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New look on the geographical variation in *Rhinolophus clivosus* with description of a new horseshoe bat species from Cyrenaica, Libya

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Abstract. Geographical variation in *Rhinolophus clivosus* was revised; the species was found to be composed of five well separated genetic lineages and six original morphotypes. A new *Rhinolophus* species is described from the former rank of this bat, known from seven localities in the Mediterranean part of Cyrenaica, Libya. Taxonomy of the *R. clivosus / R. ferrumequinum* morpho-complex is discussed.

Taxonomy, biogeography, Rhinolophidae, morphometrics, mtDNA, Mediterranean, Africa

Introduction

Rhinolophus clivosus Cretzschmar, 1828 is a medium-sized species of the family Rhinolophidae, typical by its high but bluntly rounded connecting process of the rather narrow nose-leaf, and a very small (or missing) and externally positioned minute upper premolar, P^2 (Hayman & Hill 1971, Harrison & Bates 1991, Csorba et al. 2003). It is assigned to the *R. ferrumequinum* group (Bogdanowicz 1992, Koopman 1994, Csorba et al. 2003) belonging to the Afro-Palaearctic clade of the genus *Rhinolophus* Lacépède, 1799 (Guillén Servent et al. 2003, Zhou et al. 2009).

Distribution range of this bat covers mainly drier areas of Africa with a large extension to the Arabian Peninsula (Csorba et al. 2003). While in the Palaearctic *R. clivosus* occurs mainly in desert habitats (Arabian and Sahara deserts of Israel, Jordan, Saudi Arabia, Egypt, Sudan, Libya and Algeria), in the Afrotropic region, it is mainly an inhabitant of savannah woodland (Oman, Yemen, Eritrea, Ethiopia, and South Sudan, over East Africa and Congo, to Zambia, Malawi, Mozambique, Zimbabwe and South Africa) (Csorba et al. 2003, Monadjem et al. 2010). The only area in the Palaearctic, where *R. clivosus* occurs in a similar habitat as in the Afrotropics, is the Mediterranean woodland of northern Cyrenaica, Libya.

With exception of the continuous range in eastern and southern Africa, the distribution of *R. clivosus* is patchy, creating rather isolated spots of occurrence. Perhaps due to this type of known distribution, a large number of named forms were described, which are currently assembled into seven subspecies (Koopman 1994, Csorba et al. 2003, Simmons 2005); *R. c. clivosus* Cretzschmar, 1828 (type locality [t.l.] Al Muwaylih, NW Saudi Arabia) from Yemen and Saudi Arabia; *R. c. brachygnathus* Andersen, 1905a (t.l. Ghizah, N Egypt) from Egypt and Israel to north-eastern Libya and northern Sudan; *R. c. schwarzi* Heim de Balsac, 1934 (t.l. Djanet, SE Algeria) from south-eastern Algeria and south-western Libya; *R. c. acrotis* von Heuglin, 1861 (t.l. Keren, Eritrea) from Eritrea, Ethiopia, Sudan, Djibouti, and Somalia; *R. c. keniensis* Hollister, 1916 (t.l.

Mount Kenya, Kenya) from South Sudan, Uganda, Kenya, and northern Tanzania; *R. c. zuluensis* Andersen, 1904 (t.l. Jususic valley, South Africa) from coastal parts of southern Africa; and *R. c. augur* Andersen, 1904 (t.l. Kuruman, South Africa) from southern Tanzania, Malawi, Zimbabwe, Botswana, and northern South Africa. Some older authors considered the Central Asian species *R. bocharicus* Kaŝenko et Akimov, 1917 to be a part of the *R. clivosus* species rank (Aellen 1959, Harrison 1964, Corbet 1978, Koopman 1993, 1994), however, this opinion seems to be abandoned in the present time (Hanák 1969, Strelkov 1971, Felten et al. 1977, Harrison & Bates 1991, Horáček et al. 2000, Csorba et al. 2003, Simmons 2005).

The present taxonomic intra-specific arrangement of *R. clivosus* is based on the opinion introduced by Ellerman et al. (1953), that African representatives, formerly assigned to separate species *R. acrotis* and *R. augur* (cf. e.g. Andersen 1904, 1905b, 1906, Allen 1939, Ellerman & Morrison-Scott 1951) are conspecific with the Arabian *R. clivosus* s.str., including all the names synonymised with the former two forms. This ordering has been followed by most of subsequent authors, see the reviews by Cotterill (2002) and Csorba et al. (2003). However, as Csorba et al. (2003) and Stoffberg et al. (2012) pointed out, the arrangement of this group of populations under one species cannot be considered as conclusive and realignments of subspecific assignments as well as discoverings of hidden diversities are still possible.

Most of uncertainties in taxonomic affiliations were reported from the Middle Eastern and North African populations (with exception of the central Saharan populations, steadily assigned to *R. c. schwarzi*). Although most authors recognised three subspecies in Arabia and north-eastern Africa, geographical content of these subspecies varies depending on author. Harrison (1964), Hayman & Hill (1971) and Harrison & Bates (1991) assigned populations from Sinai, Israel, north-western and central Saudi Arabia to *R. c. clivosus* and those from south-western and southern Arabia to *R. c. acrotis*. Hayman & Hill (1971) differentiated *R. c. acrotis* in Sudan, Eritrea, Ethiopia, and Somalia, *R. c. brachygnathus* in Egypt and Sudan, and in addition *R. c. andersoni* (by most authors considered a junior synonym of one of the former two names) in the Eastern Desert of Egypt. Koopman (1975) distinguished *R. c. brachygnathus* in northern Sudan and *R. c. acrotis* in central Sudan, and *R. c. acrotis* and/or *R. c. keniensis* tentatively in southern Sudan. Corbet (1978) recognised only *R. c. clivosus* in the whole area (and the names *acrotis*, *andersoni* and *brachygnathus* as its synonyms). Koopman (1994) mentioned *R. c. clivosus* to occur in the belt from Israel to north-eastern Sudan, *R. c. brachygnathus* from Egypt to north-eastern Libya and northern Sudan, and *R. c. acrotis* from central and south-western Arabia, Ethiopia, most of central and southern Sudan, Somalia, and most of Kenya. Thomas (1997) and Csorba et al. (2003) reported *R. c. clivosus* from Yemen and Saudi Arabia, *R. c. brachygnathus* from Israel over Egypt to north-eastern Libya and northern Sudan, and *R. c. acrotis* from Ethiopia, most of central and southern Sudan, and Somalia. Based solely on pelage colouration, Kock et al. (2002) differentiated two subspecies in Yemen, the paler *R. c. clivosus* and the darker *R. c. acrotis*. So, almost all opinions differ from each other in the geographical coverage of particular taxa.

Qumsiyeh (1985) has been the only who published any results of comparison of samples from the respective area (Holy Land and NE Africa). These results from his simple metric analysis detected existence of three size categories of *R. clivosus* within this region, which he assigned to three subspecies. The smallest bats from the Nile valley between northern Sudan and the delta were considered by Qumsiyeh (1985) as *R. c. brachyotis*, the medium-sized bats from southern Israel, Sinai, Egyptian-Sudanese mountainous transition (type series of *R. andersoni*), mountains of north-eastern Libya and mountains of eastern Sudan as *R. c. clivosus* (with *acrotis* and *andersoni* as synonyms), while the large-sized bats from southern and eastern Sudan were not named by him (but the available names for this form are *augur* or *keniensis*, see above). However, this interpretation was not accepted by Koopman (1994) and Csorba et al. (2003), see above. Qumsiyeh (1985) has also been the only author who examined the bats from the population of Cyrenaica, north-eastern Libya, and assigned them to the nominotypical form. This population was discovered and first described by Qumsiyeh & Schlitter (1982), they reported five bats collected at two sites in this unique Mediterranean bioregion. Until their publication appeared, only the desert populations represented by small-sized individuals of *R. clivosus* from south-western Libya were known from this country, traditionally assigned to *R. c. schwarzi* (see Hanák & Elgadi 1984).

Although specimens of *R. clivosus* are rather scarce in collections (with exceptions of Egyptian and southern African populations), we conducted a morphological examination of a set of more than 120 specimens from the Middle East and Africa, including newly collected bats from various parts of the species range. Geographically representative subsets of these bats were also subjected to molecular genetic comparisons. The first results of these two approaches are synthesised here.

Material and Methods

We analysed representative sample sets of museum specimens of *Rhinolophus clivosus* Cretzschmar, 1828 (sensu Csorba et al. 2003) from Arabia (Sinai, Jordan, Yemen, Oman) and Africa (Egypt, Libya, Algeria, Sudan, Eritrea, Ethiopia, Kenya, Uganda, Rwanda, Tanzania, Malawi, Mozambique, Lesotho, South Africa) using morphological and molecular genetic approaches. Most of the respective type material was used for morphological comparison, viz. *Rhinolophus clivosus* Cretzschmar, 1828 (from the SMF collection), *Rhinolophus andersoni* Thomas, 1904 (BMNH), *Rhinolophus augur* Andersen, 1904 (BMNH), *Rhinolophus augur zuluensis* Andersen, 1904 (BMNH), *Rhinolophus augur zambesiensis* Andersen, 1904 (BMNH), *Rhinolophus acrotis brachygnathus* Andersen, 1905a (BMNH), *Rhinolophus acrotis schwarzi* Heim de Balsac, 1934 (MNHN). For the complete list of specimens of *R. clivosus* examined for the morphological analysis see Appendix 1.

For morphological comparisons, the museum specimens were examined in the same way as described in our previous studies (e.g. Benda & Vallo 2009); we used mainly the skull and tooth metric dimensions in order to describe morphological trends in particular populations rather than individual variation. The specimens were measured in a standardised way with the use of mechanical or optical calipers. The evaluated external, cranial and dental measurements are listed in Abbreviations and Terminology. External dimensions were taken from freshly collected material in the NMP specimens, in other specimens the measurements were taken from museum preparations. Tooth-row and dental dimensions were taken on tooth cingulum margins. Bacula were extracted into 6% solution of KOH and coloured with alizarin red. Statistical analyses were performed using the Statistica 6.0 software. Stepwise discriminant function analysis was performed as a test of importance of particular dimensions and their ratios for geographical variation; statistically significant parameters most affecting morphological variation were selected and employed in a subsequent principal component analysis.

A representative subset of specimens from the morphological analysis was chosen (complemented by a set of West Palaearctic specimens of *Rhinolophus ferrumequium*) to form a dataset for molecular phylogenetic inference (see Appendix 2). Published sequences of African *R. clivosus* and Spanish and East Asian *R. ferrumequinum* were retrieved from the GenBank database to enrich geographical sampling. Newly obtained or published sequences of several other *Rhinolophus* species belonging to various species groups were included for intrafamily comparison: *R. fumigatus* Rüppell, 1842 and *R. hildebrandtii* Peters, 1878, as well as the recently described Chinese member of the Afro-Palaearctic rhinolophid lineage *R. xinanzhongguoensis* Zhou, Guillén-Servent, Lim, Eger, Wang et Jiang, 2009. The West Palaearctic *R. hipposideros* (Borkhausen, 1797) (*hipposideros* group) was used as an outgroup to root phylogenetic trees.

For molecular genetic analysis, the specimens were processed by standard laboratory procedures. Genomic DNA was extracted from alcohol preserved tissue samples with a DNeasy Blood and Tissue Kit (Qiagen) or Jetquick Tissue Kit (Top-Bio) following the manufacturer's protocol. Mitochondrial gene for cytochrome *b* (cyt *b*) was PCR amplified using primers F1 (modified; 5'-CCACGACCAATGACAYGAAAA-3') and R1 (5'-CCTTTTCTGGTTTACAAGACCAG-3') by Sakai et al. (2003) in 50 µl reaction volume containing 800 µM dNTP, 200 µM of each primer, 1U of HotMaster *Taq* DNA polymerase with an appropriate 10× buffer (Eppendorf) or in 25 µl reaction volume of Combi PPP Mastermix (Top-Bio). 2–5 µl of extracted DNA were added to the reaction as template. Reaction conditions were 3 min initial denaturation at 94 °C, 35 cycles of 40 s denaturation at 94 °C, 40 s annealing at 50 °C and 90 s extension at 65 °C, and 5 min final extension at 65 °C. Products were purified using QIAquick PCR Purification Kit (Qiagen) or Jetquick Purification Kit (Top-Bio), and sequenced on an ABI 3730XL sequencer using BigDye sequencing chemistry (Applied Biosystems) by a commercial company (Macrogen). Two ca. 800 bp long, partially overlapping fragments obtained were assembled in Sequencher 4.6 (GeneCodes) into complete sequences of cyt *b* (1140 bp). The sequences were aligned and visually inspected in BioEdit

(Hall 1999). Final sequences were submitted to the GenBank database under accession numbers KC579369–KC579400. Aligned sequences were explored for base composition and content of phylogenetic information. Phylogenetic relationships were reconstructed under maximum parsimony (MP) in program PAUP* 4.10b (Sinauer Associates). MP tree was heuristically searched with 100 random additions of sequences and tree bisection-reconnection branch-swapping (TBR) algorithm with all characters equally weighted. Nodal support was assessed by non-parametric bootstrap of 1000 pseudoreplicates. ML tree was computed in program PhyML 2.2.4. (Guindon & Gascuel 2003) under Tamura-Nei model of evolution (TN93; Tamura & Nei 1993) with a proportion of invariable sites and Γ-distributed among-site rate variation (TN93+I+Γ), and nodal support assessed by bootstrap with 1000 pseudoreplicates. This model was suggested by the AIC criterion as the best for the dataset in program Modeltest 3.7 (Posada & Crandall 1998). Phylogeny was also inferred using Bayesian method in program MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) under the nearest higher model implemented in MrBayes, i.e. the general time-reversible model of evolution (GTR; Tavaré 1986) with a proportion of invariable sites and Γ-distributed among-site rate variation (GTR+I+Γ). This model was chosen as Two simultaneous runs of four Metropolis-coupled Markovian chains with default heating values were executed in one million generations. Runs were sampled each 100 generations and the first 25% of trees were discarded as burnin. A consensus tree was built from sampled trees and support of this topology was expressed as posterior probabilities of the respective nodes.

Abbreviations and Terminology

Dimensions

External: LC = head and body length; LCd = tail length; LAt = forearm length; LA = auricle length; LaFE = horseshoe width; G = body weight.

Cranial: LCr = greatest length of skull incl. praemaxillae; LCc = condylocanine length of skull; LaZ = zygomatic width; LaI = width of interorbital constriction; LaInf = rostral width between infraorbital foramens; LaNc = neurocranium width; LaM = mastoidal width of skull; ANc = neurocranium height; ACr = cranial height (incl. tympanic bullae); LBT = largest horizontal length of tympanic bulla; CC = rostral width between canines (incl.); P^4P^4 = rostral width between last upper premolars (incl.); M^3M^3 = rostral width between third upper molars (incl.); CM^3 = length of upper tooth-row between canine and third molar (incl.); M^1M^3 = length of upper tooth-row between first and third molars (incl.); CP^4 = length of upper tooth-row between canine and large premolar (P^4) (incl.); LMd = condylar length of mandible; ACo = height of coronoid process; I_1M_3 = length of lower tooth-row between first incisor and third molar (incl.); CM_3 = length of lower tooth-row between canine and third molar (incl.); M_1M_3 = length of lower tooth-row between first and third molars (incl.); CP_4 = length of lower tooth-row between canine and large premolar (P_4) (incl.).

