Peter Vallo*, Petr Benda, Jaroslav Červený and Petr Koubek

Phylogenetic position of the giant house bat *Scotophilus nigrita* (Chiroptera, Vespertilionidae)

Abstract: The giant house bat *Scotophilus nigrita*, one of the largest vespertilioniform bat species in the world, is a poorly known taxon, especially with respect to its phylogenetic relationships to congeneric species. Its phylogenetic position was thus assessed by analysing DNA sequences of single mitochondrial and nuclear genes. Based on the mitochondrial cytochrome *b*, *S. nigrita* was found to be paraphyletic with respect to continental African species *S. colias*, *S. dinganii*, *S. nigritellus* and *S. viridis*. Analysis of sequences of the nuclear zinc finger protein gene on the Y chromosome corroborated the general pattern of the cytochrome *b* phylogeny, although phylogenetic relationships were poorly resolved. These results clearly contradict the published data on *S. nigrita* from Kenya for both markers, rendering the hypothesis of historical hybridization with *S. colias* implausible and questioning the taxonomic affiliation of the particular Kenyan sequence. A deep split in the cytochrome *b* phylogeny between *S. nigrita* from West and Southern Africa reached sequence divergence values of 7.6% to 8.1%, a finding that supports taxonomic elevation of the two currently recognized subspecies into separate species *S. nigrita* and *S. alvenslebeni*.

Keywords: cranial morphometrics; cytochrome *b*; phylogeny; zinc finger protein Y.

***Corresponding author: Peter Vallo,** Institute of Vertebrate Biology AS CR, v.v.i., Květná 8, 603 65 Brno, Czech Republic, e-mail: vallo@ivb.cz; and Institute of Experimental Ecology, University Ulm, Albert Einstein Allee 11, M25, 89069 Ulm, Germany
Petr Benda: Department of Zoology, National Museum (Natural History), Václavské nám. 68, 11579 Praha 1, Czech Republic; and Faculty of Science, Department of Zoology, Charles University, Viničná 7, 12844 Praha 2, Czech Republic
Jaroslav Červený: Faculty of Forestry and Wood Sciences, Department of Game Management and Wildlife Biology, Czech University of Life Sciences, Kamýcká 129, 16521 Praha 6, Czech Republic
Petr Koubek: Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Květná 8, 60365 Brno, Czech Republic; and Faculty of Forestry and Wood Sciences, Department of Game Management and Wildlife Biology, Czech University of Life Sciences, Kamýcká 129, 16521 Praha 6, Czech Republic

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Introduction

The giant house bat *Scotophilus nigrita* (Schreber, 1774) is the largest representative of the genus *Scotophilus* Leach, 1821 (Vespertilionidae), a common faunal element of the African and Asian tropics (Robbins et al. 1985, Simmons 2005, Horáček et al. 2006). This species is also one of the largest vespertilioniform bats in the world, with forearm length over 70 mm and body mass over 50 g (De Vree 1973, Monadjem et al. 2010, Happold 2013). Although its distribution spreads over sub-Saharan Africa from Senegal to Kenya and South Africa, data on its occurrence and biology are rather limited, which is probably associated with only about 35 specimens known to science (Dobson 1875, Dalquest 1965, De Vree 1973, Robbins et al. 1985, Trujillo et al. 2009, Monadjem et al. 2010, Bakwo et al. 2012, Cohen and Linton 2013). Characterisation of phylogenetic relationships of *S. nigrita* to its congeners remains virtually nonexistent. The only published information comes from a molecular phylogenetic study by Trujillo et al. (2009), which included one specimen of *S. nigrita* from Kenya. However, this specimen bore a mitochondrial haplotype of *S. dinganii* (Smith 1833), thus the actual phylogenetic position of *S. nigrita* remains unknown.

In this study, the phylogenetic position of *Scotophilus nigrita* within the genus *Scotophilus* is reported based on yet unpublished or recently recorded specimens. Sequences of the cytochrome *b* gene (*cytb*) are used herein as the main, broadly employed genetic marker (Baker and Bradley 2006, Tobe et al. 2010), and the paternally inherited gene for zinc finger protein on the Y chromosome (*zfy*) as a nuclear alternative for independent assessment of phylogeny (Cathey et al. 1998). Both markers have been successfully used in previous phylogenetic studies on *Scotophilus* (Trujillo et al. 2009, Vallo et al. 2011, 2013). Furthermore, some particular details of genetic variation of *S. nigrita* across Africa in connection with morphometric data are discussed with respect to current taxonomy.

