun, Fezzan, Libya	D1	–	(5)	NMP 48314
<i>Pipistrellus deserti</i>	Gabrun, Fezzan, Libya	D1	–	(5)	NMP 48315
<i>Pipistrellus deserti</i>	Murzuq, Fezzan, Libya	D1	KM252757	(2)	NMP 48319
<i>Pipistrellus deserti</i>	Germa, Fezzan, Libya	D1	–	(5)	NMP 48320
<i>Pipistrellus deserti</i>	Al Fjayj, Fezzan, Lybia	D1	KM252758	(5)	NMP 48321
<i>Pipistrellus deserti</i>	Oued Drâa, Morocco	D2	KM252759	(5)	NMP 90058
<i>Pipistrellus deserti</i>	Oued Drâa, Morocco	D3	KM252760	(5)	NMP 90059
<i>Pipistrellus deserti</i>	Tamtattouchte, Morocco	D2	KM252761	(5)	NMP 90071
<i>Pipistrellus kuhlii</i>	Khemis, Morocco	K1	KM252765	–	NMP 90024
<i>Pipistrellus kuhlii</i>	Milos, Kilkis, Greece	K1	AJ504444 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus kuhlii</i>	Sparti, Peloponnese, Greece	K1	KM252762	–	NMP 48733
<i>Pipistrellus kuhlii</i>	Sparti, Peloponnese, Greece	K1	KM252763	–	NMP 48735
<i>Pipistrellus kuhlii</i>	Bam, Kerman, Iran	K2	KM252772	–	NMP 48116
<i>Pipistrellus kuhlii</i>	Rasafah, Homs, Syria	K2	–	–	NMP 47992
<i>Pipistrellus kuhlii</i>	Rasafah, Homs, Syria	K2	KM252766	–	NMP 47993
<i>Pipistrellus kuhlii</i>	Tell Sheikh Hamad, Syria	K2	KM252767	–	NMP 48033
<i>Pipistrellus kuhlii</i>	Bastam, W Azarbaijan, Iran	K2	KM252768	–	NMP 48121
<i>Pipistrellus kuhlii</i>	Simili, Khuzestan, Iran	K2	KM252769	–	NMP 48161
<i>Pipistrellus kuhlii</i>	Choqa Zambil, Khuzestan, Iran	K2	KM252770	–	NMP 48190
<i>Pipistrellus kuhlii</i>	Karkurah, Cyrenaica, Libya	K3	KM252773	(5)	NMP 48322
<i>Pipistrellus kuhlii</i>	Al Abyar, Cyrenaica, Libya	K3	–	(5)	NMP 48332
<i>Pipistrellus kuhlii</i>	Tokrah, Cyrenaica, Libya	K4	KM252774	(5)	NMP 48326
<i>Pipistrellus kuhlii</i>	Pir Sohrab, Beluchestan, Iran	K5	AJ504445 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus kuhlii</i>	Chah Reza, Kerman, Iran	K5	KM252775	–	NMP 48428
<i>Pipistrellus kuhlii</i>	Sarvestan, Fars, Iran	K2	KM252771	–	NMP 48455
<i>Pipistrellus kuhlii</i>	Geneva, Switzerland	K1	–	(5)	MHNG 1685.018
<i>Pipistrellus kuhlii</i>	Geneva, Switzerland	K8	KM252776	(5)	MHNG 1916.061
<i>Pipistrellus kuhlii</i>	Geneva, Switzerland	K8	KM252777	(5)	MHNG 1828.067
<i>Pipistrellus kuhlii</i>	Valais, Switzerland	K1	KM252764	(5)	MHNG 1868.076
<i>Pipistrellus kuhlii</i>	Vaud, Switzerland	K1	–	(5)	MHNG 1906.049
<i>Pipistrellus kuhlii</i>	Geneva, Switzerland	K8	–	(5)	MHNG 1869.032
<i>Pipistrellus kuhlii</i>	Geneva, Switzerland	K8	–	(5)	MHNG 1885.089
<i>Pipistrellus kuhlii</i>	Valladolid, Spain	K8	AJ426619 ^a	–	Pestano et al. 2003
<i>Pipistrellus kuhlii</i>	northern Spain	C1	DQ120841 ^a	–	Ibáñez et al. 2006
<i>Pipistrellus kuhlii</i>	southern Spain	C4	DQ120844 ^a	–	Ibáñez et al. 2006
<i>Pipistrellus kuhlii</i>	Fuerteventura, Canary Islands	PK03	AJ426609 ^a	–	Pestano et al. 2003
<i>Pipistrellus maderensis</i>	Tenerife, Canary Islands	Pma1	AJ426610 ^a	–	Pestano et al. 2003