Dental: LCs = largest mesio-distal length of upper canine; LaCs = largest palato-labial width of upper canine; $LP^4 1$ = largest mesio-distal length of large upper premolar on the labial cingulum; $LP^4 2$ = mesiodistal length of large upper premolar on palatal cingulum (largest dimension taken over the palato-mesial to palato-distal points of the talon); $LP^4 3$ = smallest mesio-distal length of large upper premolar taken over the talon constriction; LaP^4 = largest palato-labial width of large upper premolar taken over the mesio-labial and palato-distal cingulum margins; LM^1 = largest mesio-distal length of first upper molar taken over parastyle and metasyle; LaM^1 = largest palato-labial width of first upper molar taken over parastyle and palato-distal part of talon; LM^3 = largest mesio-distal length of third upper molar; LaM^3 = largest palato--labial width of third upper molar taken over parastyle and palatal cingulum; LCi = largest mesio-distal length of lower canine; LP_2 = largest mesio-distal length of first lower premolar; LaP_2 = largest labio-lingual width of first lower premolar; LP_4 = largest mesio-distal length of last lower premolar; LaP_4 = largest labio-lingual width of last lower premolar; LM_1 = largest mesio-distal length of first lower molar taken over paraconid and hypoconulid.

Collections

BMNH – Natural History Museum, London, United Kingdom; BCSU – Biological Collection of the Sana'a University, Sana'a, Yemen; DM – Durban Natural Science Museum, Durban, South Africa; EBD – Doñana Biological Station, Seville, Spain; FMNH – Field Museum, Chicago, USA; IVB – Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Brno, Czech Republic; KIZ – Chinese Academy of Sciences, Beijing, China; MNHN – National Museum of Natural History, Paris, France; MSNG – Civil Natural History Museum Giacomo Doria, Genoa, Italy; MZUF – Natural History Museum, Florence, Zoology Section "La Specola", Italy; NMB – National Museum, Bloemfontein, South Africa; NMP – National Museum (Natural History), Prague, Czech Republic; NMW – Natural History Museum, Vienna, Austria; ROM – Royal Ontario Museum, Toronto, Canada; SMF – Museum and Research Institute Senckenberg, Frankfurt, Germany; TM – Transvaal Museum, Pretoria, South Africa; ZFMK – Zoological Institute and Museum Alexander Koenig, Bonn, Germany.

Other abbreviations

A = alcoholic preparation; f = female; M = mean; m = male; min, max = dimension range margins; S = skull; SD = standard deviation.

Geographical terminology
Specimens were arranged to eight geographically defined sample sets: Holy Land – specimens from southern Jordan, Sinai and north-western Saudi Arabia; Egypt – specimens from the Nile valley of Egypt between Aswan and Cairo and the holotype of *R. andersoni* coming from the Red Sea mountains of the Egyptian-Sudanese transition; Cyrenaica – specimens from the Mediterranean part of Cyrenaica, north-eastern Libya; Algeria – type series of *R. acrotis schwarzi* coming from the mountains of south-eastern Algeria; South Arabia – specimens from Yemen and Oman; Ethiopia – specimens from Ethiopia, Eritrea and Sudan; East Africa – specimens from Uganda, Kenya, Rwanda, Tanzania, and Malawi; South Africa – specimens from Mozambique, Lesotho, and South Africa.

Results

Morphological analysis

The analysis of metric characters showed several more or less distinct morphotypes within the examined set of samples of *R. clivosus*. According to a mere comparison of skull dimensions, three size types appeared among the examined geographical groups of specimens. However, they overlapped in most of their measurement ranges (Fig. 1, Table 1); (1) group of small-sized bats (LAt 44–49 mm; LCc 16.0–16.9 mm; CM^3 6.5–7.2 mm) from Egypt and Algeria; (2) group of medium-sized bats (LAt 45–53 mm; LCc 17.2–18.6 mm; CM^3 7.1–7.9 mm) from the Holy Land, Cyrenaica, South Arabia and Ethiopia; and (3) group of large-sized bats (LAt 51–58 mm; LCc 18.5–20.6 mm; CM^3 7.5–8.6 mm) from East and South Africa. The principal component analysis (PCA) based on all 22 skull and tooth-row dimesions taken (Fig. 2; PC1=76.95% of variance, PC2=6.87%) clearly separated these three size-based groups along the PC1. While the groups of small-sized and large-sized bats are relatively homogeneous and do not vary substantially in their metric traits, the group of medium-sized bats is highly variable and all geographically defined

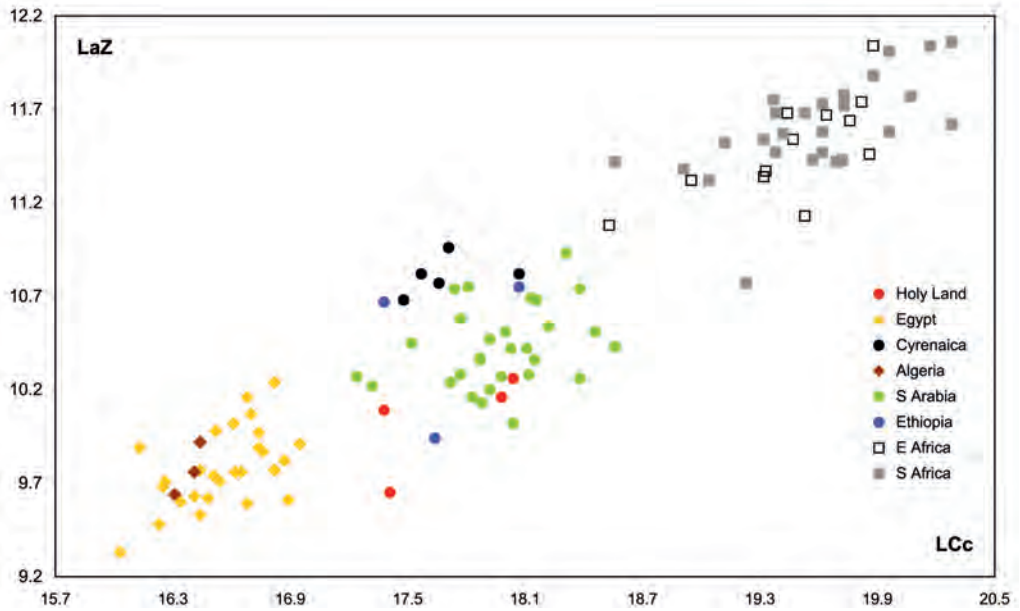


Fig. 1. Bivariate plot of the compared samples of *Rhinolophus clivosus* s.l.: condylocanine length of skull (LCc) against zygomatic width (LaZ).

Table 1. Dimensions (in mm) of the examined sample sets of *Rhinolophus clivosus* s.l. For legend see Abbreviations and Terminology

	Holy Land					Egypt					Cyrenaica					Algeria				
	n	**M**	min	max	SD	n	**M**	min	max	SD	n	**M**	min	max	SD	n	**M**	min	max	SD
LAt	7	**48.71**	46.7	49.9	1.288	30	**47.32**	44.0	49.1	1.245	5	**49.12**	48.2	50.2	0.832	2	**45.50**	45.0	46.0	0.707
LaFE	5	**8.26**	7.7	8.7	0.416	22	**6.57**	5.6	7.4	0.375	5	**7.18**	6.9	7.5	0.217	0	–	–	–	–
LCr	4	**20.86**	20.42	21.33	0.448	26	**19.39**	18.78	19.93	0.313	5	**20.54**	20.16	20.88	0.262	3	**19.06**	19.01	19.14	0.068
LCc	4	**17.70**	17.38	18.04	0.356	27	**16.54**	16.03	16.89	0.231	5	**17.70**	17.48	18.07	0.226	3	**16.37**	16.27	16.44	0.091
LaZ	4	**10.04**	9.65	10.26	0.269	26	**9.78**	9.33	10.24	0.213	5	**10.81**	10.68	10.96	0.101	3	**9.77**	9.64	9.92	0.140
LaI	7	**2.29**	2.08	2.54	0.181	28	**2.37**	2.19	2.58	0.101	5	**2.34**	2.21	2.44	0.092	3	**2.27**	2.20	2.39	0.107
LaInf	6	**5.38**	5.14	5.53	0.137	28	**4.87**	4.64	5.12	0.116	5	**5.72**	5.64	5.77	0.053	3	**5.00**	4.98	5.03	0.029
LaNc	4	**8.24**	8.14	8.38	0.104	27	**8.19**	7.92	8.47	0.140	5	**8.55**	8.43	8.64	0.095	3	**7.95**	7.88	8.06	0.095
LaM	4	**9.19**	9.05	9.48	0.199	27	**8.87**	8.65	9.09	0.119	5	**9.50**	9.32	9.63	0.117	3	**8.82**	8.74	8.87	0.068
ANc	4	**6.12**	5.86	6.39	0.287	27	**5.99**	5.64	6.35	0.173	5	**6.21**	6.07	6.44	0.144	3	**5.81**	5.74	5.84	0.058
LBT	5	**3.44**	3.22	3.59	0.151	25	**3.08**	2.81	3.42	0.166	5	**3.32**	3.07	3.43	0.146	3	**3.05**	2.98	3.12	0.070
CC	6	**5.39**	5.23	5.52	0.118	27	**5.09**	4.82	5.36	0.149	5	**5.94**	5.84	6.07	0.103	3	**5.14**	5.07	5.19	0.061
M^{3}M^3	7	**7.45**	7.18	7.65	0.190	27	**7.18**	6.93	7.66	0.192	5	**7.82**	7.71	8.08	0.150	3	**7.23**	7.15	7.29	0.074
CM^3	6	**7.33**	7.12	7.48	0.133	28	**6.85**	6.53	7.16	0.154	5	**7.40**	7.28	7.57	0.106	3	**6.83**	6.74	6.92	0.090
M^{1}M^3	6	**4.61**	4.42	4.75	0.134	24	**4.40**	4.25	4.63	0.086	5	**4.77**	4.67	4.87	0.083	3	**4.47**	4.47	4.48	0.006
CP^4	6	**3.14**	2.87	3.52	0.233	25	**2.69**	2.52	2.89	0.117	5	**3.18**	2.93	3.32	0.146	3	**2.54**	2.52	2.56	0.020
LMd	7	**13.23**	12.93	13.56	0.247	28	**12.48**	12.04	12.98	0.228	5	**13.51**	13.24	13.79	0.230	3	**12.36**	12.21	12.48	0.137
ACo	7	**3.32**	3.16	3.57	0.152	28	**2.94**	2.75	3.12	0.085	5	**3.44**	3.28	3.61	0.121	3	**2.93**	2.92	2.94	0.012
CM$_3$	6	**7.87**	7.61	8.13	0.181	28	**7.37**	7.05	7.62	0.149	5	**8.13**	7.98	8.29	0.148	3	**7.41**	7.31	7.51	0.100
M^{1}M$_3$	6	**5.27**	4.96	5.38	0.157	25	**5.00**	4.76	5.28	0.117	5	**5.42**	5.39	5.47	0.035	3	**5.17**	5.02	5.34	0.162
CP$_4$	6	**2.86**	2.57	3.96	0.541	25	**2.74**	2.38	7.54	1.005	5	**2.96**	2.84	3.06	0.087	3	**2.49**	2.31	2.67	0.180
LCs	6	**1.78**	1.69	1.85	0.069	19	**1.65**	1.50	1.77	0.066	5	**1.89**	1.83	1.94	0.047	3	**1.60**	1.57	1.62	0.028
LaCs	6	**1.42**	1.31	1.61	0.102	18	**1.37**	1.24	1.49	0.073	5	**1.56**	1.53	1.60	0.037	3	**1.35**	1.34	1.35	0.006
LP^{4}1	6	**1.45**	1.34	1.50	0.063	19	**1.43**	1.32	1.56	0.070	5	**1.43**	1.37	1.53	0.073	3	**1.38**	1.35	1.40	0.026
LP^{4}2	6	**0.88**	0.75	1.01	0.094	19	**0.90**	0.81	1.01	0.056	5	**0.97**	0.91	1.03	0.055	3	**0.88**	0.87	0.89	0.010
LP^{4}3	6	**0.73**	0.61	0.81	0.092	19	**0.71**	0.66	0.79	0.034	5	**0.89**	0.79	0.96	0.068	3	**0.67**	0.67	0.68	0.006
LaP^4	6	**2.25**	2.15	2.32	0.071	19	**2.13**	1.97	2.35	0.094	5	**2.43**	2.37	2.51	0.057	3	**2.16**	2.14	2.18	0.024
LM^1	6	**1.92**	1.82	2.02	0.071	19	**1.80**	1.71	1.93	0.055	5	**1.87**	1.82	1.92	0.041	3	**1.85**	1.83	1.90	0.036
LaM^1	6	**2.78**	2.65	2.94	0.101	19	**2.64**	2.38	2.83	0.121	5	**3.01**	2.96	3.05	0.037	3	**2.83**	2.80	2.88	0.041
LM^3	6	**1.13**	1.04	1.24	0.066	19	**1.08**	0.98	1.14	0.045	5	**1.21**	1.20	1.24	0.014	3	**1.10**	1.10	1.10	0.000
LaM^3	5	**1.94**	1.63	2.11	0.185	19	**1.82**	1.31	1.98	0.143	5	**2.08**	2.07	2.09	0.008	3	**1.93**	1.90	1.98	0.044
LCi	6	**1.07**	0.98	1.18	0.074	19	**0.99**	0.92	1.08	0.050	5	**1.15**	1.08	1.20	0.046	3	**1.04**	0.97	1.07	0.054
LP$_2$	6	**0.62**	0.49	0.72	0.080	19	**0.63**	0.54	0.70	0.042	5	**0.72**	0.69	0.73	0.017	3	**0.64**	0.57	0.73	0.087
LaP$_2$	6	**0.80**	0.60	0.96	0.131	19	**0.79**	0.74	0.87	0.032	5	**0.84**	0.81	0.88	0.028	3	**0.90**	0.82	0.95	0.076
LP$_4$	6	**1.10**	1.02	1.15	0.055	19	**1.13**	1.05	1.24	0.054	5	**1.33**	1.29	1.39	0.040	3	**1.03**	0.98	1.07	0.044
LaP$_4$	6	**1.03**	0.86	1.17	0.123	19	**0.94**	0.82	1.04	0.065	5	**1.08**	1.04	1.14	0.039	3	**1.03**	1.01	1.09	0.048
LM$_1$	6	**1.99**	1.85	2.10	0.090	19	**1.91**	1.83	2.01	0.051	5	**2.05**	1.98	2.12	0.049	3	**1.89**	1.85	1.93	0.037

Table 1. (continued)

