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A new species of pipistrelle bat (Chiroptera: Vespertilionidae) from southern Arabia

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A new species of the genus *Pipistrellus* is described from the Dhofar region, southern Arabia. The new species occurs in a very limited area lesser than 1,000 km^2, situated in the belt of relative humid savannah habitats of coastal Arabia between easternmost Yemen and south-western Oman. This bat represents the eighth pipistrelle species known from Arabia and fourth bat species endemic to southern Arabia. The new species is positioned morphologically and genetically very close to the group of the Oriental species of the genus *Pipistrellus* and represents the westernmost offshoot of the Oriental vespertilionid bat fauna, isolated for more than 1,500 km across the Indian Ocean from the area of continuous distribution of this fauna in the Indian Subcontinent.

Key words: mtDNA, morphometry, taxonomy, pipistrelle bats, Middle East

INTRODUCTION

In Arabia, pipistrelle bats or dwarf vespertilionid bats are represented by four genera, *Pipistrellus* Kaup, 1829, *Hypsugo* Kolenati, 1856, *Neoromicia* Roberts, 1926, and *Vansonia* Roberts, 1946. Only one species of the genus *Neoromicia* is known from the Peninsula, *N. guineensis* (du Bocage, 1889); it occurs only marginally in south-western Yemen, i.e., in the Afro-tropic corner of Arabia (Benda *et al*., 2011*a*). *Vansonia rueppellii* (Fischer, 1829) is known from two separate and limited areas in northern Arabia, Palestine in the west and lower Mesopotamia in the east (Harrison and Bates, 1991). Species of the two remaining genera are widely distributed in both eremic and arboreal parts of the Peninsula. *Pipistrellus pipistrellus* (Schreber, 1774) and *Hypsugo savii* (Bonaparte, 1837), both broadly distributed in the European, Maghrebian and Asian sections of the Mediterranean, are known from the arboreal habitats of north-western Arabia, from Palestine, Lebanon, and Syria (Harrison and Bates, 1991; Benda *et al*., 2006, 2010; Horáček *et al*., 2008). Two other *Hypsugo* species occur in restricted areas of the semi-eremic parts of the Peninsula; *H. ariel* (Thomas, 1904) is known from the western part of Arabia, it lives in the belt between Palestine and south-western Oman and in Egypt (Benda *et al*., 2008, 2010, 2011*a*), and *H. arabicus* (Harrison, 1979) is known from eastern Arabia, it occurs in the Al Hajar Mts., north-eastern Oman, and also in south-eastern Iran (Harrison and Bates, 1991; Benda *et al*., 2011*a*, 2012). *Pipistrellus kuhlii* (Kuhl, 1817) is the only bat widespread across the Peninsula (Harrison and Bates, 1991), it occurs in all parts of Arabia, including central areas of the Arabian Desert, mountains of western Yemen and Saudi Arabia, or coastal regions of north-eastern Oman. The only Arabian area, from which *P. kuhlii* is absent, is the Dhofar region on the Omani-Yemeni transition, in the central part of the south-Arabian coastal zone.

The mountainous Dhofar region (ca. 1,500 km^2) represents an island of tropic savannah vegetation isolated from the rest of the Arabian mainland by harsh deserts of the Empty Quarter. Due to direct exposition to the south-Asian summer monsoon, the phenology of the region sharply contrasts with the climatic cycles of other parts of southern Arabia (Sale, 1980). The bat fauna of Dhofar comprises

14 species of nine families (Harrison and Bates, 1991; Benda *et al*., 2013) and of the Arabian pipistrelles, only *H. ariel* has been reported to occur marginally in the region (Benda *et al*., 2011*a*). On the other hand, the broader Dhofar region is known as a zone of a certain level of endemism, apparent even in mammals, where at least five endemic species are recognised (Hutterer and Harrison, 1988; Benda *et al*., 2009, 2011*b*; Benda and Vallo, 2009; Frynta *et al*., 2010).