<i>Pipistrellus maderensis</i>	La Gomera, Canary Islands	Pma5	AJ426614 ^a	–	Pestano et al. 2003
<i>Pipistrellus maderensis</i>	La Palma, Canary Islands	Pma11	AJ426632 ^a	–	Pestano et al. 2003
<i>Pipistrellus abramus</i>	Chiayi Co, Taiwan		AJ504448 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus abramus</i>	Miyazaki, Japan		AB085739 ^a	–	Sakai et al. 2003
<i>Pipistrellus hanaki</i>	Cyrenaica, Libya		AY316333 ^a	–	Hulva et al. 2004
<i>Pipistrellus hesperidus</i>	Knysna, South Africa		AJ841968 ^a	–	Stadelmann et al. 2004a
<i>Pipistrellus cf. javanicus</i>	Miao-Li Co, Taiwan		AJ504447 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus nathusii</i>	Lausanne, Switzerland		AJ504446 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus pipistrellus</i>	Macedonia, Greece		AJ504443 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus pipistrellus</i>	Tamtattouchte, SW Morocco		KM252778	–	NMP 90076
<i>Pipistrellus pipistrellus</i>	Azrou, Morocco		AY582283 ^a	–	Benda et al. 2004b
<i>Pipistrellus pygmaeus</i>	Macedonia, Greece		AJ504441 ^a	–	Stadelmann et al. 2004b
<i>Pipistrellus pygmaeus</i>	Mt Trodos, Cyprus		AJ504442 ^a	–	Stadelmann et al. 2004b

The collecting locality, haplotype designation, GenBank accession number, multilocus genotype (i.e., number of microsatellite loci, if available) and location of voucher specimens (NMP – National Museum, Prague, Czech Republic; MHNG – Natural History Museum, Geneva, Switzerland) are also given. Accession numbers followed by an ^a are taken from the literature.

Appendix 3

Experimental conditions used to amplify five microsatellite loci in 22 samples of *Pipistrellus kuhlii* s.l. from North Africa and Switzerland.

Primer name	Dye on forward	Multiplex number	Annealing temperature	Number of alleles
EF6	DY751 (black)	1	55–50°C	9
NN8	BMN6 (green)	1	55–50°C	19
Paur05	DY751 (black)	2	65–60°C	8
L45	DY751 (black)	3	65–60°C	10
Ppip05	BMN6 (green)	3	65–60°C	7

Full genotypes of all samples can be obtained upon request to the senior author.

References

- Aggundey, I.R. and D.S. Schlitter. 1984. Annotated checklist of the mammals of Kenya. I. Chiroptera. Ann. Carnegie Mus. 53: 119–161.
- Allen, G.M. 1911. Bats of the British East Africa. Bull. Mus. Comp. Zoöl. Harvard Coll. 54: 321–331.
- Allen, G.M. 1939. A checklist of African mammals. Bull. Mus. Comp. Zoöl. Harvard Coll. 83: 1–763.
- Anciaux de Faveaux, M. 1976. Distribution des Chiroptères en Algérie, avec notes écologiques et parasitologiques. Bull. Soc. Hist. Natur. Afr. Nord 67: 69–80.
- Anderson, J. 1902. Zoology of Egypt: Mammalia. Revised and completed by W. E. de Winton. Hugh Rees, Ltd., London, UK. pp. 374.
- Artyushin, I.V., A.A. Bannikova, V.S. Lebedev and S.V. Kruskop. 2009. Mitochondrial DNA relationships among North Palaearctic *Eptesicus* (Vespertilionidae, Chiroptera) and past hybridization between common serotine and northern bat. Zootaxa 2262: 40–52.