	Ethiopia					South Arabia					East Africa					South Africa				
	n	**M**	min	max	SD	n	**M**	min	max	SD	n	**M**	min	max	SD	n	**M**	min	max	SD
LAt	13	**50.24**	44.6	53.2	3.092	37	**49.55**	47.2	52.2	1.249	12	**54.83**	52.5	56.7	1.323	34	**54.12**	51.3	57.4	1.544
LaFe	8	**7.76**	6.8	8.8	0.655	24	**8.28**	7.3	8.9	0.357	11	**7.97**	6.8	8.9	0.672	9	**8.04**	7.4	8.6	0.436
LCr	7	**20.67**	19.93	21.40	0.585	29	**20.96**	20.12	21.62	0.384	10	**22.60**	21.42	23.25	0.561	18	**22.80**	21.69	23.57	0.437
LCc	3	**17.70**	17.38	18.07	0.348	30	**17.96**	17.24	18.56	0.309	12	**19.46**	18.53	19.88	0.399	27	**19.62**	18.56	20.57	0.452
LaZ	5	**10.45**	9.94	10.75	0.316	30	**10.41**	10.02	10.93	0.220	12	**11.50**	11.08	12.04	0.273	27	**11.62**	10.77	12.06	0.274
LaI	8	**2.50**	2.22	2.75	0.191	30	**2.16**	1.81	2.61	0.232	12	**2.63**	2.39	3.11	0.198	29	**2.66**	2.29	2.93	0.174
LaInf	8	**5.24**	4.95	5.43	0.155	30	**5.53**	5.27	5.82	0.161	12	**5.82**	5.34	6.14	0.205	28	**5.71**	5.56	5.92	0.108
LaNc	7	**8.40**	8.22	8.84	0.219	30	**8.35**	8.04	8.67	0.152	12	**9.28**	8.82	9.81	0.268	27	**9.23**	8.87	9.65	0.234
LaM	7	**9.36**	9.01	9.58	0.207	30	**9.33**	8.95	9.68	0.194	11	**10.20**	9.92	10.49	0.149	27	**10.17**	9.93	10.60	0.147
ANc	6	**6.01**	5.64	6.47	0.299	31	**6.13**	5.52	6.57	0.264	11	**6.64**	6.38	7.07	0.222	27	**6.70**	6.29	7.18	0.218
LBT	6	**3.48**	3.16	3.79	0.324	22	**3.62**	3.21	3.84	0.143	11	**3.27**	2.93	3.75	0.250	27	**3.41**	3.07	3.82	0.195
CC	8	**5.44**	5.19	5.64	0.149	30	**5.63**	5.25	5.94	0.156	12	**6.04**	5.64	6.31	0.189	28	**6.16**	5.68	6.60	0.234
M^{3}M^3	8	**7.62**	7.29	7.98	0.211	30	**7.75**	7.34	8.22	0.181	12	**8.33**	7.88	8.74	0.263	28	**8.44**	7.76	8.96	0.314
CM^3	8	**7.52**	7.31	7.75	0.136	32	**7.53**	7.16	7.85	0.144	12	**8.09**	7.58	8.54	0.304	29	**8.22**	7.56	8.82	0.331
M^{1}M^3	8	**4.82**	4.68	4.97	0.120	30	**4.78**	4.54	5.01	0.120	12	**5.13**	4.74	5.58	0.216	29	**5.14**	4.72	5.59	0.232
CP^4	8	**2.93**	2.74	3.17	0.136	20	**2.98**	2.74	3.28	0.155	12	**3.17**	3.05	3.33	0.087	29	**3.22**	2.82	3.58	0.188
LMd	8	**13.39**	12.92	14.01	0.341	32	**13.70**	12.98	14.21	0.303	12	**14.84**	13.98	15.31	0.385	29	**14.83**	13.93	15.68	0.443
ACo	8	**3.25**	2.91	3.48	0.183	32	**3.40**	2.98	3.68	0.186	12	**3.61**	3.38	3.74	0.117	29	**3.64**	3.16	3.93	0.186
CM$_3$	8	**8.02**	7.77	8.49	0.263	32	**8.14**	7.76	8.49	0.168	12	**8.63**	8.28	9.09	0.265	29	**8.84**	8.14	9.56	0.361
M$_1$M$_3$	8	**5.48**	5.33	5.79	0.144	30	**5.47**	5.16	5.74	0.123	12	**5.78**	5.51	6.19	0.230	29	**5.89**	5.45	6.43	0.253
CP$_4$	8	**2.72**	2.58	2.88	0.104	20	**2.81**	2.66	3.08	0.113	12	**2.97**	2.63	3.19	0.178	29	**3.10**	2.79	3.43	0.154
LCs	4	**1.77**	1.72	1.86	0.065	17	**1.81**	1.71	1.92	0.059	12	**2.01**	1.86	2.12	0.092	12	**2.12**	1.94	2.27	0.102
LaCs	4	**1.41**	1.28	1.59	0.133	17	**1.55**	1.46	1.70	0.062	12	**1.70**	1.56	1.87	0.101	12	**1.69**	1.50	2.03	0.148
LP^{4}1	4	**1.41**	1.29	1.51	0.106	17	**1.58**	1.49	1.64	0.044	12	**1.49**	1.30	1.62	0.111	12	**1.64**	1.38	1.74	0.095
LP^{4}2	4	**1.06**	1.01	1.13	0.055	17	**1.04**	0.94	1.13	0.067	12	**1.05**	0.90	1.16	0.072	12	**1.13**	1.01	1.26	0.095
LP^{4}3	4	**0.80**	0.73	0.88	0.068	17	**0.83**	0.73	0.90	0.047	12	**0.87**	0.79	1.01	0.065	12	**0.88**	0.72	1.02	0.093
LaP^4	4	**2.18**	2.03	2.40	0.156	17	**2.40**	2.28	2.51	0.062	12	**2.45**	2.23	2.63	0.126	12	**2.63**	2.03	2.83	0.217
LM^1	4	**1.90**	1.81	2.03	0.094	17	**1.99**	1.93	2.05	0.040	12	**2.10**	1.97	2.29	0.093	12	**2.15**	1.94	2.32	0.110
LaM^1	4	**2.75**	2.62	2.93	0.146	17	**2.96**	2.85	3.07	0.076	12	**3.04**	2.80	3.28	0.129	12	**3.17**	2.82	3.31	0.141
LM^3	4	**1.23**	1.19	1.26	0.028	17	**1.21**	1.13	1.29	0.044	12	**1.30**	1.17	1.39	0.066	12	**1.33**	1.19	1.42	0.072
LaM^3	4	**1.94**	1.89	2.04	0.069	17	**2.00**	1.87	2.12	0.072	12	**2.18**	1.95	2.34	0.108	12	**2.24**	2.07	2.40	0.106
LCi	4	**1.12**	1.02	1.28	0.113	16	**1.11**	1.03	1.21	0.062	12	**1.16**	1.01	1.24	0.080	12	**1.23**	1.09	1.36	0.087
LP$_2$	4	**0.76**	0.68	0.82	0.059	16	**0.71**	0.60	0.88	0.066	12	**0.82**	0.73	0.92	0.067	12	**0.92**	0.74	1.03	0.083
LaP$_2$	4	**0.91**	0.81	0.95	0.070	16	**0.93**	0.83	1.08	0.071	12	**0.94**	0.80	1.05	0.074	12	**1.03**	0.90	1.13	0.079
LP$_4$	4	**1.08**	0.98	1.12	0.063	16	**1.20**	1.13	1.28	0.040	12	**1.24**	1.13	1.37	0.081	12	**1.29**	1.12	1.36	0.068
LaP$_4$	4	**1.09**	0.88	1.32	0.184	16	**1.11**	0.98	1.19	0.068	12	**1.18**	1.06	1.32	0.073	12	**1.24**	1.09	1.34	0.082
LM$_1$	4	**1.96**	1.93	2.00	0.030	16	**2.06**	1.98	2.15	0.051	12	**2.16**	2.07	2.28	0.071	12	**2.28**	2.10	2.39	0.075

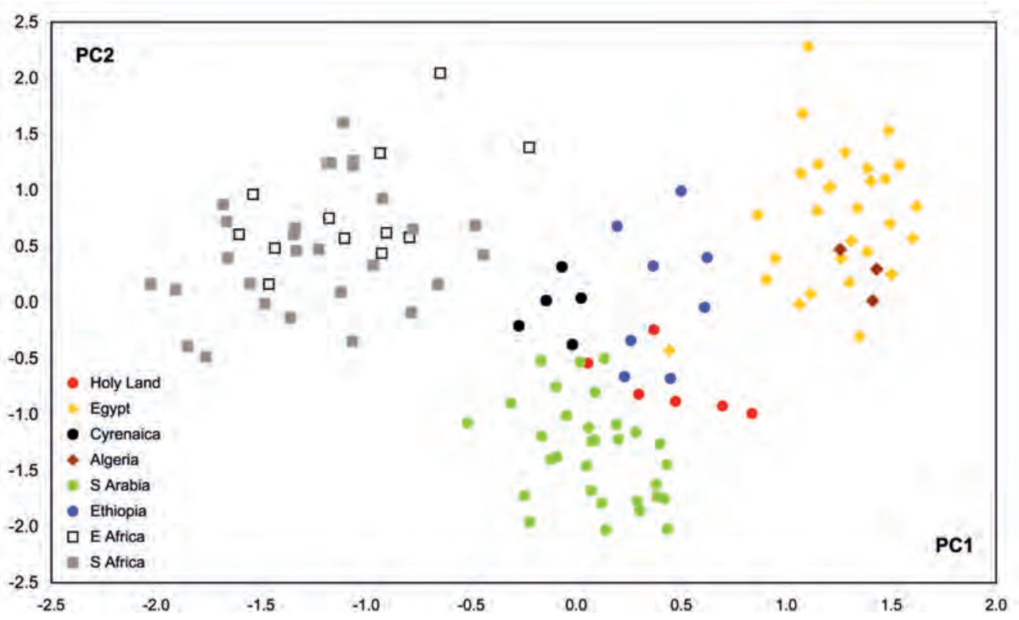


Fig. 2. Bivariate plot of the compared samples of *Rhinolophus clivosus* s.l.: results of principal component analysis of 22 skull dimensions.

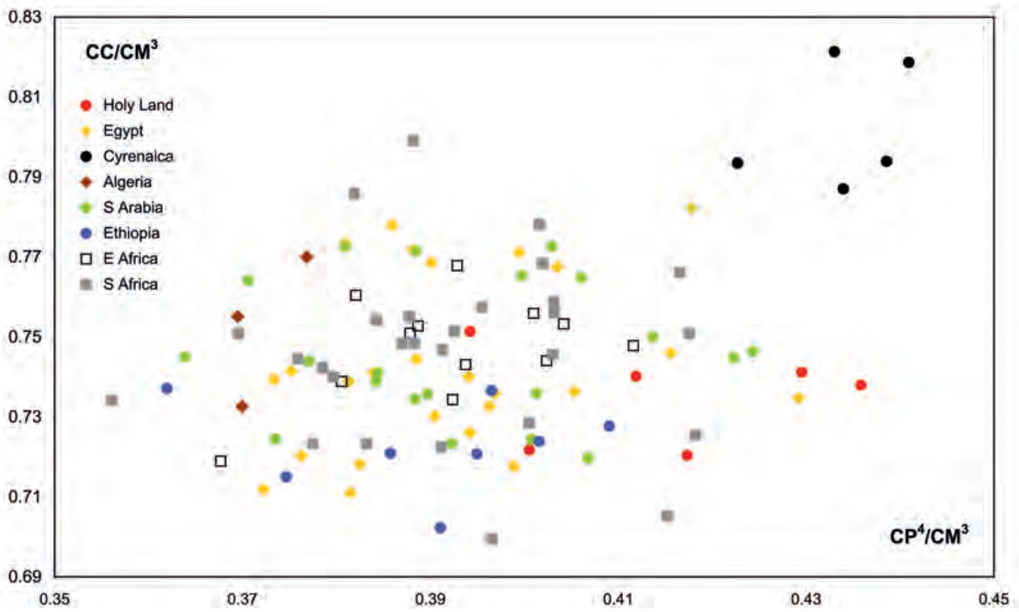


Fig. 3. Bivariate plot of the compared samples of *Rhinolophus clivosus* s.l.: relative width of rostrum (CC/CM^3) against relative length of the mesial part of the upper tooth-row (CP^4/CM^3).

sets of samples differ from each other in certain characters (see below). This suggests that the metric change from the small-sized bats in the north of the species range to the large-sized bats in the south is not simply clineal, but is characterised by steps of several different morphotypes (see below and Table 2). Nevertheless, among the Egyptian specimens belonging almost completely to the group of small-sized bats, one specimen was positioned to the group of medium-sized bats by the PCA results, the holotype of *R. andersoni*.

Within the whole compared series of geographical sets of specimens, the medium-sized bats from Cyrenaica showed the most massive skulls; their skulls were relatively widest (LaZ/LCc 0.599–0.619) and in absolute values of the width dimensions (LaInf, LaNc, CC, M^3M^3) they were as large as the large-sized bats (Table 1). On the other hand, the medium-sized bats from the Holy Land demonstrated relatively narrowest skulls (LaZ/LCc 0.554–0.581) from all compared geographical sets, only the bats from South Arabia were similar in this character (LaZ/LCc 0.555–0.605). The samples from the Holy Land also showed relatively short rostra (CM^3/LCc 0.438–0.454), similarly as the group of small-sized bats from Egypt and Algeria (CM^3/LCc 0.435–0.464), while the Cyrenaican and Ethiopian samples possessed rather long rostra (CM^3/LCc 0.454–0.468 and 0.447–0.472, respectively). However, the Cyrenaican bats demonstrated the most massive rostra, namely their mesial parts, among all compared samples (Fig. 3); their rostra were relatively widest (CC/CM^3 0.787–0.821) and in the part bearing the unicuspidal teeth also the longest (CP^4/CM^3 0.423–0.441). Other sample sets only slightly overlapped with the Cyrenaican bats, namely in the width dimensions, although the Holy Land and Ethiopian samples showed relatively very narrow rostra (CC/CM^3 0.702–0.751). In the shape of braincase, the compared sample sets showed two basic types; the group of bats with a relatively high and wide braincase (LaN/LCc 0.480–0.515; ANc/LCc 0.334–0.379) from Egypt and Algeria and the group of bats with a relatively low and narrow braincase (LaN/LCc 0.444–0.481; ANc/LCc 0.306–0.365) from the Holy Land, South Arabia and Ethiopia, and most of bats from East

Table 2. Matrix of states of relative dimensions in the particular sets of samples of *Rhinolophus clivosus* s.l.

character \ sample set	Holy Land	Egypt	Cyrenaica	Algeria	S Arabia	Ethiopia	E Africa	S Africa
horseshoe width	large	small	medium	?	large	medium	medium	medium
skull width	very small	large	very large	large	small	medium	medium	large
rostrum length	small	small	large	medium	medium	large	small	medium
rostrum width	small	medium	large	medium	medium	small	medium	medium
nasal swellings width	medium	small	large	medium	medium	small	medium	small
mesial tooth-row length	large	medium	very large	small	small	small	small	small
braincase width	small	large	medium	medium	small	small	small	small
braincase height	medium	large	medium	medium	medium	small	medium	medium
tympanic bulla size	large	medium	medium	medium	large	large	small	small
P^4 length	medium	large	small	medium	large	large	small	small
P^4 medial length	small	small	large	small	medium	medium	large	medium
P_4 length	large	large	large	medium	medium	small	small	small
M^1 width	small	medium	large	medium	medium	small	medium	medium

Table 3. Presence (and its percentage) of small premolars in the examined sample sets of *Rhinolophus clivosus* s.l. (presence confirmed at least from one half of jaw)

sample set \ presence of	P^2	%	P_3	%
Holy Land	–	0	–	0
Egypt	–	0	1	3.1
Cyrenaica	4	80.0	1	20.0
Algeria	–	0	–	0
South Arabia	1	6.3	1	6.3
Ethiopia	2	50.0	3	75.0
East Africa	11	91.7	3	25.0
South Africa	11	91.7	–	0

and South Africa. The latter two African sets, however, partly overlapped with the previous group (LaN/LCc 0.447–0.497; ANc/LCc 0.323–0.368). The set of specimens from Cyrenaica created a transition between the two main braincase types (LaN/LCc 0.478–0.488; ANc/LCc 0.346–0.356). In the relative size of tympanic bulla, the compared sets also created two basic types, which partly overlapped; the group of bats with relatively large bullae (LBT/LaM 0.334–0.416; LBT/ANc 0.511–0.659) from the Holy Land, South Arabia and Ethiopia, and the group of relativelly small bullae (LBT/LaM 0.291–0.385; LBT/ANc 0.436–0.611) from Egypt, Algeria, East and South Africa. The set of specimens from Cyrenaica created a transition between these two bulla size types (LBT/LaM 0.329–0.360; LBT/ANc 0.498–0.561), similarly as in the braincase shape.