During several recent field trips to Dhofar, we recorded another pipistrelle bat in the most humid parts of the region. Already at the first sight, these bats do not fit by their characters to any other bat known from the Middle East (cf. Harrison and Bates, 1991), their body size is larger than that of other Arabian pipistrelles and their generally brown pelage colouration possesses a slight silverish tinge, similar to the African pipistrelles of the genus *Neoromicia*. Further detailed analyses of morphological and genetic traits revealed these bats as a new species, which represents the eighth pipistrelle bat species occurring in Arabia and fourth bat species endemic to Dhofar. Its description is provided here.

Materials and Methods

Analyses

For morphological comparisons of 66 available specimens of the new pipistrelle bat from Dhofar, we used around 300 specimens of the Arabian populations of pipistrelle bats housed in the National Museum (Natural History), Prague, Czech Republic (NMP). The examined museum material is listed in Appendix I. The specimens were measured in a standard way with the use of mechanical or optical callipers. Horizontal dental dimensions were taken on cingulum margins. Particular teeth are denoted according to the convention proposed by e.g., Bates and Harrison (1997), i.e. I^2 and I^3 for the upper incisors, P^2 and P_2 for the mesial premolars. For the evaluated external and cranial measurements see Abbreviations below. Bacula were extracted in a 6% solution of KOH and coloured with alizarin red. Statistical analyses were performed using the Statistica 6.0 software.

We analysed partial sequences of the mitochondrial gene for cytochrome *b* (cyt *b*) of 32 specimens from Dhofar, combined with 49 newly obtained sequences from the Arabian and African populations of various species of pipistrelle bats and 30 previously published cyt *b* sequences deposited in the GenBank (see Appendix II for details on newly sequenced specimens and the corresponding GenBank accession numbers).

Material for genetic analyses was obtained from pectoral muscles or wing punches preserved in alcohol. Total genomic DNA was extracted using Geneaid Genomic DNA Mini Kit (Taipei, Taiwan) and following the manufacturer's protocol. The partial sequence of mitochondrial cyt *b* was amplified with forward L15162 (5'-GCAAGCTTCTACCATGAGGACAAATATC-3' and reverse H15915 (5'-AACTGCAGTCATCTCCGGTTTACAAGAC-3') primers. For PCR amplification a 25 µl coctail of 2 µl DNA template, 8.5 µl of ddH_2O, 12.5 µl of PPP Master Mix and 1 µl of each primer was used. Thermal profile of amplification was described elsewhere (Stadelmann *et al*., 2004*a*). All PCR products were purified by ethanol/sodium acetate precipitation before the sequenation with amplification primers was carried out by Macrogen Inc. (Seoul, South Korea).

Chromatograms of all sequences which are new for this study were checked by eye and assembled in Geneious v.6.0.6 (Biomatters, http://www.geneious.com). Multiple sequence alignment was carried out in MAFFT 7.017 (Katoh and Standley, 2013) producing 721 bp high quality alignment with no stop codons detected when translation into amino acids was obtained. A final 641 bp alignment was used for phylogenetic analyses after combining new sequences with those from GenBank. Both AIC and BIC model selection criteria as implemented in jModelTest v.2.1.10 (Darriba *et al.*, 2012) recognised HKY+Γ+I as the best substitution model of nucleotide evolution. Phylogenetic trees of unique haplotypes were constructed using the maximum likelihood (ML) and Bayesian inference (BI) methods. ML analysis was performed in RAxML v.8.0.0 (Stamatakis, 2014) using raxmlGUI v.1.5 interface (Silvestro and Michalak, 2012), with GTRGAMMAI model selected as the closest alternative to HKY+Γ+I model. The branch support was assessed using the thorough bootstrapping algorithm from 1,000 pseudoreplicates. BI analyses were performed in MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001). Two runs, four Monte Carlo Markov Chains for each run were run simultaneously for ten million generations. Tree samples were recorded every 500 generation and a 50% majority-rule consensus tree was constructed after discarding the first 25% trees as burn-in. Uncorrected *p*-distances between species were calculated in MEGA 6.0 (Tamura *et al.*, 2013). A 95% connectivity limit parsimony haplotype network from 721 bp alignment of all Dhofar samples was built using TCS 1.21 (Clement *et al.*, 2000) software and overlapped with geographical structure in tcsBU (Murias Dos Santos *et al.*, 2016).