Materials and methods

Three specimens of *Scotophilus nigrita* originating from West Africa (Table 1, Figures 1 and 2) were included: two were captured in 2008 in northwestern Senegal and the other in 2007 in western Benin. These specimens are housed as ethanol-preserved vouchers with their skulls extracted in the collections of the Institute of Vertebrate Biology in Brno (IVB) and National Museum in Prague (NMP), Czech Republic. Only one specimen was included from Southern Africa (Table 1, Figure 1). It was captured in 2009 in Hectorspruit, South Africa, and was examined and tissue sampled as an ethanol-preserved voucher with its skull extracted in the collection of the Durban Natural Science Museum in Durban, South Africa (DM). An additional specimen from the Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa (TM), was reviewed for morphological comparison (Tables 1 and Table 2). This specimen can be matched with an unpublished fragment of *cytb* sequence available in GenBank (D. Jacobs, pers. comm.). The type specimen of *S. gigas* Dobson, 1875 from Nigeria housed in the Natural History Museum, London, UK (BMNH), was also included in the morphological comparison. Specimens were measured for one external and 15 cranial dimensions using mechanical callipers as described in Vallo et al. (2011, 2013). Given that the number of the examined specimens was low and that all of them were males except for one specimen, sexual dimorphism was not considered in the morphological comparison.

Total genomic DNA was extracted from ethanol-preserved tissue samples (spleen, muscle) of the four available specimens using commercial kits, and the complete *cytb* and a fragment of *zfy* were PCR amplified, sequenced, assembled and aligned as described in Vallo et al. (2011, 2013). Additional sequences of congeneric species published by Trujillo et al. (2009), including those of *Scotophilus nigrita* from Kenya (Table 1), and Vallo et al. (2011, 2013) were included into the alignment, with *S. nux* Thomas, 1904 and *S. kuhlii* Leach, 1821 used as outgroup taxa for rooting phylogenetic trees. Phylogenetic analysis was done using PAUP* 4.10b (Sinauer Associates, Sunderland, MA, USA) under maximum parsimony (MP) using heuristic search with tree bisection-reconnection swapping algorithm on 100 random additions of sequences. Reliability of branching pattern was assessed by bootstrapping using 1000 pseudoreplicates.

Phylogeny was further estimated using Bayesian inference (BI) in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) under the general time-reversible model with gamma-distributed evolutionary rates (GTR+Γ; Tavaré 1986, Yang 1996), as suggested by the program Modeltest 3.7 (Posada and Crandall 1998). Two independent simultaneous Metropolis-coupled MCMC runs of four chains were run for 10^6 generations, sampled every 100 generations, starting from random trees. The first 2500 sampled trees were discarded as burn-in and a 50% majority rule consensus tree was constructed. Sequence divergences were expressed as percentual pairwise Kimura two-parameter genetic distances (K2P; Kimura 1980) to allow comparison with other bat groups and particularly with members of the genus *Scotophilus* (Baker and Bradley 2006, Vallo et al. 2011, 2013). Nuclear *zfy* sequences were also analyzed using MP and BI methods. Gaps were treated either as missing data or as fifth state in MP analysis and coded as standard data in mixed model assay together with Bayesian analysis to include insertion-deletion signal into phylogenetic reconstruction (Simmons and Ochoterena 2000). Additionally, median-joining network (Bandelt et al. 1999) was constructed from the *zfy* haplotypes in Network 4.6.0.0 (Fluxus Technology, Clare, Suffolk, UK; fluxus-engineering.com).

Table 1 List of specimens of *Scotophilus nigrita* used in the study and their accession numbers in GenBank.