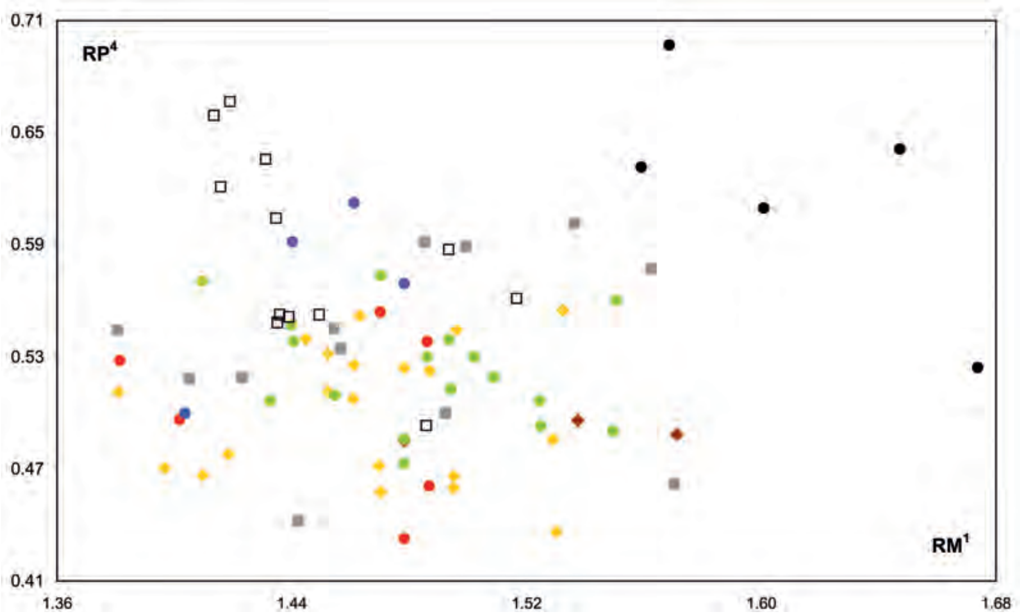


Fig. 4. Bivariate plot of the compared samples of *Rhinolophus clivosus* s.l.: relative width of the first upper molar (RM^1) against relative medial length of the last upper premolar (RP^4). For legend see Figs. 1–3 and 5.

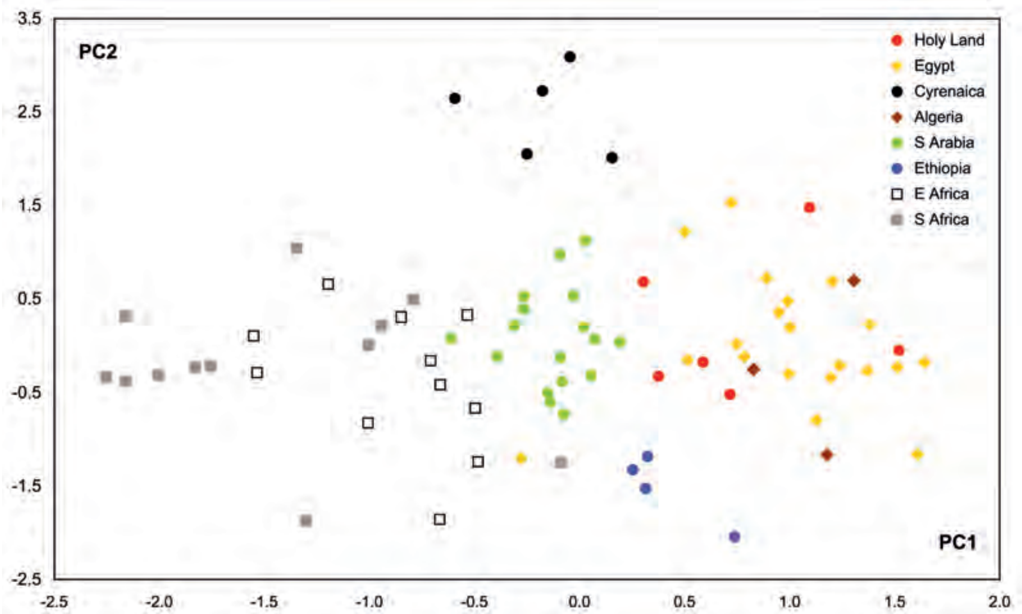


Fig. 5. Bivariate plot of the compared samples of *Rhinolophus clivosus* s.l.: results of principal component analysis of selected 12 tooth dimensions and relative dimensions (see Results for details).

Table 3 shows the presence of small premolars documented in specimens of the compared geographical sets. At least one of the upper small premolars (P^2) was present in most of Cyrenaican, East and South African specimens and in 50% of bats from Ethiopia, while in the sample sets from the Holy Land, Egypt and Algeria this tooth was absent. At least one of the lower small premolars (P_3) was found in most of the Ethiopian sample set, while in the Holy Land, Algerian and South African bats this tooth was missing and in the sets from Egypt, Cyrenaica, South Arabia and East Africa it was found only in minority of specimens per set.

The molariform teeth were shown to be extremely variable among the compared sets of specimens (Table 1). In the Cyrenaican and East African bats, the large upper premolars (P^4) were relatively shortest (in the mesio-distal dimension), but in the Cyrenaican samples also with the relatively largest length at the talon constriction (i.e. with the smallest concavity in the distal margin of talon) (Fig. 4). Relatively and absolutely largest last lower premolars (P_4) were found in the Cyrenaican bats, while the smallest were in the Ethiopian samples (Table 1). In the Cyrenaican bats the last lower premolars (P_4) were also relatively largest related to the size of the first lower premolar (P_2) ($LP_2 \times LaP_2/LP_4 \times LaP_4$ 0.397–0.466). In the Cyrenaican and Ethiopian samples, the first upper molars (M^1) were short, while the last upper molars (M^3) were relatively long. However, in the Cyrenaican samples the first upper molars (M^1) were relatively shortest (in the mesio-distal dimension) and widest (Fig. 4; LaM^1/LM^1 1.559–1.674). The last upper molars were relatively widest in the Holy Land samples.

The PCA of the most variable six tooth dimensions and their six ratios (LCs, LP^41, LP^42, LM^1, LaM^1, LP_4, P_2sq [= $LP_2 \times LaP_2$], P_4sq [= $LP_4 \times LaP_4$], $RP_{2/4}$ [= P_2sq/P_4sq], RM^1 [= LaM^1/LM^1], RP^4 [= LP^43/LP^41], RC^1 [= LC^1/LM^1]), selected by a discriminant function analysis from all 16 tooth

Table 4. Relative pairwise uncorrected genetic distances among and within reconstructed *Rhinolophus*

p-distance [%]	Europe & Maghreb	Middle East	Egypt & Holy Land	South Arabia	Socotra
ferrumequinum Europe & Maghreb	–				
ferrumequinum Middle East	0.9–1.1	0.5			
clivosus Egypt & Holy Land	1.1–1.8	1.2–1.5	0.2–1.1		
clivosus South Arabia	3.2–3.9	3.1–3.9	3.5–4.4	0.3–2.3	
clivosus Socotra	3.2–3.5	3.1–3.4	3.3–3.6	2.1–2.8	–
clivosus South & East Africa	3.5–5.1	3.9–5.3	3.9–5.6	4.4–6.5	4.9–6.1
clivosus Ethiopia	4.1–5.1	4.1–5.0	4.8–5.7	4.9–6.1	5.4–6.2
ferrumequinum SW & C China	4.7–5.2	4.9–5.3	5.3–5.6	5.3–5.8	5.4–5.6
ferrumequinum Japan & China	4.9–5.4	5.2–5.4	5.5–6.0	5.6–6.3	5.4–6.0
clivosus Cyrenaica	8.6–8.9	8.2–8.7	8.9–9.1	8.2–8.8	8.9
fumigatus	9.0–10.3	8.9–10.1	9.4–10.7	9.0–10.0	9.5–10.2
hildebrandtii	9.5–10.0	9.2–9.6	9.7–10.0	8.4–9.3	9.0–9.3
xinanzhongguoensis	8.6–9.1	8.1–8.5	8.5–8.9	8.2–9.0	7.9–8.3
hipposideros	11.6–11.8	11.9–12.1	11.9–12.1	11.2–11.9	12.1

dimensions taken and from their ten ratios (Fig. 5; PC1=54.82% of variance, PC2=12.88%), indicated similar relations among the sample sets as shown above. The PCA arranged the specimens into three size-based groups along the PC1; unlike the results of body and skull dimension analyses, the group of small-sized bats was created by Egyptian, Algerian and also Holy Land samples, and the group of medium-sized bats was clearly separated into three clusters representing the geographically delimited sets. The most distinct set along the PC2 was the group of specimens from Cyrenaica.

Genetic analysis

We processed 56 samples of *Rhinolophus*, of which 47 belonged to *R. clivosus* and its close relative *R. ferrumequinum* and nine to other species. We obtained 32 unique complete sequences of cyt *b*, of which 27 were of the *R. ferrumequinum* / *R. clivosus* morpho-group. After appending GenBank sequences, the whole dataset contained 43 sequences including the outgroup sequence of *R. hipposideros*.

Genetic divergences among ingroup haplotypes ranged from 0.1 to 11.0%, among ingroup and outgroup haplotypes from 11.2 to 13.4% (Table 4). Within ingroup, divergences among the *R. ferrumequinum* / *R. clivosus* morpho-group and other *Rhinolophus* species ranged from 9.4 to 11.0%, within the *R. ferrumequinum* / *R. clivosus* morpho-group from 0.1 to 9.2%.

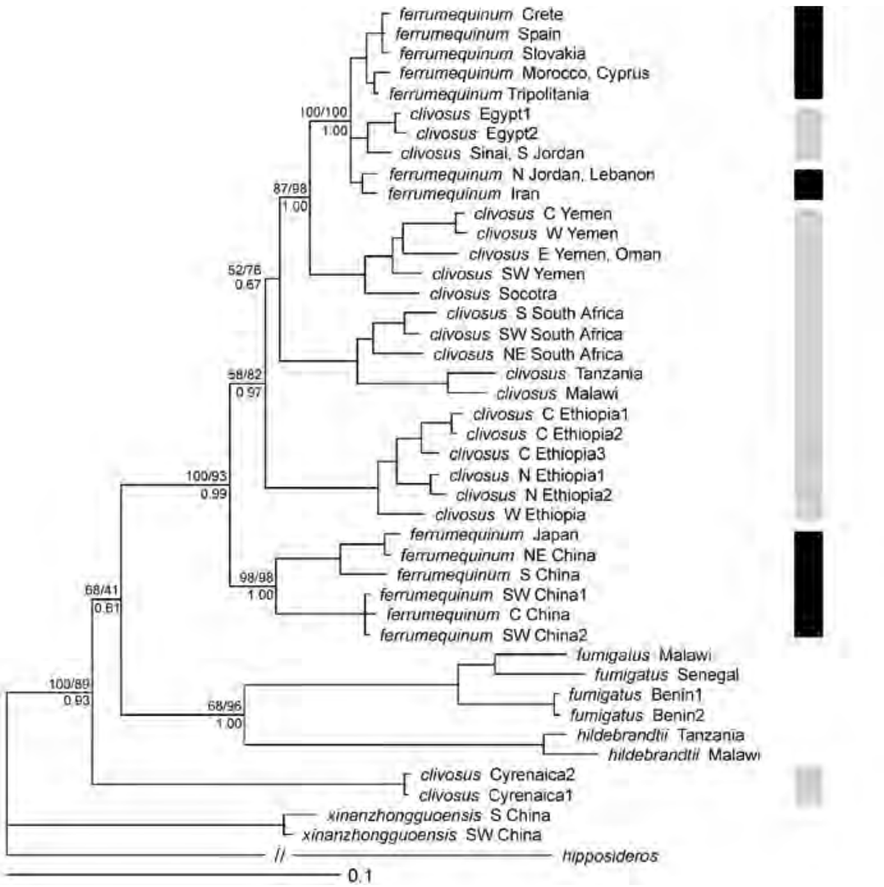
MP analysis revealed four equally parsimonious trees of 785 steps. These MP trees differed in minor arrangement of haplotypes within West-Palaearctic and African *R. ferrumequinum / R. clivosus* lineages, but it did not influence the general topology. Majority of nodes showed a good bootstrap support (BS>70%), and revealed phylogroups corresponding with taxonomic or geographical affiliation of the respective species and forms (Fig. 6). Identical phylogroups with similarly significant support were revealed also by ML and BA (Fig. 6).

The basal phylogroup in the reconstructed phylogeny was *R. xinanzhongguoensis* from China. The sequences from Cyrenaican *R. clivosus* diverged as next under all three methods used.