- Aulagnier, S., P. Haffner, A.J. Mitchell-Jones, F. Moutou and J. Zima. 2008. Guide des mammifères d'Europe, d'Afrique du Nord et du Moyen-Orient. Delachaux et Niestlé SA, Paris, France. pp. 271.
- Ballard, J.W.O. and M.C. Whitlock. 2004. The incomplete natural history of mitochondria. Mol. Ecol. 13: 729–744.
- Barlow, K.E., G. Jones and E.M. Barratt. 1997. Can skull morphology be used to predict ecological relationships between bat species? A test using two cryptic species of pipistrelle. Proc. R. Soc. Lond. B 264: 1695–1700.
- Benda, P. and P. Vallo. 2012. New look on the geographical variation in *Rhinolophus clivosus* with description of a new horseshoe bat species from Cyrenaica, Libya. Vespertilio 16: 69–96.
- Benda, P., M. Ruedi and S. Aulagnier. 2004a. New data on the distribution of bats (Chiroptera) in Morocco. Vespertilio 8: 13–44.
- Benda, P., P. Hulva and J. Gaisler. 2004b. Systematic status of African populations of *Pipistrellus pipistrellus* complex (Chiroptera: Vespertilionidae), with a description of a new species from Cyrenaica, Libya. Acta Chiropterol. 6: 193–217.
- Benda, P., J. Červený, A. Konečný, A. Reiter, M. Ševčík, M. Uhrin and P. Vallo. 2010. Some new records of bats from Morocco (Chiroptera). Lynx, n.s. 41: 151–166.
- Benda, P., P. Vallo and A. Reiter. 2011. Taxonomic revision of the genus *Asellia* (Chiroptera: Hipposideridae) with a description of a new species from southern Arabia. Acta Chiropterol. 13: 245–270.
- Benda, P., K. Faizolâhi, M. Andreas, J. Obuch, A. Reiter, M. Ševčík, M. Uhrin, P. Vallo and S. Ashrafi. 2012. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 10. Bat fauna of Iran. Acta Soc. Zool. Bohem. 76: 163–582.
- Berthier, P., L. Excoffier and M. Ruedi. 2006. Recurrent replacement of mtDNA and cryptic hybridization between two sibling bat species *Myotis myotis* and *Myotis blythii*. Proc. R. Soc. Lond. B 273: 3101–3109.
- Bradley, R.D. and R.J. Baker. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. J. Mammal. 82: 960–973.
- Bray T.C., O.B. Mohammed and A.N. Alagaili. 2013. Phylogenetic and demographic insights into Kuhl's pipistrelle, *Pipistrellus kuhlii*, in the Middle East. Plos One 8: e57306.
- Burland, T.M., E.M. Barratt and P.A. Racey. 1998. Isolation and characterization of microsatellite loci in the brown long-eared bat, *Plecotus auritus*, and cross-species amplification within the family Vespertilionidae. Mol. Ecol. 7: 136–138.
- Çoraman, E., A. Furman, A. Karataş and R. Bilgin. 2013. Phylogeographic analysis of Anatolian bats highlights the importance of the region for preserving the Chiropteran mitochondrial genetic diversity in the Western Palaearctic. Conserv. Genet. 14: 1205–1216.
- Corbet, G.B. 1978. The Mammals of the Palaearctic Region: a taxonomic review. British Museum (Natural History) and Cornell University Press, London, UK and Ithaca, USA. pp. 314.
- Corbet, G.B. 1984. The Mammals of the Palaearctic Region: a taxonomic review. Supplement. British Museum (Natural History), London, UK. pp. 46.
- Dalhousi, R., P. Aissa and S. Aulagnier. 2011. Taxonomie et répartition des Chiroptères de Tunisie. Rev. Suisse Zool. 118: 1–28.
- De Beaux, O. 1923. Di alcuni chiropteri africani del museo civico di Milano. Atti Soc. Ital. Sci. Natur. Milano 62: 91–101.