Specimen	Sex	Country	Locality	Coordinates	*cytb*	*zfy*
IVB Sen1967	♂	Senegal	Diadam	16° 22′ N, 16° 16′ W	KF305855	KF305858
IVB Sen1968	♂	Senegal	Diadam	16° 22′ N, 16° 16′ W	–	–
NMP 91889	♂	Benin	Maningri	08° 59′ N, 01° 42′ E	KF305856	–
BMNH 72.10.24.5[a]	♀	Nigeria	Lagos	06° 27′ N, 03° 24′ E	–	–
DM 9873	♂	South Africa	Hectorspruit	25° 25′ S, 31° 41′ E	KF305857	–
TM 47626	♂	South Africa	Komatiepoort	25° 26′ S, 31° 56′ E	DQ459068	–
CM 102256[b]	♂	Kenya	Taveta	03° 23′ S, 37° 42′ E	EU750955	EU751020

[a]Type specimen of *S. gigas* Dobson, 1875.

[b]Specimen published by Trujillo et al. (2009); for the collection acronyms in specimen numbers see Materials and methods.

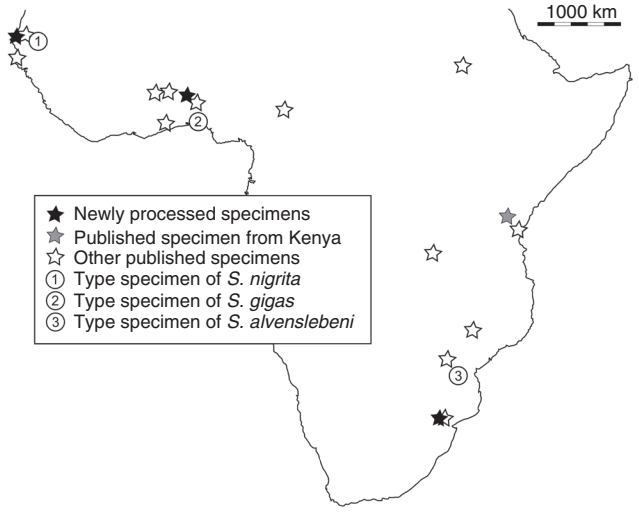

Figure 1 Distribution of *Scotophilus nigrita* with new and published localities reliably verified from references cited in this study and linked to particular voucher specimens. Type localities of *S. nigrita* and *S. alvenslebeni* are placed approximately in the regions of Senegal River, Senegal and Zinave, Save River, Mozambique according to the respective descriptions by Schreber (1774) and Dalquest (1965).

Results

Complete *cytb* sequences were obtained from all four newly processed *Scotophilus nigrita* specimens and corresponded to three unique haplotypes from Senegal, Benin and South Africa (Table 1, Figure 1). The South African haplotype was found to be identical with the unpublished partial sequence of the South African *S. nigrita* with Genbank accession number DQ459068 on the corresponding 534 bp. Partial *zfy* sequences were obtained only from the West African specimens and corresponded to one unique haplotype (Table 1). Amplification from the South African specimen did not yield any product despite intensive effort. All new unique sequences were submitted to GenBank and can be retrieved under accession numbers KF305855–KF305858 (Table 1).

In the MP tree, *Scotophilus nigrita* haplotypes were supported as a monophyletic clade, positioned in unsupported sister relationship to *S. robustus* Milne-Edwards, 1881 from Madagascar. In the BI tree (Figure 2), *S. nigrita* was actually reconstructed within a polytomy of several lineages representing individual species and a lineage containing strongly supported crown group of *S. colias* Thomas, 1904, *S. dinganii*, *S. nigritellus* de Winton, 1899, and *S. viridis* (Peters 1852). Genetic divergence between *S. nigrita* and other *Scotophilus* species ranged from 9.8 to 15.4%. Within the *S. nigrita* clade, a deep split divided the West African and Southern African lineages, with genetic divergence values of 7.6–8.1%. The published *cytb* sequence of *S. nigrita* specimen from Kenya clustered within the *S. colias* clade (*sensu* Vallo et al. 2011), thus in paraphyletic relationship to the West and South African specimens. Similarly, difference in the *zfy* fragment between the Kenyan haplotype and the new *S. nigrita* haplotype was rather marked. Not only did the sequences differ by four substitutions and one 1-bp