→

Fig. 6. Bayesian consensus tree depicting positions of the examined *Rhinolophus clivosus* s.l. (grey vertical bars) samples and their relationships to morphologically similar populations of the genus, including *R. ferrumequinum* s.l. (black bars). Nodal support for ML and ML is indicated above, and posterior probabilities below respective branches.

phylogroups							
South & East Africa	Ethiopia	SW & C China	Japan & China	Cyrenaica	*fumigatus*	*hildebrandtii*	*xinanzhong-guoensis*
0.9–3.8							
5.1–6.5	0.4–2.2						
4.9–7.1	5.3–5.9	0.2					
5.4–7.5	5.8–6.3	3.7–4.1	0.3–2.2				
8.2–9.8	8.6–9.2	8.9	8.7–8.9	0.1			
8.9–10.1	9.6–10.4	9.7–9.8	9.7–10.2	9.2–9.6	0.1–4.3		
9.6–10.6	9.4–10.0	9.6–9.7	9.5–9.9	9.3–9.7	8.6–9.6	1.5	
8.5–10.0	8.4–9.4	8.7–9.1	8.3–9.0	10.2–10.7	9.9–11.0	9.6–10.0	0.8
11.8–12.9	11.2–12.2	11.3	11.6–12.2	12.3–12.4	12.5–13.4	12.1–12.6	11.4–11.7



Monophyly at the sister node, however, was weakly supported, thus, the relationship among the Cyrenaican *R. clivosus*, the *fumigatus* lineage grouping two sister species *R. fumigatus* and *R. hildebrandtii*, and the lineage comprising all other haplotypes from *R. clivosus* s.str. and *R. ferrumequinum* (the *ferrumequinum/clivosus* complex), remains an unresolved trichotomy. The latter lineage was strongly supported as monophyletic, differing from *R. clivosus* from Cyrenaica at rather high genetic divergence of 8.2–9.8%. The particular phylogroups within the *ferrumequinum/clivosus* complex comprised morphotypes of either *R. ferrumequinum* or *R. clivosus* or of both species. The group of East Asian *R. ferrumequinum* sequences was the first to diverge, showing an internal split into two well supported and up to 4.1% divergent clades from Japan, north-eastern China and the Hainan island, and central and south-western China, respectively. Within the remaining monophylum of African and West-Palaearctic bats of both species, four basic phylogroups could be recognised: *R. clivosus* from Ethiopia, *R. clivosus* from South and East Africa, *R. clivosus* from South Arabia including the Socotra island, and a mixed clade of *R. ferrumequinum* and *R. clivosus*, which contained three subclades with unresolved relationships: *R. ferrumequinum* from the Middle East, *R. clivosus* from Egypt and the Holy Land, and *R. ferrumequinum* of a mostly west-Mediterranean origin (Europe, Maghreb incl. western Libya, Cyprus). Divergences among the four main phylogroups of the *ferrumequinum/clivosus* complex ranged from 3.1 to 6.5%. Within the respective phylogroups, the Socotran *R. clivosus* differed by 2.1–2.8% from the Yemeni continental samples, and the three crown subclades diverged by 0.9–1.5% from each other (Table 4).

Discussion

The morphological and molecular genetic analyses revealed remarkable variation among populations within the species rank of *Rhinolophus clivosus*. This species is composed of several lineages, representing six various morphotypes (Table 2) and separated by various genetic distances in the analysed mitochondrial marker (Tables 2, 4). The results of the molecular genetic analysis conform with the findings by Guillén Servent et al. (2003) and Zhou et al. (2009) on the close position of *R. clivosus* and *R. ferrumequinum*. Moreover, the latter authors found *R. clivosus* to be an inner group of *R. ferrumequinum* s.l. and the whole clade can thus represent one broadly distributed species or three separate species (cf. Zhou et al. 2009). Our results of the genetic analysis rather conform to the latter opinion as they indicate the East Asian populations of *R. ferrumequinum* to be substantially separated from the West Palaearctic ones (4.7–5.4%, see Table 4); a separate position of the East Asian form was also supported by morphological evidence by Thomas (1997). The specimens nominally assigned to *R. clivosus* except the Cyrenaican bats showed a closer relationship to the West Palaearctic specimens of *R. ferrumequinum* (1.1–5.3%) than to East Asian *R. ferrumequinum* (5.3–7.1%). This result also supports the above opinion, that the contemporarily considered widely distributed bat *R. ferrumequinum* (sensu e.g. Csorba et al. 2003 and Simmons 2005) comprises two species, the West Palaearctic *R. ferrumequinum* and East Palaearctic and Oriental *R. nippon* Temminck, 1835 (cf. Csorba et al. 2003).

In addition, the populations of *R. clivosus* from the Holy Land, representing a well defined morphotype (medium-sized bats with very gracile teeth, see above), were shown by genetic comparison to be an inner group within the West Palaearctic lineage of *R. ferrumequinum* (being distant from other haplotypes of this lineage by 1.1–1.8%). This suggests that the metrically most distant forms of the *ferrumequinum/clivosus* complex, traditionally considered as *R. f. ferrumequinum* and *R. c. clivosus* and living in close parapatry (see Csorba et al. 2003, Benda et al. 2010), represent neither two species nor subspecies, but only one morphologically extremely variable taxon. In such case, other forms currently assigned to *R. clivosus* from southern Arabia and sub-Saharan Africa comprise a group of separate taxa (species or subspecies) under different species name/s (as supposed originally, see Introduction and Stoffberg et al. 2012), since the Holy Land population represents the topo-typical form of *R. clivosus* Cretzschmar, 1828. However, such extensive taxonomic reconsideration of the complex contemporarily composed of two morphologically well differentiated (although generally very similar) and geographically widely distributed species cannot be carried out based on the results of analysis of one mitochondrial marker only.

Thus, until a new evidence concerning the phylogenetic position of the respective populations is available, we suggest the complex to be tentatively considered as three allopatric/parapatric species, *R. ferrumequinum*, *R. clivosus*, and *R. nippon*. Nevertheless, while *R. nippon* and *R. ferrumequinum* are rather unvariable forms, at least in their genetic characters, *R. clivosus* is extremely deeply diversified in genetic traits and variable in morphology (see also Stoffberg et al. 2012).

However, the above described pattern of mutual positions of *R. ferrumequinum* and *R. clivosus* is not followed by the Cyrenaican populations of horseshoe bats, originally assigned to *R. clivosus* by Qumsiyeh & Schlitter (1982). In our morphological analysis, this form was demonstrated to be similar in most of absolute metric traits to the medium-sized forms of *R. clivosus* from Ethiopia and South Arabia (Figs 1, 2) but in its relative parameters of skull and teeth as the most divergent form among all compared samples of *R. clivosus* (see Figs 3–5 and Table 2). The molecular genetic analysis showed these bats to represent a separate lineage, deeply divergent within the Afro-Palaearctic clade, both from the bats of the *ferrumequinum/clivosus* complex of the three above defined species (8.2–9.8%) and of the *fumigatus* group (sensu Csorba et al. 2003), i.e. here *R. fumigatus* and *R. hildebrandtii* (9.2–9.7%). In summary, the synthesis of the results from both approaches shows the Cyrenaican form to represent a taxon substantially separated from its closest relatives and thus, deserving a description as a discrete species (see below). This species, along with *Pipistrellus h. hanaki* Hulva et Benda, 2004 (Benda et al. 2004) is an endemic of Cyrenaica and both bats demonstrate the uniqueness of this relatively small area within the biogeographic region of Mediterranean arboreal zone.

The above analyses also showed several other rather unexpected relations within *R. clivosus* s.str. (i.e. without the Cyrenaican populations). The results of morphological and genetic analyses indicate that the Ethiopian and South Arabian populations of the medium-sized bats of *R. clivosus* do not belong to an identical taxon (contra Harrison 1964, Harrison & Bates 1991, Al-Jumaily 1998, Kock et al. 2002). Although occurring in closely localised areas on the opposite sides of the Red Sea, both populations possess their specific morphological characters (see Table 2) and belong to lineages separated by 4.9–6.2% of genetic distances. Whereas the name *acrotis* von Heuglin, 1861 is available for the Ethiopian populations, the South Arabian bats perhaps represent a yet undescribed form. On the other hand, morphological and genetic analyses of a limited number of samples from East and South Africa did not reveal any substantial characters which would justify their division into three separate subspecies and perhaps all populations occurring in the savannah belt from the Cape to Kenya belong to one taxon (contra Stoffberg et al. 2012); *augur* Andersen, 1904 is the prior available name.

The central Saharan populations known from mountainous plateaus of south-eastern Algeria and south-western Libya (Heim de Balsac 1934, Hufnagl 1972), currently assigned to a separate subspecies *R. c. schwarzi*, were shown to be almost identical in their morphological traits to the Egyptian populations living in the Saharan part of the Nile Valley, traditionally considered *R. c. brachygnathus*. However, the latter form was further showed by results of the morphological analysis of dental traits and of the molecular genetic analysis (1.1% of distance) to be closely related to the populations from the Holy Land, representing the nominotypical subspecies. According to this arrangement, all these populations represent one taxon (subspecies) and we consider both the names *brachygnathus* Andersen, 1905a and *schwarzi* Heim de Blasac, 1934 as junior synonyms of the name *clivosus* Cretzschmar, 1928. Another Egyptian population, described as *Rhinolophus andersoni* Thomas, 1904 on the basis of a series of immature specimens, has been variably assigned to various subspecies of *R. clivosus*. The comparison mainly of tooth characters (incl. tooth-row lengths) showed the type specimen of this form to be most similar to the Ethiopian samples of *R. c. acrotis*, and we thus consider these names synonymous, since also the ecological conditions of the occurrences of both populations are very similar (dry mountain ranges along the western Red Sea shore).

Herein presented data provide a new and inspiring look on the relationships within the *R. ferrumequinum / R. clivosus* morpho-group. While the new status of the Cyrenaican populations could be suggested beyond doubt, a decisive taxonomic revision of the whole group requires a more extensive sampling over its vast distribution area, and a more detailed phylogenetic analysis using other genetic markers in order to evaluate alternative explanations of possible changes (see also Stoffberg et al. 2012).

Taxonomic Description

Rhinolophus horaceki sp. n.

Rhinolophus clivosus Cretzchmar, 1828: Qumsiyeh 1981: 49; Qumsiyeh & Schlitter 1982: 384; Le Berre 1990: 78 [partim]; Horáček et al. 2000: 100 [partim]; Simmons 2005: 353 [partim]; Aulagnier et al. 2008: 72 [partim].

Rhinolophus clivosus clivosus Cretzchmar, 1828: Qumsiyeh 1985: 32.

Rhinolophus clivosus brachygnathus Andersen, 1905: Koopman 1994: 54; Csorba et al. 2003: 35.

Type material. **Holotype**: ♂ ad. (NMP 49880, field No. pb2124 [S+A]), Wadi Darnah, 6 km S of Darnah, 15 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin. – **Paratypes**: ♂ ad. (NMP 49861, field No. pb2104 [S+A]), Al Burdi, 12 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – ♂ ad. (NMP 49879, field No. pb2123 [S+A]), Wadi Darnah, 6 km S of Darnah, 15 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – ♀ ad. (NMP 49882, field No. pb2127 [S+A]), Wadi Darnah, 10 km S of Darnah,16 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – ♀ ad. (NMP 49915, field No. pb2163 [S+A]), Wadi Al Kuf, 20 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin.

Type locality. Wadi Darnah, 32° 42’ 06” N, 22° 36’ 40” E, ca. 6 km S of Darnah, Darnah Dist., Cyrenaica, Libya.

Description. *Rhinolophus horaceki* sp. n. is a medium-sized horseshoe bat, in most respects similar to the medium-sized forms of *R. clivosus* Cretzschmar, 1828 from the Middle East and north-eastern Africa, including the structure and relative size of the nose-leaf. Forearm length 48–50 mm, ear length 20.8–22.7 mm, horseshoe width 6.9–7.5 mm, condylocanine length of skull 17.5–18.1 mm, length of the upper tooth-row 7.3–7.6 mm.

The horseshoe of *R. horaceki* sp. n. is relatively narrow (Fig. 7), the connecting process of the nose-leaf is high and rounded, the sella is constricted in the middle, tip of the sella is pointed, lancet is hairy and regularly triangular in shape. One medial groove is present in the lower lip.

Skull is relatively wide (LaZ 11.1–12.1 mm; LaZ/LCc 0.599–0.619), rostral part of the skull inluding the nasal swellings is massive (LaInf 5.3–6.1 mm; CC 5.6–6.3 mm; LaInf/CM^3 0.762–0.786; CM^3/LCc 0.454–0.468), relatively long and wide (CC/CM^3 0.787–0.821; CP^4/CM^3 0.423–0.441). Sagittal crest is medium developed, infraorbital foramen is large and infraorbital bar

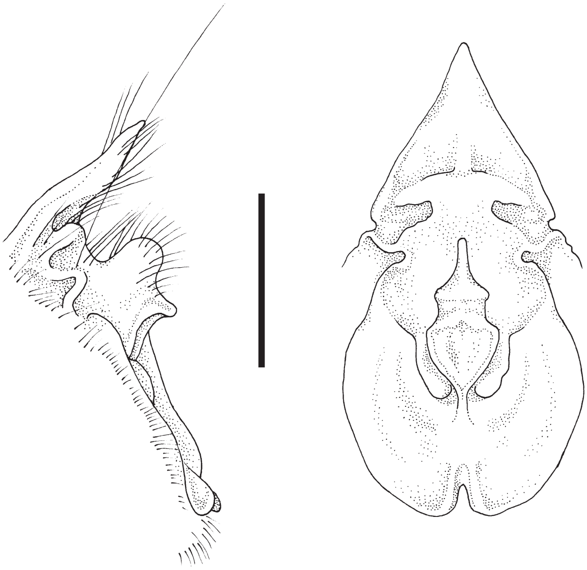


Fig. 7. Nose-leaf of *Rhinolophus horaceki* sp. n. (NMP 49880, holotype), lateral (left) and frontal (right) views. The frontal view is depicted without hairs. Scale bar – 5 mm.

is long and thin (Fig. 8). Nasal swellings are rather undeveloped, the posterior median swellings are equally long to the anterior swellings, the anterior lateral swellings are almost equal to the anterior median swellings (Fig. 8).

The teeth are relatively massive (Figs. 9, 10); upper molars are relatively wide (LaM^1/LM^1 1.559–1.674; LaM^3/LM^3 1.691–1.735), large upper premolars (P^4) are relatively wide and mesio-distally short (LP^4/LaP^4 0.569–0.610), with relatively very shallow concavity in the distal

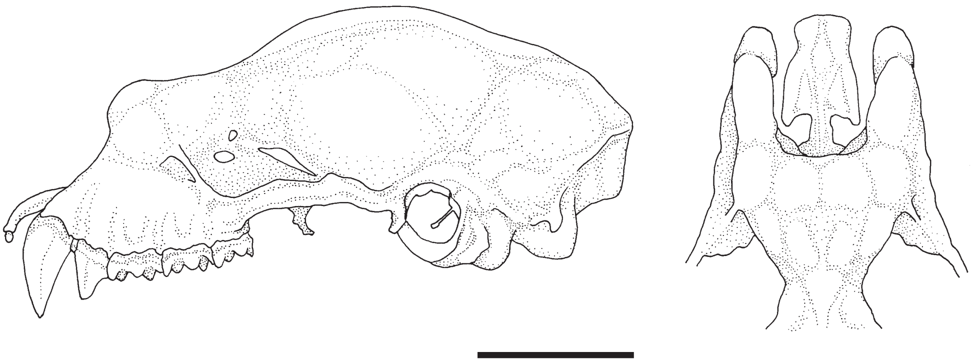


Fig. 8. Skull in lateral view (left) and rostral part of the skull in dorsal view (right) of *Rhinolophus horaceki* sp. n. (NMP 49880, holotype). Scale bar – 5 mm.