- Decher, J., D.A. Schlitter and R. Hutterer. 1997. Noteworthy records of small mammals from Ghana with special emphasis on the Accra plains. Ann. Carnegie Mus. 66: 209–227.
- Deleuil, R. and A. Labbé. 1955a. Contributions à l'étude des chauves-souris de Tunisie. Bull. Soc. Sci. Natur. Tunisie 8: 39–55.
- Deleuil, R. and A. Labbé. 1955b. Sur la variabilité de la Pipistrelle de Kuhl (*Pipistrellus Kuhl*). Bull. Soc. Sci. Natur. Tunisie 8: 237–241.
- de Queiroz, K. 2007. Species concepts and species delimitation. Syst. Biol. 56: 879–886.
- Dollman, G. 1914. Notes on a collection of East African mammals presented to the British Museum by Mr. G. P. Cosens. Proc. Zool. Soc. Lond. 1914: 307–318.
- Ellerman, J.R. and T.C.S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian Mammals 1758 to 1946. British Museum (Natural History), London, UK. pp. 810.
- Evin, A., V. Nicolas, G. Beuneux, R. Toffoli, C. Cruchaud, A. Couloux and J.M. Pons. 2011. Geographical origin and endemism of Corsican Kuhl's pipistrelles assessed from mitochondrial DNA. J. Zool. 284: 31–39.

- Fischer, J.B. 1829. Synopsis mammalium. J.G. Cottae, Stuttgart, Württemberg. pp. 527.
- Foley, J.A., M.T. Coe, M. Scheffer and G.L. Wang. 2003. Regime shifts in the Sahara and Sahel: Interactions between ecological and climatic systems in northern Africa. *Ecosystems* 6: 524–539.
- Gaisler, J. and K. Kowalski. 1986. Results of the netting of bats in Algeria (Mammalia: Chiroptera). *Věst. Čs. Společ. Zool.* 50: 161–173.
- Gaisler, J., G. Madkour and J. Pelikán, 1972. On the bats (Chiroptera) of Egypt. *Acta Sci. Natur. Acad. Sci. Bohemoslov. Brno, S.N.* 6: 1–40.
- Geffroy Saint-Hilaire, E. 1818. Description des mammifères qui se trouvent en Égypte. In: Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française. Histoire naturelle. Imprimerie Impériale, Paris, France. pp. 99–135.
- Goudet, J. 1999. PCA-GEN, Version 1.2 URL: <http://www.unil.ch/izea/softwares/pcagen.html>, Lausanne, Switzerland. Accessed on 16 June 2014.
- Grimmberger, E. and K. Rudloff. 2009. Atlas der Säugetiere Europas, Nordafrikas und Vorderasiens. Natur und Tier – Verlag GmbH, Münster, Germany. pp. 495.
- Grubb, P., T.S. Jones, A.G. Davies, E. Edberg, E.D. Starin and J.E. Hill. 1998. Mammals of Ghana, Sierra Leone and Gambia. The Trendline Press, Zennor, UK. pp. vi+265.
- Guillaumet, A., P.A. Crochet and J.M. Pons. 2008. Climate-driven diversification in two widespread *Galerida* larks. *BMC Evol. Biol.* 8(32): 1–22.
- Hanák, V. and A. Elgadi. 1984. On the bat fauna (Chiroptera) of Libya. *Věst. Čs. Společ. Zool.* 48: 165–187.
- Hayman, R.W. and J.E. Hill. 1971. Part 2. Order Chiroptera. In: (J. Meester and H. W. Setzer, eds.) *The mammals of Africa: an identification manual*. Smithsonian Institution Press, Washington, DC, USA. pp. 1–73.
- Heim de Balsac, H. 1934. Mission saharienne Augérias-Drapper 1927–1928. *Ann. Mus. Natn. Hist. Natur.* 6: 482–489.
- Heim de Balsac, H. 1936. Biogéographie des mammifères et des oiseaux de l'Afrique du Nord. *Bull. Biol. Fr. Belg.* 21(Suppl.): 1–446.
- Hill, J.E. 1977. A review of the Rhinopomatidae (Mammalia: Chiroptera). *Bull. Brit. Mus. (Natur. Hist.), Zool. Ser.* 32: 29–43.