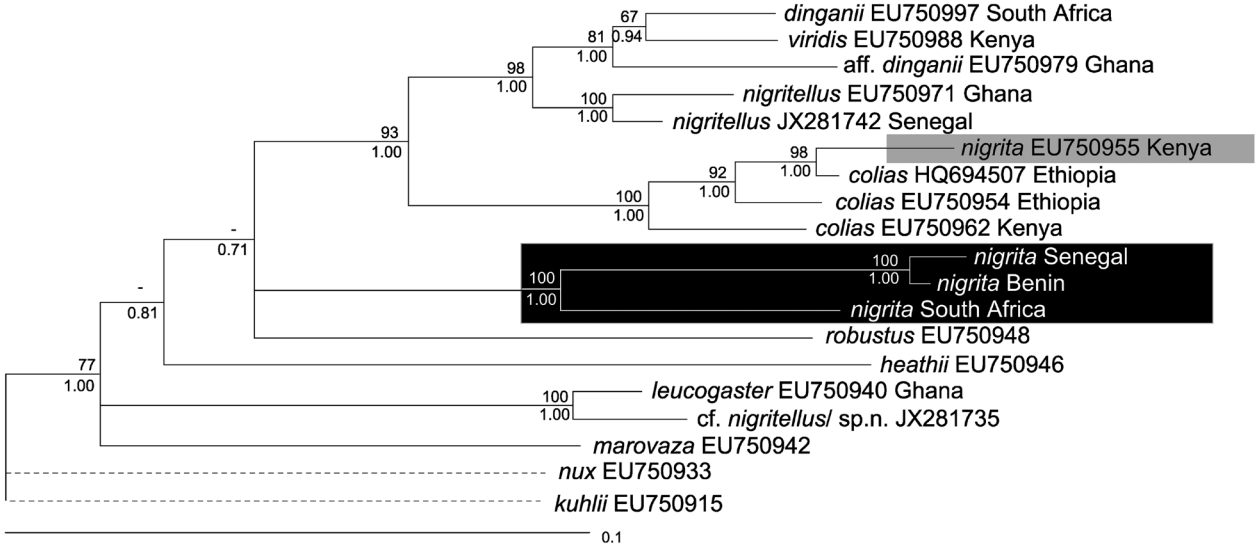

Figure 2 Bayesian *cytb* tree showing phylogenetic position of *Scotophilus nigrita* within the genus *Scotophilus*. Nodal support is given for MP above and for BI below the respective nodes. Grayscale highlighting indicates paraphyletic relationship between *S. nigrita* s. str. from West and South Africa (black) and published *S. nigrita* from Kenya (gray).

Table 2 External and cranial measurements of the examined specimens of *Scotophilus nigrita*.

Specimen	IVB Sen1967	IVB Sen1968	NMP 91889	BMNH 72.10.24.5[a]	DM 9873	TM 47626	CM 102256[b]
Forearm length	84.8	85.1	87.8	86.0	80.0	78.8	78.4
Greatest length of skull	31.11	31.02	31.08	32.31	28.42	27.58	–
Condylobasal length	27.44	27.54	27.67	28.09	26.01	24.87	25.4
Zygomatic width	20.89	20.46	21.04	21.31	20.67	20.13	19.9
Interorbital width	6.83	6.46	6.75	6.48	6.62	6.34	6.6
Infraorbital width	10.47	10.26	10.74	10.79	10.82	10.45	–
Braincase width	13.85	13.33	13.44	13.31	12.76	13.21	–
Mastoidal width	17.62	17.47	17.41	18.44	17.72	16.75	–
Braincase height	12.73	13.23	12.44	13.31	12.41	12.13	–
Tympanic bulla length	5.24	5.52	5.18	5.57	5.43	5.53	–
Rostrum width across upper canines	10.55	10.51	10.68	10.67	10.32	10.27	–
Rostrum width across third upper molars	13.21	12.67	13.22	13.14	12.65	12.58	–
Length of upper tooth-row (C-M3)	11.06	11.08	11.52	11.52	10.36	10.36	10.4
Mandible length	22.85	23.13	23.04	23.17	21.07	20.75	–
Coronoid height of mandible	9.08	9.07	9.66	9.48	8.95	8.54	–
Length of lower tooth-row (C-M3)	12.86	12.84	13.47	13.02	11.57	11.82	–

[a]Type specimen of *S. gigas* Dobson, 1875; forearm length taken from De Vree (1973). [b]Comparative measurements of the Kenyan specimen provided by D. Schlitter.

indel, but they also were not recovered in a monophyletic group in both the MP and BI trees (not shown). Resolution of both *zfy* trees was poor, showing a comb-like pattern without nodal support, which was likely due to the low number of variable and parsimony informative sites (two without, six with consideration of gaps). Alternative reconstruction of relationships between haplotypes using median-joining network also did not indicate close relationship between the two *S. nigrita zfy* haplotypes (Figure 3).