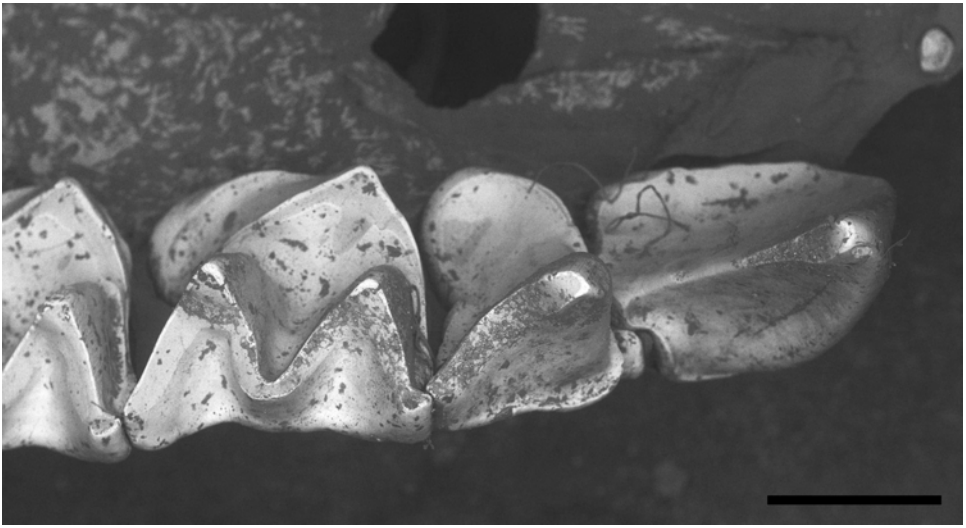


Fig. 9. Occlusal view on the mesial part of the left upper tooth-row (I^1–M^1) of *Rhinolophus horaceki* sp. n. (NMP 49880, holotype). Scale bar – 1 mm.

margin of talon (LP^43/LP^41 0.524–0.697). Large lower premolars (P_4) are absolutely very large (LP_4 1.31–1.39 mm) as well as very large in relation to the size of smaller lower premolars (P_2) ($LP_2 \times LaP_2/LP_4 \times LaP_4$ 0.397–0.466). The minute second lower premolar (P_3) is frequently missing, while the minute first upper premolar (P^2) is frequently present (LP^2 0.35–0.38 mm); if present, P_3 lies out of the the tooth-row, P_2 and P_4 are in contact.

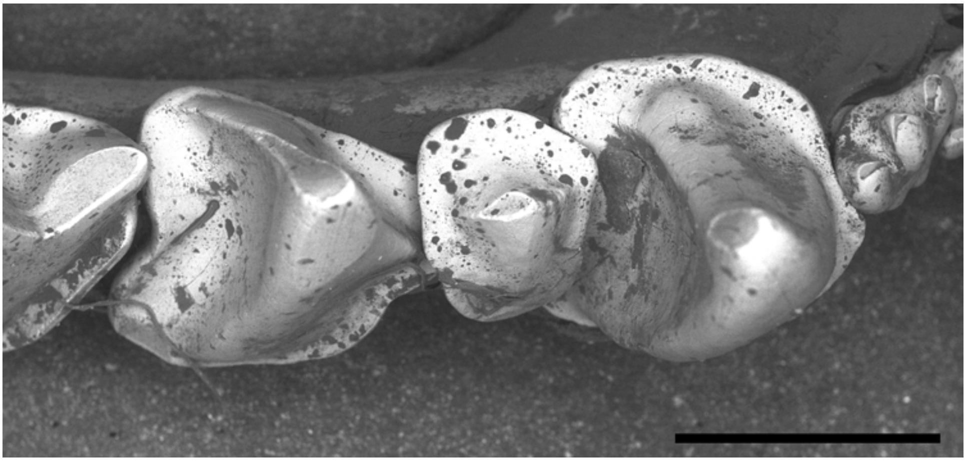


Fig. 10. Occlusal view on the right lower unicuspidal teeth (C–P_4) of *Rhinolophus horaceki* sp. n. (NMP 49880, holotype). Scale bar – 1 mm.

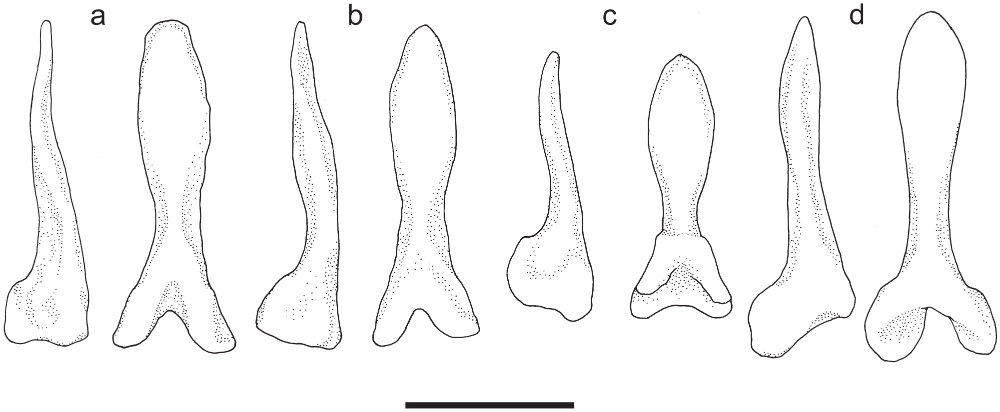
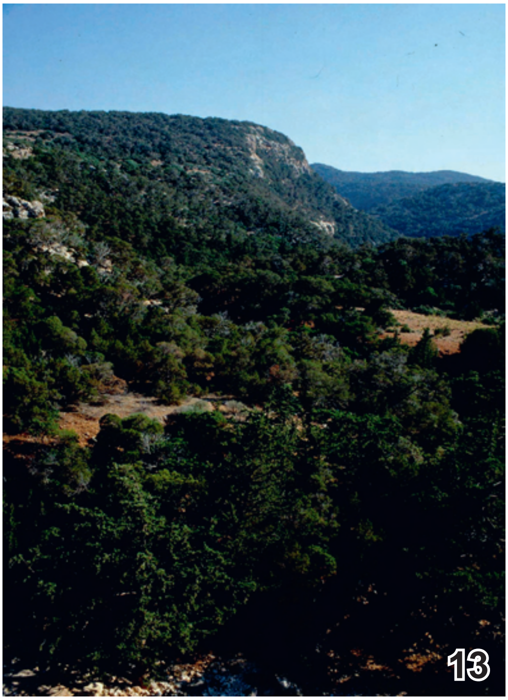


Fig. 11. Baculum preparations of *Rhinolophus horaceki* sp. n. and two comparative samples of the *ferrumequinum/clivosus* group (for other examined samples of this group see Hanák 1969, Strelkov 1971, Thomas 1997, and Csorba et al. 2003). Explanations: a – *R. horaceki* sp. n., Libya (Cyrenaica), Wadi Darnah, NMP 49879 (left – lateral view, right – ventral view); b – *R. horaceki* sp. n., Libya (Cyrenaica), Al Burdi, NMP 49861 (left – lateral view, right – dorsal view); c – *R. clivosus*, Egypt, Cairo, Abu Rawash, ZFMK 59.292 (left – lateral view, right – ventral view); d – *R. ferrumequinum*, Syria, As Salihiyyah, NMP 48974 (left – lateral view, right – dorsal view). Scale bar – 2 mm.

Baculum of *R. horaceki* sp. n. is a relativelly large bone, dorso-ventrally flattened in its distal two-thirds, creating a lancet-form shape, while its proximal epiphysis is massive and laterally bifurcated (Fig. 11). Total length of baculum 3.7–3.9 mm, largest width of the proximal epiphysis

Fig. 12. Portrait of *Rhinolophus horaceki* sp. n. (photo by A. Reiter).



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1.2–1.5 mm, largest (dorso-ventral) height of the proximal epiphysis 1 mm, largest width of the lancet 0.8–0.9 mm.

The dorsal pelage of *R. horaceki* sp. n. is brown to brownish-grey, ventral pelage is greyish-beige (Fig. 12). Nose-leaf and ears are dark brown or dark greyish-brown, distal parts darker than the proximal. Wing membranes are dark brown or greyish-brown.

Genetics. In the group of horseshoe bats of the *ferrumequinum/clivosus* complex (*R. ferrumequinum* (Schreber, 1774), *R. nippon* Temminck, 1835 and *R. clivosus* Cretzschmar, 1828 s.str.), *R. horaceki* sp. n. shows a unique base position within the mitochondrial gene for cytochrome *b* (1140 bp) at 34 sites: 1071 (A→C), 36, 127, 378, 562, 750, 808, 972, 1107, 1134 (A→G), 117 (C→A), 5, 57, 190, 201, 285, 390, 468, 564, 730, 894, 969, 982, 1057 (C→T), 698, 907 (G→A), 126, 459, 873 (T→C), 864, 1089 (A/C→T), 282, 462 (A/G→C), and 708 (A/C/G→T). With the *fumigatus* group (here, *R. fumigatus* Rüppell, 1842 and *R. hildebrandtii* Peters, 1878), *R. horaceki* sp. n. shares unique base positions at four sites, which it does not share with bats of the *ferrumequinum/clivosus* complex: 57, 564 (T), 459, and 873 (C); only with *R. fumigatus* at two sites: 907 (A) and 969 (T); and only with *R. hildebrandtii* at three sites: 190, 1089 (T), and 697 (A). With the *ferrumequinum/clivosus* complex, *R. horaceki* sp. n. shares unique base positions at seven sites, which it does not share with bats of the *fumigatus* group: 141, 591, 681 (A), 105 (C), 640, 835 (G), and 49 (T).

DIMENSIONS OF THE HOLOTYPE (in millimetres). **External**: LC 60; LCd 34; LAt 18.4, LA 21.3; LaFE 6.9.

Cranial: LCr 20.16; LCc 17.48; LaZ 10.68; LaI 2.42; LaInf 5.69; LaNc 8.43; LaM 9.32; ANc 6.17; ACr 7.54; LBT 3.07; CC 5.84; P^4P^4 6.48; M^3M^3 7.71; CM^3 7.42; M^1M^3 4.74; CP^4 3.22; LMd 13.24; ACo 3.28; IM_3 8.79; CM_3 8.03; M_1M_3 5.39; CP_4 2.94.

Dental: LCs 1.92; LaCs 1.53; LP^2 0.35; $LP^4$1 1.50; $LP^4$2 0.91; $LP^4$3 0.79; LaP^4 2.46; LM^1 1.82; LaM^1 3.05; LM^3 1.20; LaM^3 2.07; LCi 1.20; LP_2 0.69; LaP_2 0.83; LP_3 –; LP_4 1.31; LaP_4 1.10; LM_1 2.06.

MITOCHONDRIAL SEQUENCE OF THE HOLOTYPE (complete sequence of the mitochondrial gene for cytochrome *b*; GenBank Accession Number KC579375; 5' end). atg atc aac att cgc aag tcc cac cca cta ttc aag att atc aac gac tca ttc gtt gac cta cct gcc cca tca agt atc tct tcc tga tga aacttc gga tcc ctc cta ggg gta tgc cta gcc gtc caa att ctc aca gga ctt ttc cta gca ata cac tac aca tca gat act gcc aca gcc ttc tac tcc gta act cat att tgc cga gac gtc aac tat ggc tga gtc cta cgc tac ctc cac gcc aac gga gcc tct ata ttc ttc atc tgc ctc ttt cta cac gta gga cga gga atc tac tac ggc tcc tat aca ttc tca gaa aca tga aac att gga att atc ctc ctc ttc gcc gtc atg gcc acg gca ttc ata ggt tac gta ctc cca tga ggc caa atg tcc ttc tga ggg gca aca gtc atc aca aac ctt ctc tca gcc atc ccc tac gtt gga aca acc cta gtc gaa tga gtc tga ggc gga ttc tca gtt gat aaa gcc aca ctc acc cga ttc ttc gcc ctg cac ttc cta cta ccc ttt gtt atc gca gcc ata gtt ata gtc cat cta ctt ttc ctc cat gaa aca gga tca aac aac cca acc gga atc cca tca gac gca gac ata atc cca ttc cac ccc tac tac acc att aaa gac atc cta ggc ctc ata cta ata ctt aca gca cta ctg tcc ctg gtc tta ttt gcc ccc gac cta ctg ggc gac cca gac aac tac act cca gcc aac cca cta aat act cca ccc cac att aag cca gaa tga tac ttt cta ttt gcc tac gca atc cta cgc tca atc cca aac aaa ctt ggt gga gtc gta gcc ctg gtc cta tcc att ctc atc cta gcc acc att cca cta ctc cac aca tca aaa caa cgc agc ata gca ttc cga ccc cta agt caa tgt ctg ttc tga ctc tta gta gca gac ctt ctt aca cta acc tga atc gga ggc caa cct gtc gaa cac ccg ttc atc atc atc gga caa tta gcc tcc att ctc tat ttc cta att atc ctt gtc cta ata cca ctt gcg ggc atc gca gaa aac cat cta ttg aag tga aga.

DERIVATIO NOMINIS. Patronymic; named in honour of Professor Ivan Horáček (Prague, Czech Republic) who has significantly contributed to the fauna, taxonomy and ecology of the Mediterranean bats.

←

Figs. 13–16. Sites of occurrence of *Rhinolophus horaceki* sp. n. in Cyrenaica, Libya (photos by A. Reiter). 13 – dense coniferous forest in the central part of Wadi Al Kuf. 14 – Qasr Ash Shahdayn ruins, roost of *R. horaceki* sp. n., surrounded by dense mountain forests. 15 – Wadi Darnah, mosaic of agricultural areas and Mediterranean woodlands. 16 – Al Burdi, shrubland valley in a plateau of dry steppes.

DISTRIBUTION. *Rhinolophus horaceki* sp. n. is known from seven sites in northern Cyrenaica (Qumsiyeh & Schlitter 1982, original findings), from ca. 350 km long belt of Mediterranean woodlands and steppes between Wadi Al Kuf in the west and Al Burdi in the east (Figs. 13–16). The records are available from altitudes stretching from the sea level up to 660 m a. s. l., from the following sites: Al Burdi (31° 45' N, 25° 05' E), Qasr Ash Shahdayn (32° 37' N, 21° 35' E), ruins 6 km SE of Qasr [Al] Maqdam (32° 38' N, 21° 36' E; Qumsiyeh & Schlitter 1982), Roman aquaduct at Kufanta (32° 46' N, 21° 34' E; Qumsiyeh & Schlitter 1982), Wadi Darnah, gallery ca. 6 km S of Darnah (type locality, 32° 42' N, 22° 37' E), Wadi Darnah, cave ca. 10 km S of Darnah (32° 41' N, 22° 36' E), and Wadi Al Kuf, unnamed cave (32° 41' N, 21° 34' E). At four sites, *R. horaceki* sp. n. was found roosting; viz., in two natural caves, in an underground part of castle ruins (Fig. 14) and in an abandoned cellar.

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References

AELLEN V., 1959: Contribution à l'étude de la faune d'Afghanistan 9. Chiroptères. *Revue Suisse de Zoologie*, **66**: 353–386.

AL-JUMAILY M. M., 1998: Review of the mammals of the Republic of Yemen. *Fauna of Arabia*, **17**: 477–502.