- Hill, J.E. and D.L. Harrison. 1987. The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus. *Bull. Brit. Mus. (Natur. Hist.), Zool. Ser.* 52: 225–305.
- Hollister, N. 1918. East African mammals in the United States National Museum. I. Insectivora, Carnivora, and Chiroptera. *Bull. US Natl. Mus.* 99: 1–194.
- Horáček, I., V. Hanák and J. Gaisler. 2000. Bats of the Palaearctic region: a taxonomic and biogeographic review. In: (B. W. Wozoszyn, ed.) *Proceedings of the VIIIth European Bat Research Symposium. Volume I. Approaches to biogeography and ecology of bats*. Chiropterological Information Center, Kraków, Poland. pp. 11–157.
- Hufnagl, E. 1972. *Libyan Mammals*. Oleander Press, London, UK. pp. 85.
- Huelsenbeck, J.P. and F. Ronquist. 2001. MrBAYES: Bayesian inference of phylogenetic trees. *Bioinform. Appl. Note* 17: 754–755.
- Hulva, P., I. Horáček, P.P. Strelkov and P. Benda. 2004. Molecular architecture of *Pipistrellus pipistrellus/Pipistrellus pygmaeus* complex (Chiroptera: Vespertilionidae): further cryptic species and Mediterranean origin of the divergence. *Mol. Phylogenet. Evol.* 32: 1023–1035.
- 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). *BMC Evol. Biol.* 7: 1–15.
- Ibáñez, C., J.L. García-Mudarra, M. Ruedi, B. Stadelmann and J. Juste. 2006. The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterol.* 8: 277–297.
- Jones, J.K. Jr., K.F. Koopman, N. Sullivan, J. Ramirez-Pulido, O.L. Rossolimo and S. Wang. 1982. Family Vespertilionidae. In: (J.H. Honacki, K.E. Kinman, and J.W. Koepl, eds.) *Mammal species of the world. A taxonomic and geographic reference*. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, KA, USA. pp. 170–205.
- Juste, J., P. Benda, J.L. García-Mudarra and C. Ibáñez. 2013. Phylogeny and systematics of Old World serotine bats (genus *Eptesicus*, Vespertilionidae, Chiroptera): an integrative approach. *Zool. Scripta* 42: 441–457.
- Klapotcz, B. 1909. Beitrag zur Kenntnis der Säuger von Tripolis und Barka. *Zool. Jb., Abth. Syst., Geograph. Biol. Tiere* 1909: 237–272.
- Kocher, T.D., W.K. Thomas, A. Meyer, S.V. Edwards, S. Pääbo, F.X. Villablanca and A.C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proc. Natl. Acad. Sci. NY* 86: 6196–6200.
- Kock, D. 1969. Die Fledermaus-Fauna des Sudan (Mammalia, Chiroptera). *Abh. Senckenberg. Naturforsch. Gesell.* 521: 1–238.
- Kock, D. 1999. The Egyptian *Vespertilio pipistrellus aegyptius* Fischer 1829, a nomen dubium (Mammalia, Chiroptera, Vespertilionidae). *Senckenberg. Biol.* 79: 101–105.
- Kock, D. 2001. Identity of the African *Vespertilio hesperida* Temminck 1840 (Mammalia, Chiroptera, Vespertilionidae). *Senckenberg. Biol.* 81: 277–283.
- Koopman, K.F. 1975. Bats of The Sudan. *Bull. Am. Mus. Natur. Hist.* 154: 355–443.
- Koopman, K.F. 1993. Order Chiroptera. In: (D.E. Wilson and D.M. Reeder, eds.) *Mammal species of the world. A taxonomic and geographic reference. Second edition*. Smithsonian Institution Press, Washington, DC, USA and London, UK. pp. 137–241.
- Koopman, K.F. 1994. Chiroptera: systematics. *Handbook of zoology. Volume VIII. Mammalia. Part 60*. Walter de Gruyter, Berlin, Germany and New York, NY, USA. pp. 224.