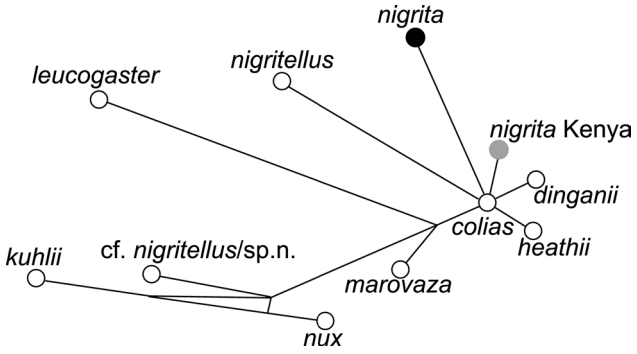

Figure 3 Median-joining network based on *zfy* sequences depicting relationship of *Scotophilus nigrita* to congeneric species. Gaps are considered as fifth state characters. Branches of *S. kuhlii* and *S. leucogaster* are shortened for representational purposes, thus their lengths do not fully reflect the 17 bp and 150 bp insertions, respectively. Grayscale highlighting indicates *S. nigrita* s. str. from West Africa (black) and published *S. nigrita* from Kenya (gray).

Morphological data confirm the correct identification of all examined specimens as the giant house bat *Scotophilus nigrita* (Tables 1 and 2). Although the small number of examined specimens does not allow for statistical analysis, comparison of forearm and skull dimensions shows a trend of a larger size in the West African specimens, on average exceeding the Southern African bats by 6.5 mm in forearm length and by 0.9–3.4 mm in the skull and tooth-row lengths (Table 2), i.e., a difference of 8.2% and 8.8% to 12.1%, respectively.

Discussion

Despite its wide distribution across much of sub-Saharan Africa and impressive physical appearance, *Scotophilus nigrita* remains poorly known even 240 years after its description. After the revisions by De Vree (1973) and Robbins et al. (1985), which comprised most of the recorded specimens of *S. nigrita*, five additional specimens have subsequently become known (Trujillo et al. 2009, Monadjem et al. 2010, Bakwo et al. 2012, Cohen and Linton 2013). Only one of these specimens has been previously used in a genetic analysis (Trujillo et al. 2009), the outcome of which obscured rather than elucidated the phylogenetic position of this species within the genus *Scotophilus*. The DNA sequence data from the newly collected specimens from Senegal, Benin and South Africa

represent an important contribution to the knowledge on the species.

The topology of the *cytb* tree generally conforms to the phylogeny of *Scotophilus* as shown by Trujillo et al. (2009) and Vallo et al. (2011, 2013). The *zfy* tree slightly differs from trees presented in the previous studies, but this disparity is likely due to a shorter fragment amplified and lower number of variable and parsimony informative sites. Moreover, relationships based on the *zfy* tree remained mostly unresolved but clearer information can be gained rather from the *zfy* network, which roughly corroborated the tree topology. The phylogenetic position of *S. nigrita* points at a major radiation event in Africa (Horáček et al. 2006, Trujillo et al. 2009), where *S. nigrita* likely represents a basal lineage of the African crown group, whose further diversification led to current morphologically similar yellow-bellied forms currently recognized as species *S. colias*, *S. dinganii*, *S. nigritellus* and *S. viridis*.