ALLEN G. M., 1939: A checklist of African mammals. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, **83**: 1–763.

ANDERSEN K., 1904: Five new *Rhinolophi* from Africa. *Annals and Magazine of Natural History*, Series 7, **14**: 378–388.

ANDERSEN K., 1905a: Further descriptions of new *Rhinolophi* from Africa. *Annals and Magazine of Natural History*, Series 7, **15**: 70–76.

ANDERSEN K., 1905b: A list of the species and subspecies of the genus *Rhinolophus*, with some notes on their geographical distribution. *Annals and Magazine of Natural History*, Series 7, **16**: 648–662.

ANDERSEN K., 1906: On some new or little-known bats of the genus *Rhinolophus* in the collection of the Museo Civico, Genoa. *Annali del Museo Civico di Storia Naturale di Genova*, **3**: 173–195.

AULAGNIER S., HAFFNER P., MITCHELL-JONES A. J., MOUTOU F. & ZIMA J., 2008: *Guide des mammifères d'Europe, d'Afrique du Nord et du Moyen-Orient*. Delachaux et Niestlé SA, Paris, 271 pp.

BENDA P. & VALLO P., 2009: Taxonomic revision of the genus *Triaenops* (Chiroptera: Hipposideridae) with description of a new species from southern Arabia and definitions of a new genus and tribe. *Folia Zoologica*, **53**(Monograph 1): 1–45.

BENDA P., HULVA P. & GAISLER J., 2004: Systematic status of African populations of *Pipistrellus pipistrellus* complex (Chiroptera: Vespertilionidae), with a description of a new species from Cyrenaica, Libya. *Acta Chiropterologica*, **6**: 193–217.

BENDA P., LUČAN R. K., OBUCH J., REITER A., ANDREAS M., BAČKOR P., BOHNENSTENGEL T., EID E. K., ŠEVČÍK M., VALLO P. & AMR Z. S., 2010: Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 8. Bats of Jordan: fauna, ecology, echolocation, ectoparasites. *Acta Societatis Zoologicae Bohemicae*, **74**: 185–353.

Bogdanowicz W., 1992: Phenetic relationships among bats of the family Rhinolophidae. *Acta Theriologica*, **37**: 213–240.

Corbet G. B., 1978: *The Mammals of the Palaearctic Region*: *A Taxonomic Review*. British Museum (Natural History) & Cornell University Press, London & Ithaca, 314 pp.

Cotterill F. P. D., 2002: A new species of horseshoe bat (Microchiroptera: Rhinolophidae) from south-central Africa: with comments on its affinities and evolution, and the characterization of rhinolophid species. *Journal of Zoology*, *London*, **256**: 165–179.

Cretzschmar J., 1826–1830: Säugethiere. Pp.: 1–78+30 tbl. In: Senckenbergische Naturforschende Gesellschaft (ed.): *Atlas zu der Reise im nördlichen Afrika von Eduard Rüppell*. *Erste Abtheilung*. *Zoologie*. Comission bei Heinr. Ludw. Brönner, Frankfurt am Main, [not continuously paginated]. [NB: The sheet concerning the description of *Rhinolophus clivosus* was issued in 1928, see Mertens 1925.]

Csorba G., Ujhelyi P. & Thomas N., 2003: *Horseshoe Bats of the World* (*Chiroptera*: *Rhinolophidae*). Alana Books, Bishop's Castle, xxxii+160 pp.

Ellerman J. R. & Morrison-Scott T. C. S., 1951: *Checklist of Palaeartic and Indian Mammals 1758 to 1946*. British Museum, London, 810 pp.

Ellerman J. R., Morrison-Scott T. C. S. & Hayman R. W., 1953: *Southern African Mammals 1758 to 1951*: *A Reclassification*. British Museum, London, 363 pp.

Felten H., Spitzenberger F. & Storch G., 1977: Zur Kleinsäugerfauna West-Anatoliens. Teil IIIa. *Senckenbergiana Biologica*, **58**: 1–44.

Guillén Servent A., Francis C. M. & Ricklefs R. E., 2003: Phylogeny and biogeography of the horseshoe bats. Pp.: xii–xxiv. In: Csorba G., Ujhelyi P. & Thomas N. (eds.): *Horseshoe Bats of the World* (*Chiroptera*: *Rhinolophidae*). Alana Books, Bishop's Castle, xxxii+160 pp.

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

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

Hanák V., 1969: Zur Kenntnis von *Rhinolophus bocharicus* Kastchenko et Akimov, 1917 (Mammalia: Chiroptera). *Věstník Československé Společnosti Zoologické*, **33**: 315–327.

Hanák V. & Elgadi A., 1984: On the bat fauna (Chiroptera) of Libya. *Věstník Československé Společnosti Zoologické*, **48**: 165–187.

Harrison D. L., 1964: *The Mammals of Arabia*. *Volume I*. *Indroduction*, *Insectivora*, *Chiroptera*, *Primates*. Ernest Benn Limited, London, 192 pp.

Harrison D. L. & Bates P. J. J., 1991: *The Mammals of Arabia*. *Second Edition*. Harrison Zoological Museum, Sevenoaks, 354 pp.

Hayman R. W. & Hill J. E., 1971. Part 2. Order Chiroptera. Pp.: 1–73. In: Meester J. & Setzer H. W. (eds.): *The Mammals of Africa*. *An Identification Manual*. Smitsonian Institution Press, Washington, [not paginated continuously].

Heim de Balsac H., 1934: Mission Saharienne Augièras-Draper 1927–1928. Mammifères. *Bulletin du Muséum National d'Histoire Naturelle*, **6**: 482–489.

von Heuglin T., 1861: Beiträge zur Fauna der Säugethiere N.O.-Afrika's. I. Chiroptera. *Novorum Actorum Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum*, **29**: 1–18.

Hollister N., 1916: Description of a new genus and eight new species and subspecies of African mammals. *Smitsonian Miscelaneous Collections*, **66**: 1–8.

Horáček I., Hanák V. & Gaisler J., 2000: Bats of the Palearctic Region: a taxonomic and biogegraphic review. Pp.: 11–157. In: Wołoszyn W. (ed.): *Proceedings of the VIIIth European Bat Research Conference*. *Volume I*. *Approaches to Biogeography and Ecology of Bats*. Institute of Systematics and Evolution of Animals PAS, Kraków, 280 pp.

Hufnagl E., 1972: *Libyan Mammals*. The Oleander Press, Stoughton & Harrow, 85 pp.

Kaŝenko N. F. & Akimov M. P., 1917: *Rhinolophus bocharicus* sp. n. *Ežegodnik Zoologičeskago Muzeâ Akademii Nauk*, **22**: 221–223 (in Russian).

Kock D., Al-Jumaily M. & Nasher A. K., 2002: Horseshoe bats, genus *Rhinolophus* Lacépède, 1799 (Mammalia: Chiroptera: Rhinolophidae), of Yemen. *Fauna of Arabia*, **19**: 517–515.

Koopman K. F., 1966: Taxonomic and distributional notes on southern African bats. *The Puku*, **4**: 155–165.

Koopman K. F., 1975: Bats of The Sudan. *Bulletin of the American Museum of Natural History*, **154**: 353–444.

Koopman K. F., 1993: Order Chiroptera. Pp.: 137–241. In: Wilson D. E. & Reeder D. M. (eds.): *Mammal Species of the World*. *A Taxonomic and Geographic Reference*. *Second Edition*. Smithsonian Institution Press, Washington & London, xviii+1206 pp.

Koopman K. F., 1994: Chiroptera: Systematics. In: Niethammer J., Schliemann H. & Starck D. (eds.): *Handbook of Zoology*. *Volume VIII*. *Mammalia*. Walter de Gruyter, Berlin & New York, 217 pp.

Le Berre M., 1990: *Faune du Sahara*. *2*. *Mammifères*. Chabaud & Lechevalier, Paris, 360 pp.

Li G., Jones G., Rossiter S. J., Chen S.-F., Parsons S. & Zhang S., 2006: Phylogenetics of small horseshoe bats from East Asia based on mitochondrial DNA sequence variation. *Journal of Mammalogy*, **87**: 1234–1240.

Mertens R., 1925: Verzeichnis der Säugetier-Typen des Senckenbergischen Museums. *Senckenbergiana*, **7**: 18–37.

Monadjem A., Taylor P., Cotterill F. P. D. (W.) & Schoeman M. C., 2010: *Bats of Southern and Central Africa*. *A Biogeographic and Taxonomic Synthesis*. Wits University Press, Johannesburg, xii+596 pp.

Peters W., 1878: Über die von Hrn. J. M. Hildebrandt während seiner letzen ostafrikanischen Reise gesammelten Säugethiere und Amphibien. *Monatsberichte der Königlich Preußischen Akademie der Wissenschaften zu Berlin*, **1878**: 194–209.

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

Qumsiyeh M. B., 1981: The bat fauna of Jebel Al Akhdar, N.E. Libya. *Bat Research News*, **22**(4): 49.

Qumsiyeh M. B., 1985: The bats of Egypt. *Special Publications*, *The Texas Tech University*, **23**: 1–102.

Qumsiyeh M. B. & Schlitter D. A., 1982: The bat fauna of Jabal Al Akhdar, Northeast Libya. *Annals of Carnegie Museum*, **51**: 377–389.

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

Rüppell E., 1842: Beschreibung mehrerer neuer Säugethiere in der Sammlung der senckenbergischen naturforschenden Gesellschaft befindlich. *Museum Senckenbergianum*, **3**: 129–144.

Sakai T., Kikkawa Y., Tsuchiya K., Harada M., Kanoe M., Yoshiyuki M. & Yonekawa H., 2003: Molecular phylogeny of Japanese Rhinolophidae based on variations in the complete sequence of the mitochondrial cytochrome b gene. *Genes and Genetic Systems*, **78**: 179–189.

Simmons N. B., 2005: Order Chiroptera. Pp.: 312–529. In: Wilson D. E. & Reeder D. M. (eds.): *Mammal Species of the World*. *A Taxonomic and Geographic Reference*. *Third Edition*. *Volume 1*. The Johns Hopkins University Press, Baltimore, xxxv+743 pp.

Stoffberg S., Schoeman M. C. & Matthee C. A., 2012: Correlated genetic and ecological diversification in a widespread southern African horseshoe bat. *Public Library of Science One*, **7**(2): 1–11

Strelkov P. P., 1971: Bol'šie (*Rhinolophus ferrumequinum*) i buharskie (*Rh. bocharicus*) podkovonosy (Chiroptera) iz pustyni Karakumy [Greater (*Rhinolophus ferrumequinum*) and Bukhara (*Rh. bocharicus*) horseshoe bats (Chiroptera) from the Karakum Desert]. *Zoologičeskij Žurnal*, **50**: 893–906 (in Russian, with a summary in English).

Tamura K. & Nei M., 1993: Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, **10**: 512–526.

Tavaré S., 1986: Some probabilistic and statistical problems in the analysis of DNA sequences.*Lectures on Mathematics in the Life Sciences*, **17***:* 57–86.

Temminck C. J., 1835: *Monographies de mammalogie*, *ou description de quelques genres de mammifères*, *don't les espèces ont été observées dans les différens musées de l'Europe*. *Tome Second*. *Huitième monographie sur le genre rhinolophe*; *Rhinolophus* (*Geoff*. *Cuv*. *Illig*. *Desm*.), *Vespertilio* (*Linn*. *Erxleb*.), *Noctilio* (*Kuhl*.). C. C. Van Der Hoek, Leiden, 45 pp.

Thomas O., 1904: On some small mammals collected by Mr. A. M. Mackilligin in the Eastern Desert of Egypt. *Annals and Magazine of Natural History*, Series 7, **14**: 155–159.

Thomas N. M., 1997: *A Systematic Review of Selected Afro-Asiatic Rhinolophidae* (*Mammalia*: *Chiroptera*): *An Evaluation of Taxonomic Methodologies*. Unpubl. PhD Thesis. Harrison Zoological Museum, Seveoaks, v+211 pp.

Zhou Z.-M., Guillén-Servent A., Lim B. K., Eger J. L., Wang Y.-X. & Jiang X.-L., 2009: A new species from southwestern China in the Afro-Palearctic lineage of the horseshoe bats (*Rhinolophus*). *Journal of Mammalogy*, **90**: 57–73.

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Appendix 1

List of the specimens examined

Algeria: 3 ♀♀ (MNHN 2006-246–248 [S], holotype and two paratypes of *Rhinolophus acrotis schwarzi* Heim de Blasac, 1934), Djanet, Tassili des Adjers, date unlisted, leg. Dr. H. Foley.
Egypt: 1 ♀ (NMP 91994 [S]), Abu Rawash, 15 April 1959, leg. H. Roer; – 1 ♂ (NMP 92584 [S+A]), Aswan, 24 January 2010, leg. P. Benda, I. Horáček & R. Lučan; – 1 ♂ (BMNH 4.11.4.2. [S+B]), E. Egypt Desert, 22° N, 35° E, holotype of *Rhinolophus andersoni* Thomas, 1904), 3 August 1903, leg. M. Mackilligin; – 1 ♀ (NMP 92596 [S+A]), El A'aqab, 25 January 2010, leg. P. Benda, I. Horáček & R. Lučan; – 1 ♂ (BMNH 92.9.9.7. [S], holotype of *Rhinolophus acrotis brachygnathus* Andersen, 1905a), Ghizeh, 16 December 1891, leg. J. Anderson; – 24 ♂♂ (ZFMK 59.274–59.278, 59.290–59.297, 59.299, 59.300, 59.301, 59.304, 59.306–59.308 [S+A], 59.298, 59.302, 59.303, 59.305 [A]), Kairo, Aburawasch, 15 April 1959, leg. H. Roer; – 1 ♂ (MSNG 44290 [S+A]), Korosko, Alto Egitto, date unlisted, leg. Messedaglia Bey; – 1 ♂ (MSNG 44854 [S+A]), Sakkara presso il Cairo, 5 May 1906, leg. W. Innes Bey; – 1 ♂ (SMF 41810 [S+A]), Saqqara, 14 June 1971, leg. I. Helmy & D. Kock; – 1 ♀ (NMP 90498 [S+A]), Sinai, Wadi El Feiran, 10 September 2005, leg. M. Andreas, P. Benda, J. Hotový & R. Lučan; – 1 ind. (NMP 91987 [S+B]), W of Abu Rihal, 90 km E of Idfn Shalatein, date & collector unlisted.
Eritrea: 1 ♀ (MZUF 6000 [A]), Asmara, October 1937, leg. Ignesti; – 1 ♂ (MSNG 44312 [S+A]), Assab, July 1893, leg. G. Pestalozzo; – 1 ♂ (MSNG 27583 [S+B]), Assab, Dancalia, February 1929, leg. S. Patrizi.
Ethiopia: 1 ♂ (NMP pb5503 [A]), Aksum, 1 November 2012, leg. P. Benda; – 1 ♂ (NMP pb5574 [A]), 15 km E of Bonga, 26 November 2012, leg. P. Benda; – 3 ♀♀ (NMP pb5549–5551 [A]), Dangola Washa Caves, 5 km SW of Kesa, 12 November 2012, leg. P. Benda; – 1 ♂ (MZUF 6029 [S]), Gorgora, Lago Tana, 1828 m, 13 March 1937, leg. G. Dainelli; – 3 ♀♀ (MSNG 18243 [S+B], MSNG 45630a, 45630b [S+A]), Harrar, date unlisted, leg. P. Felter, 1893, leg. Salimbeni; – 1 ♂ (MZUF 5649 [S]), Lago Tana, 1937, leg. G. Dainelli; – 1 ♀ (NMP pb5525 [A], Simien National Park, Aman Amba, 5 November 2012, leg. P. Benda.
Jordan: 2 ♀♀ (NMP 92495 [S+A], 92496 [A]), Jabal Al Bayda, 19 May 2009, leg. P. Benda, J. Obuch & A. Reiter; – 1 ♂ (NMP 92447 [S+A]), Jebel Masuda, Ain Amshit, 15 May 2009, leg. P. Benda, J. Obuch & A. Reiter; – 1 ♂ (NMP 92843 [S+B]), Petra, 4 May 1983, leg. P. Boye; – 1 ♂ (NMP 92425 [S+A]), Wadi Ghuweir, 2 km E of Khirbet Feynan, 13 May 2009, leg. P. Benda, J. Obuch & A. Reiter.
Kenya: 1 ♂, 2 ♀♀ (SMF 38521 [A], 39427, 39431 [S]), Naibei's Great Cave, Kapasakwany, Süd Seite des Mt. Elgon, 12 and 16 December 1970, 17 May 1971, leg. Dr. Mutuku.
Lesotho: 2 ♂♂, 1 ♀ (MSNG 42305, 44908a, 44908b [A]), Hermon (Basutoland), October 1891, leg. Rev. Christol; – 1 ♂ (NMB 8222 [S+B]), Mount Moorosi, Quthing, 13 November 1991, collector unlisted; – 1 ♀ (NMB 8300 [S+B]), Phallang, Maseru (Semonkong), 12 December 1991, collector unlisted; – 1 ♂ (NMB 8418 [S+B]), Ski Lodge, Butha-Buthe (Oxbow), 20 February 1992, collector unlisted.