- Koopman, K., R.E. Mumford and J.F. Heisterberg. 1978. Bat records from Upper Volta, West Africa. *Am. Mus. Novit.* 2643: 1–6.
- Kowalski, K. and B. Rzebik-Kowalska. 1991. *Mammals of Algeria*. Zakład Narodowy im. Ossolińskich, Wrocław, Poland. pp. 371.
- Kuhl, H. 1817. *Die deutschen Fledermäuse*. Privately published, Hanau, Prussia. pp. 67.
- Lanza, B. 1959. Notizie sull'osso peniale dei chiroterri europei e su alcuni casi di paralelismo morfologico. *Monit. Zool. Ital.* 67: 3–14.
- Le Berre, M. 1990. *Faune du Sahara. 2. Mammifères*. Lechevalier and R. Chabaud, Paris, France. pp. 360.
- Lewis, R.E. and D.L. Harrison. 1962. Notes on bats from the Republic of Lebanon. *Proc. Zool. Soc. Lond.* 138: 473–486.
- Madkour, G. 1977. Further observations on bats (Chiroptera) of Egypt. *Agricult. Res. Rev.* 55: 173–184.

- Mayer, F., C. Dietz and A. Kiefer. 2007. Molecular species identification boosts bat diversity. *Front. Zool.* 4(4): 1–5.
- Miller, S.A., D.D. Dykes and H.F. Polesky. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Res.* 16: 1215.
- Nowak, R.M. 1994. Walker's bats of the world. The Johns Hopkins University Press, London, UK. pp. 288.
- Nylander, J.A.A. 2004. MrModeltest v. 2.3. Programm distributed by the author. Uppsala University, Sweden.
- Owen, R.D. and M.B. Qumsiyeh. 1987. The subspecies problem in the trident leaf-nosed bat, *Asellia tridens*: homomorphism in widely separated populations. *Ztschr. Säugetierk.* 52: 329–337.
- Panouse, J. 1951. Les chauves-souris du Maroc. *Trav. Inst. Sci. Chérif.* 1: 1–121.
- Pavlinov I.Ā, A.V. Borisenko, S.V. Kruskop and E.L. Āhontov. 1995. Mlekopitaŭšie Evrazii. II. Non-Rodentia. Sistematiko-geografičeskii spravočnik [Mammals of Eurasia. II. Non Rodentia. Systematic-geographical review]. *Arch. Zool. Mus. Moscow State Univ.* 33: 1–336 (in Russian).
- Petri, B., S. Pääbo, A. von Haeseler and D. Tautz. 1997. Paternity assessment and population subdivision in a natural population of the Larger Mouse-eared bat *Myotis myotis*. *Mol. Ecol.* 6: 235–242.
- Pestano, J., R.P. Brown, N.M. Suárez and S. Fajardo. 2003. Phylogeography of pipistrelle-like bats within the Canary Islands, based on mtDNA sequences. *Mol. Phylogenet. Evol.* 26: 56–63.
- Qumsiyeh, M.B. 1985. The bats of Egypt. *Spec. Publ. Mus. Texas Tech Univ.* 23: 1–102.
- Racey, P.A., E.M. Barratt, T.M. Burland, R. Deaville, D. Gotelli, G. Jones and S.B. Pierny. 2007. Microsatellite DNA polymorphism confirms reproductive isolation and reveals differences in population genetic structure of cryptic pipistrelle bat species. *Biol. J. Linn. Soc.* 90: 539–550.
- Rambaut, A. and A.J. Drummond. 2009. Tracer v1.5. URL: <http://beast.bio.ed.ac.uk/Tracer>. Accessed on 20 January 2014.
- Rode, P. 1947. Les mammifères de l'Afrique du Nord. I. La Terre et la Vie 94: 120–142.
- Ruedi, M. and F. Mayer. 2001. Molecular systematics of bats of the genus *Myotis* (Vespertilionidae) suggests deterministic ecomorphological convergences. *Mol. Phylogenet. Evol.* 21: 436–448.
- Sakai, T., Y. Kikkawa, K. Tschuchiya, M. Harada, M. Kanoe, M. Yoshiyuki and H. Yonekawa. 2003. Molecular phylogeny of Japanese Rhinolophidae based on variations in the complete sequence of the mitochondrial cytochrome b gene. *Genes Genet. Syst.* 78: 179–189.