However, the position of the *Scotophilus nigrita* specimens analyzed herein clearly contradicts the published position of the Kenyan sequence of this bat within the East African *S. colias* by Trujillo et al. (2009), to which the unambiguously identified specimens occur in paraphyly. Nevertheless, reasons for such discordance remain obscure because the Kenyan specimen actually conforms in size to *S. nigrita* (D. Schlitter and S. McLaren, pers. comm.; Table 2), which excludes its possible misidentification. Nevertheless, this particular specimen has to be revised and additional evidence has to be collected to support the hypothesis of introgressive hybridization between *S. nigrita* and *S. colias* in East Africa as suggested by Trujillo et al. (2009). The proposed explanation of the phylogenetic pattern actually seems rather implausible given the new data. Conversely, sympatric occurrence of these species and the large body size of *S. colias* (forearm length up to 58 mm, body mass up to 30 g) may facilitate such an interspecific relationship. Indeed, recently published studies suggest several cases of introgressive hybridization between bat species (Berthier et al. 2006, Artyushin et al. 2009, Nesi et al. 2011, Juste et al. 2013), including between members of the genus *Scotophilus* (Vallo et al. 2013).

Despite its unmistakable physical appearance, *Scotophilus nigrita* significantly contributed to taxonomic confusion, which has been a proverbial attribute of the genus *Scotophilus* (e.g., Hayman and Hill 1971, Robbins et al. 1985, Koopman 1994, Jacobs et al. 2006). However, in this particular case, the issue concerned inappropriate use of its name, under which several currently acknowledged species had once been known (see Robbins 1978 for a review). Moreover, for over a century, the giant house bat had been called *S. gigas* Dobson, 1875 until Robbins (1978) showed it to be a junior synonym of *S. nigrita*, which represents as the valid designation of this giant bat species. Significant morphological distinction of specimens from Southern Africa further led De Vree (1973) to delimit a smaller-sized subspecies known under the currently valid name *S. nigrita alvenslebeni* Dalquest, 1965, while restricting the West and East African populations to the nominate, larger-sized subspecies *S. n. nigrita*.

Species identity of all specimens analyzed herein can be unambiguously confirmed based on their morphological traits. Their measurements further corroborated the variation ranges of the respective subspecies (De Vree 1973), which together with their geographical proximity to type localities (Figure 1) allows a reliable assignment of taxonomic labels to the two revealed sublineages of *Scotophilus nigrita*. However, a deep split between them with 7.6–8.1% sequence divergence enables a more substantial assumption regarding taxonomic distinction. The divergence values not only fall into acknowledged interspecific range in bats as reported by Baker and Bradley (2006), but also correspond to published values of divergence among house bat species (Trujillo et al. 2009, Vallo et al. 2011, 2013). Thus, the evidence presented herein supports a possible taxonomic distinction of these West and Southern African lineages as two separate species *S. nigrita* and *S. alvenslebeni*. Nevertheless, this suggestion on taxonomic change should be considered rather preliminary, and conclusive statement can be made only after relevant information is obtained through more extensive genetic sampling and corresponding morphological analysis.

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verifying the size of and providing additional information on the Kenyan specimen. We also thank Victor Van Cakenberghe (University of Antwerp, Antwerp, Belgium) for comments and discussion on the taxonomy of *Scotophilus*, Heather Baldwin (University Ulm, Ulm, Germany) for improvement of language, and an anonymous referee for suggestions enhancing clarity of the manuscript. The study was supported by grants from the Czech Science Foundation (# 206/09/P624), Grant Agency of the Academy of Sciences of the Czech Republic (# IAA6093404) and by the Ministry of Culture of the Czech Republic (# DKRVO 013/14, National Museum, 00023272).

References

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.

Baker, R.J. and R.D. Bradley. 2006. Speciation in mammals and the genetic species concept. J. Mammal. 87: 643–662.

Bakwo, E.M. fils, A.B.A. Anong and F.-N.T. Fohouo. 2012. First record of the giant house bat *Scotophilus nigrita* in Cameroon (Mammalia, Chiroptera). Biodiv. J. 3: 55–58.

Bandelt H.-J., P. Forster and A. Röhl. 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. 16: 37–48.

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.

Cathey, J.C., J.W. Bickham and J.C. Patton. 1998. Introgressive hybridization and nonconcordant evolutionary history of maternal and paternal lineages in North American deer. Evolution 52: 1224–1229.

Cohen, K. and D. Linton. 2013. http://www.inaturalist.org/observations/250839.html (accessed July 30, 2013).

Dalquest, W.W. 1965. Mammals from the Save River, Mozambique, with descriptions of two new bats. J. Mammal. 46: 254–268.

De Vree, F. 1973. New data on *Scotophilus gigas* Dobson, 1875 (Microchiroptera,Vespertilionidae). Z. Säugetierk. 38: 189–196.