Malawi: 1 ♂ (BMNH 97.10.1.18. [S+B], holotype of *Rhinolophus augur zambesiensis* Andersen, 1904), Fort Hill, N. Nyasa, July 1896, leg. A. Whyba; – 1 ♂, 2 ♀♀ (NMP mw199, mw231, mw232 [S+A]), Ntchisi Forest Reserve, 8 and 9 July 2008, leg. J. Šklíba.

Mozambique: 1 ♀ (MSNG 18316 [S+B]), Quilimane, 5 November 1908, collector unlisted.

Oman: 1 ♂ (NMP 92736 [A]), Ain Tabruq, 28 December 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (NMP 92755 [S+A]), Mirbat, 30 October 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (NMP 92695 [S+A]), Mudhai, 25 October 2009, leg. P. Benda, A. Reiter & M. Uhrin.

Rwanda: 1 ind. (SMF 92961 [S+Sk]), Lava-Höhle Ubuvumo, 11 December 2004, leg. Laumanns.

Saudi Arabia: 2 inds. (SMF 4371, 12296 [S+B], lectotype and paralectotype of *Rhinolophus clivosus* Cretzschmar, 1828), Mohila [= Al Muwaylih], 1826, leg. E. Rüppell.

South Africa: 1 ♀ (SMF 55037 [S+B]), Doornhoek, Pietermaritzburg, Natal, 27 March 1976, leg. I. W. Espie; – 1 ♂, 1 ♀ (NMB 7626, 7638 [S+B], Free State, Jagersfontein, Commonage, 12–16 February 1990, collector unlisted; – 2 ♀♀ (NMB 10573, 10638 [S+B]), Free State, Merrimietzie, Winburg Dist., 6 February 1996, collector unlisted; – 4 ♂♂, 3 ♀♀ (NMW 26126–26132 [S+B]), Guano Cave, Tsitsikama, Coastal NP, Cape Prov., 4 December 1975, leg. F. Spitzenberger & B. Herzig; – 1 ♀ (BMNH 4.5.1.8. [S+B], holotype of *Rhinolophus augur zuluensis* Andersen, 1904), Jususic Valley, 20 mi NW of Eshowe, Zululand, 17 November 1903, leg. C. H. B. Grant; – 1 ♂ (MSNG 44467 [S+A]), Kenilworth, soborgo della Citta del Capo, 15 March 1906, leg. W. L. Sclater; – 1 ♂ (BMNH 4.10.1.1. [S+B], holotype of *Rhinolophus augur* Andersen, 1904), Kuruman, Bechuana, 19 April 1904, leg. R. B. Woosnam; – 4 ♂♂, 3 ♀♀ (DM 8373–8379 [S+A]), KwaZulu-Natal, Eshowe-Melmoth, Entumeni Dist., Fort Yolland Farm, 14–15 May 2005, leg. P. J. Taylor et al.; – 1 ♂ (TM 46882 [S+A]), Limpopo, Haffenden Heights, 3 November 2002, leg. L. Cohen; – 1 ♂ (TM 47619 [S+A]), Mpumalanga, Kaalrug, 25 October 2004, leg. L. Cohen; – 1 ♀ (TM 46643 [S+A]), Mpumalanga, Sudwala Caves, 18 December 2008, leg. H. C. Schoeman & S. Stoffberg; – 2 ♂♂ (NMB 11072, 11075 [S+B]), Northern Cape, Koegelbeen Caves, Hay (Griekwastad), 22 February 1997, collector unlisted; – 1 ♂ (MSNG 73 [A]), Ookiep, Namaqualand, 1906, collector unlisted; – 1 ♂ (MSNG 42112 [A]), Sud Africa, Rhodesia Mus., date and collector unlisted; – 1 ♂ (SMF 44809 [S+A]), Transvaal, Rhin. Z., 27 December 1952, leg. Zumpt; – 1 ♀ (SMF 19557 [S]), Transvaal, Uitkoms, 19 January 1958, leg. J. Meester.

Sudan: 1 ♀ (MSNG 46965 [S+A]), Port Sudan, Mar Rosso, January 1908, leg. G. Nicolosi.

Tanzania: 2 ♂♂ (SMF 91227, 91228 [S+A]), Amani-Sigi Forest Reserve, E Usambara Mts., Tanga Reg., 5° 07’ S, 38° 39’ E, 14 March 1999, leg. Frontier; – 1 ♂ (SMF 92505 [S+A]), Nilo Forest Reserve, 3 August 2000, leg. Frontier; – 1 ♀ (NMW 19822 [S]), Ugano, Ruvumq Prov., 1935–1936, leg. H. Zerny.

Uganda: 1 ♀ (SMF 44092 [S+A]), Kisoro, Kigezi Dist., 1° 17’ S, 29° 42’ E, 30 October 1975, leg. A. B. C. Killango.

Yemen: 6 ♀♀ (NMP pb3079, pb3081–pb3084 [S+A], pb3080 [A]), 7 km S of Najd an Nashamah, 25 October 2005, leg. P. Benda; – 2 ♀♀ (NMP pb3060, pb3061 [S+A]), Al Hadr, 8 km W of Lawdar, 22 October 2005, leg. P. Benda; – 1 ♂ (NMP pb3059 [S+A]), Al Nueimah, 20 October 2005, leg. P. Benda; – 1 ♀ (BCSU 272 [S+B]), Al Theeba, 28 January 2002, leg. A. Al-Dumaini; – 1 ♂ (BCSU 173 [B]), Bani Ash-Shamakh, Al-Miftah, 13 November 2000, leg. I. Ash-Shamakh; – 1 ♂ (BCSU 250 [S+B]), Bani Ukab, 28 January 2002, leg. A. Al-Dumaini; – 1 ♂ (NMP pb3042 [S+A]), Damqawt, 16 October 2005, leg. P. Benda; – 5 ♂♂, 4 ♀♀ (NMP pb2962, pb2963, pb2992, pb2993, pb3000, pb3001, pb3032, pb3033 [S+A], pb2994 [A]), Hawf, 13–15 October 2005, leg. P. Benda; – 1 ind. (SMF 91025 [S+B]), Iss Khurd, coastal Hadramaut, 13 March 2000, leg. A. K. Nasher; – 1 ♀ (SMF 91024 [S+B]), Jarf Uraiq Cave, Madam, Hamdan, Sana’a Prov., 9 August 2000, leg. M. Alban; – 1 ♂ (NMP pb3120 [S+A]), Jebel Bura, W of Riqab, 30 October 2005, leg. P. Benda; – 1 ♂, 3 ♀♀ (BCSU 085, 088, 094, 096 [S+B]), Madam, Hamdan, 9 May 1999, leg. M. Alyan; – 1 ♂ (BCSU 175 [S+B]), Saraf, Bani Hashaish, 11 June 2001, leg. N. Al-Sarfi; – 1 ♂ (BCSU 230 [S+B]), Shahara, 15 March 2002, leg. M. Kaswa; – 2 ♂♂ (BCSU 251, 252 [S+B]), Shamsan, 15 February 2002, leg. A. Al-Dumaini; – 1 ♀ (SMF 55331 [A]), Strasse zwischen Hodeidah und Sanaa, 5 February 1978, leg. J. U. Heckel; – 1 ♂, 2 ♀♀ (MZUF 13175–13177 [A]), Umm Laylah, ca. 50 km NW of Sa’dah, 2350 m, September 1979, leg. C. Borri, B. Lanza & M. Poggesi.

Appendix 2

List of the specimens examined in genetic analysis. The geographical data are in form to be co-identified with haplotypes in Fig. 6

voucher	acc. number	species	country	site (source)
NMP 90498	KC579392	*clivosus*	Egypt	Sinai, Wadi El Feiran
NMP 92447	–	*clivosus*	S Jordan	Jebel Masuda, Ain Amshit
NMP 92811	–	*clivosus*	S Jordan	Wadi Al Dharih
ZFMK 59.297	KC579393	*clivosus*	Egypt1	Cairo, Abu Rawash
ZFMK 59.304	KC579394	*clivosus*	Egypt2	Cairo, Abu Rawash
NMP 49861	KC579374	*clivosus*	Libya	Cyrenaica2, Al Burdi
NMP 49879	KC579375	*clivosus*	Libya	Cyrenaica1, Wadi Darnah, 6 km S Darnah
NMP 49880	–	*clivosus*	Libya	Cyrenaica1, Wadi Darnah, 6 km S Darnah
NMP 49882	–	*clivosus*	Libya	Cyrenaica1, Wadi Darnah, 10 km S Darnah
NMP 49915	–	*clivosus*	Libya	Cyrenaica1, Wadi al Kuf
NMP pb2994	KC579388	*clivosus*	E Yemen	Hawf
NMP 92695	–	*clivosus*	Oman	Mudhai
NMP pb3060	KC579389	*clivosus*	C Yemen	Al Hadr, W Lawdar
NMP pb3079	KC579390	*clivosus*	SW Yemen	Najd An Nashamah
NMP pb3120	KC579391	*clivosus*	W Yemen	Jebel Bura, W Riqab
NMP pb2733	KC579387	*clivosus*	Yemen	Socotra, Diksam Plateau
NMP pb2750	–	*clivosus*	Yemen	Socotra, Keisu
NMP pb5503	KC579377	*clivosus*	N Ethiopia1	Aksum
NMP pb5525	KC579378	*clivosus*	N Ethiopia2	Simien National Park, Aman Amba area
NMP pb5549	KC579379	*clivosus*	C Ethiopia1	Dangola Washa Caves, 5 km SW Kesa
NMP pb5550	KC579380	*clivosus*	C Ethiopia2	Dangola Washa Caves, 5 km SW Kesa
NMP pb5551	KC579381	*clivosus*	C Ethiopia3	Dangola Washa Caves, 5 km SW Kesa
NMP pb5574	KC579382	*clivosus*	W Ethiopia	15 km E Bonga
FMNH 151424	EU436674	*clivosus*	Tanzania	Chome Forest (Zhou et al. 2009)
NMP mw199	KC579386	*clivosus*	Malawi	Ntchisi Forest Reserve
NMP mw230	–	*clivosus*	Malawi	Ntchisi Forest Reserve
NMP mw3069	–	*clivosus*	Malawi	Kasito Lodge
NMW 26132	KC579383	*clivosus*	S South Africa	Tsitsikama, Coastal NP, Guano Cave
NMW 26131	–	*clivosus*	S South Africa	Tsitsikama, Coastal NP, Guano Cave
biopsy	KC579385	*clivosus*	NE South Africa	Sudwala Cave, Kruger Park
biopsy	KC579384	*clivosus*	SW South Africa	Die Hel, Windhoek Mts.
NMP 91178	KC579399	*ferrumequinum*	Greece	Crete, Omalos, Tzani Cave
NMP pb831	KC579400	*ferrumequinum*	Slovakia	Silická Brezová, Milada Cave
EBD 24818	EU436673	*ferrumequinum*	Spain	Cádiz (Zhou et al. 2009)
NMP 90035	KC579397	*ferrumequinum*	Morocco	Talkout, Oued Tessaout valley
NMP 90425	–	*ferrumequinum*	Cyprus	Cinarli, Incirli Cave
NMP 49856	KC579398	*ferrumequinum*	Libya	Tripolitania, Ain Az Zarqa
NMP 49967	–	*ferrumequinum*	Libya	Tripolitania, Nanatalah
NMP 92404	KC579395	*ferrumequinum*	N Jordan	Zubiya Cave
NMP 91892	–	*ferrumequinum*	Lebanon	Afqa Cave
NMP 48122	KC579396	*ferrumequinum*	Iran	7 km SE Chuplu
NMP 90551	KC579376	*ferrumequinum*	C China	7 km N Foping, cave
–	DQ351848	*ferrumequinum*	SW China1	Yunnan (Feng et al. unpubl.)
–	DQ297575	*ferrumequinum*	SW China2	Yunnan (Li et al. 2006)
–	EF544404	*ferrumequinum*	S China	Henan (Niu et al. unpubl.)
–	DQ351847	*ferrumequinum*	NE China	Jilin (Feng et al. unpubl.)
–	AB085724	*ferrumequinum*	Japan	Taga, Shiga Pref. (Sakai et al. 2003)
FMNH 151422	EU436676	*hildebrandtii*	Tanzania	East Usambara Mts. (Zhou et al. 2009)
NMP mw134	KC579370	*hildebrandtii*	Malawi	Mulanje-Chitakali
NMP mw3048	KC579371	*fumigatus*	Malawi	Nyika-Jallawe valley

voucher	acc. number	species	country	site (source)
NMP 91837	KC579372	*fumigatus*	Benin1	Awaya, 10 km E Dassa
NMP 91838	KC579373	*fumigatus*	Benin2	Awaya, 10 km E Dassa
IVB Sen817	FJ457614	*fumigatus*	Senegal	Dindéfélo (Benda & Vallo 2009)
ROM 117760	EU750753	*xinanzhongguoensis*	S China	Suiyang County, Guizhou (Zhou et al. 2009)
KIZ 0505003	EU391626	*xinanzhongguoensis*	SW China	Yongde, Yunnan (Zhou et al. 2009)
NMP 49028	KC579369	*hipposideros*	Greece	Kombotades