- Setzer, H.W. 1957. A review of Libyan mammals. *J. Egypt. Publ. Health Assoc.* 32: 41–82.
- Simmons, N.B. 2005. Order Chiroptera. In: (D.E. Wilson, and D.M. Reeder, eds.) *Mammal species of the world. A taxonomic and geographic reference. Third edition. Volume 1.* The Johns Hopkins University Press, Baltimore, MD, USA. pp. 312–529.
- Smith, M.F. and J.L. Patton. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. *Biol. J. Linn. Soc.* 50: 149–177.
- Stadelmann, B., D.S. Jacobs, C. Schoeman and M. Ruedi. 2004a. Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences. *Acta Chiropterol.* 6: 177–192.
- Stadelmann, B., G. Herrera, J. Arroyo-Cabrales and M. Ruedi. 2004b. Molecular systematics of the piscivorous bat *Myotis (Pizonyx) vivesi*. *J. Mammal.* 85: 133–139.
- Stamatakis, A. 2006. RAXML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Thomas, O. 1902. On the mammals collected during the Whitaker expedition to Tripoli. *Proc. Zool. Soc. Lond.* 1902: 2–13.
- Toschi, A. 1954. Elenco preliminare dei mammiferi della Libia. *Suppl. Ric. Zool. Appl. Caccia, Univ. Bologna* 2: 241–273.
- Vallo, P., P. Benda, J. Červený and P. Koubek. 2013. Conflicting mitochondrial and nuclear paralogy in small-sized West African house bats (Vespertilionidae). *Zool. Scr.* 42: 1–12.
- Van Cakenberghe, V. and P. Benda. 2013. *Pipistrellus deserti* Desert Pipistrelle. In: (M. Happold and D.C.D. Happold, eds.) *Mammals of Africa. Volume IV. Hedgehogs, shrews and bats.* Bloomsbury, London, UK. pp. 619–621.
- Van Cakenberghe, V. and F. De Vree. 1994. A revision of the Rhinopomatidae Dobson 1872, with the description of a new subspecies (Mammalia: Chiroptera). *Senckenberg. Biol.* 73: 1–24.
- Van Cakenberghe, V. and M. Happold. 2013. *Pipistrellus aero* Mt Gargues Pipistrelle. In: (M. Happold and D.C.D. Happold, eds.) *Mammals of Africa. Volume IV. Hedgehogs, shrews and bats.* Bloomsbury, London, UK. pp. 608–610.
- Veith, M., M. Mucedda, A. Kiefer and E. Pidinchetta. 2011. On the presence of pipistrelle bats (*Pipistrellus* and *Hypsugo*; Chiroptera: Vespertilionidae) in Sardinia. *Acta Chiropterol.* 13: 89–99.
- Vonhof, M.J., C.S. Davis, M.B. Fenton and C. Strobeck. 2002. Characterization of dinucleotide microsatellite loci in big brown bats (*Eptesicus fuscus*), and their use in other North American vespertilionid bats. *Mol. Ecol. Notes* 2: 167–169.
- Wassif, K. and G. Madkour. 1972. The structure of the os penis in Egyptian bats (Microchiroptera). *Bull. Zool. Soc. Egypt* 24: 45–51.
- Watson, J.M. 1951. The wild mammals of Teso and Karamoja. VI. Insectivora and Chiroptera. *Uganda J.* 15: 92–106.
- Wei, L., P.Y. Hua, W.W. Shao, C.M. Miller-Butterworth and S.Y. Zhang. 2009. Isolation and characterization of microsatellite loci in the Japanese pipistrelle (*Pipistrellus abramus*). *Conserv. Genet.* 10: 677–679.
- Zavattari, E. 1934. Prodomo della fauna della Libia. Tipografia già cooperativa, Pavia, Italy. pp. viii+1234.
- Zavattari, E. 1937. I Vertebrati della Libia. In: *Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand. Vol. II. Latvija, Riga, Latvia.* pp. 526–560.