Dobson, G.E. 1875. Description of a very large species of *Scotophilus* from West Africa. Ann. Mag. Nat. Hist. Ser. 416: 122–123.

Happold, M. 2013. *Scotophilus nigrita*. Giant House-bat. In: (M. Happold and D. Happold, eds.) Mammals of Africa. Vol. IV. Hedgehogs, shrews and bats. Bloomsbury, London-New Delhi-New York-Sydney. pp. 678–679.

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

Horáček I., O. Fejfar and P. Hulva. 2006. A new genus of vespertilionid bat from Early Miocene of Jebel Zelten (Libya) with comments on *Scotophilus* and early history of vespertilionid bats. Lynx, n. s. 37: 131–150.

Jacobs, D.S., G.N. Eick, M.C. Schoeman and C.A. Mathee. 2006. Cryptic species in an insectivorous bat, *Scotophilus dinganii*. J. Mammal. 87: 161–170.

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. Scr. 42: 441–457.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16: 111–120.

Koopman, K.F. 1994. Chiroptera: systematics. In: (J. Niethammer, H. Schliemann and D. Stark, eds.) Handbook of zoology. Mammalia. Vol. VIII. Part 60. Walter de Gruyter, Berlin, Germany. pp. 1–217.

Monadjem, A., P.J. Taylor, F.D.P. Cotterill and M.C. Schoeman. 2010. Bats of Southern and Central Africa. A biogeographic and taxonomic synthesis. Wits University Press, Johannesburg, South Africa. pp. 596.

Nesi, N., E. Nakouné, C. Cruaud and A. Hassanin. 2011. DNA barcoding of African fruit bats (Mammalia, Pteropodidae). The mitochondrial genome does not provide a reliable discrimination between *Epomophorus gambianus* and *Micropteropus pusillus*. C. R. Biol. 334: 544–554.

Posada, D. and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14: 817–818.

Robbins, C.B. 1978. Taxonomic identification and history of *Scotophilus nigrita* (Schreber) (Chiroptera: Vespertilionidae). J. Mammal. 59: 212–213.

Robbins, C.B., F. De Vree and V. Van Cakenberghe. 1985. A systematic revision of the African bat genus *Scotophilus* (Vespertilionidae). Ann. Mus. R. Afr. Centrale, Sci. Zool. 246: 51–84.

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

Schreber, J.C.D. von. 1774. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen. Vol. 1. Wolfgang Walther, Erlangen, Germany. pp. 194.

Simmons, N. 2005. Order Chiroptera. In: (D.E. Wilson and D.M. Reeder, eds.) Mammal species of the World: a taxonomic and geographic reference. 3rd ed. The Johns Hopkins University Press, Baltimore, MD. pp. 312–529.

Simmons, M.P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. Syst. Biol. 49: 369–381.

Tavaré, S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. In: (R.M. Miura, ed.) Some mathematical questions in biology: DNA sequence analysis. Lectures on mathematics in the life sciences. American Mathematical Society, Providence, RI. pp. 57–86.

Tobe, S.S., A.C. Kitchener and A.M.T. Linacre. 2010. Reconstructing mammalian phylogenies: a detailed comparison of the cytochrome *b* and cytochrome oxidase subunit I mitochondrial genes. PloS One 5: 1–14.

Trujillo, R.G., J.C. Patton, D.A. Schlitter and J.W. Bickham. 2009. Molecular phylogenetics of the bat genus *Scotophilus* (Chi-

roptera: Vespertilionidae): perspectives from paternally and maternally inherited genomes. J. Mammal. 90: 548–560.

Vallo, P., P. Benda and A. Reiter. 2011. Yellow-bellied or white-bellied? Identity of Arabian house bats (Vespertilionidae: *Scotophilus*) revealed from mitochondrial DNA and morphology. Afr. Zool. 46: 350–361.

Vallo P., P. Benda, J. Červený and P. Koubek. 2013. Conflicting mitochondrial and nuclear paraphyly in small-sized West African house bats (Vespertilionidae). Zool. Scr. 42: 1–12.

Yang, Z. 1996. Among-site variation and its impact on phylogenetic analysis. Trends Ecol. Evol. 11: 367–372.