Acoustic recordings were made using a portable ultrasound detector D-240x (Pettersson Elektronik AB, Uppsala, Sweden) set on the time-expansion mode connected to Edirol R-09HR recorder (Roland Corporation, Los Angeles, USA). The analysed bat calls were recorded in free flight under natural conditions (foraging bats), usually near the sites where the bats were also mist-netted which allowed us to confirm the bat species determination. Several echolocation call sequences were recorded when hand-releasing the bats at capturing sites. The recordings were analysed with the BatSound Pro 4.00 software (Pettersson Elektronik AB). Time-expanded sequences (expansion factor 10) were digitised at the sampling rate 48 kHz with 16-bit precision and saved as *wav files. A 1,024 pt. FFT with Hanning window was used for the analyses; oscillograms, power spectra and spectrograms were evaluated. For the parameters measured for each echolocation call see Table 4. For analysis, we used only the high quality recordings of the search phase calls.

Abbreviations

External dimensions (in mm): LC = head and body length, LCd = tail length, LAt = forearm length including wrist, LAu = ear length, LTr = tragus length.

Cranial dimensions (in mm): LCr = greatest length of skull, LCb = condylobasal length, LaZ = zygomatic width, LaI = width of interorbital constriction, LaInf = rostral width between foramina infraorbitalia, LaN = braincase width, LaM = mastoidal width, ANc = braincase height, LBT = largest horizontal length of tympanic bulla, CC = rostrum width across upper canines at crowns, M^3M^3 = width across third upper molars, CM^3 = length of upper tooth-row from front of canine to back of third molar, M^1M^3 = length of upper tooth-row from front of first molar to back of third molar, CP^4 = length of upper tooth-row from front of canine to back of the second premolar, P^2 = mesio-distal length of the first upper premolar, LMd = condylar length of mandible, ACo = height of coronoid process, CM_3 = length of lower tooth-row from front of canine to back of third molar, M_1M_3 = length of lower tooth-row from front of first molar to back of third molar, CP_4 = length of lower tooth-row from front of canine to back of second premolar, P_2 = mesio-distal length of the first lower premolar.

Other abbreviations: A = alcoholic preparation, B = skin (balg), ind. = specimen of sex unidentified, M = mean, max., min. = range margins, S = skull, SD = standard deviation.

Comparisons

The Dhofar bats are large pipistrelles, in body and skull size similar to the samples of north-Arabian populations of *P. kuhlii* and *H. savii* (and *V. rueppellii* — cf. Harrison and Bates, 1991) and much larger — without any remarkable dimension overlap — than other south-Arabian pipistrelle bats, *P. kuhlii*, *H. ariel*, *Hypsugo arabicus*, and *N. guineensis*, as well as north-Arabian *P. pipistrellus* (Fig. 1 and Table 1). The Dhofar bats are on average the largest pipistrelle bats from Arabia and absolutely the largest from southern Arabia.

In the dorsal pelage colouration, the Dhofar bats are generally brownish with two basic colour morphs (Fig. 2), greyish-brown with a slight silverish tinge and reddish-brown with the silverish tinge less apparent. The ventral pelage is markedly paler than the dorsal pelage and the difference between the dorsal colour morphs is much more apparent in the ventral colouration (Fig. 2). The colouration of the wing membranes, ears and face is rather uniformly dark greyish brown, with only slightly paler membrane parts along bones. This colouration pattern differs completely from that of other Arabian pipistrelles, which is much paler in most of species — both in the pelage and naked parts (*P. kuhlii*, *H. ariel*, *H. arabicus*), with the exceptions of *P. pipistrellus* and *N. guineensis*, which are dark coloured similarly as the Dhofar bats (although with a different tinge of the brown pelage colouration), and *H. savii* and some individuals of *V. rueppellii* with pale pelage and black or blackish-brown naked

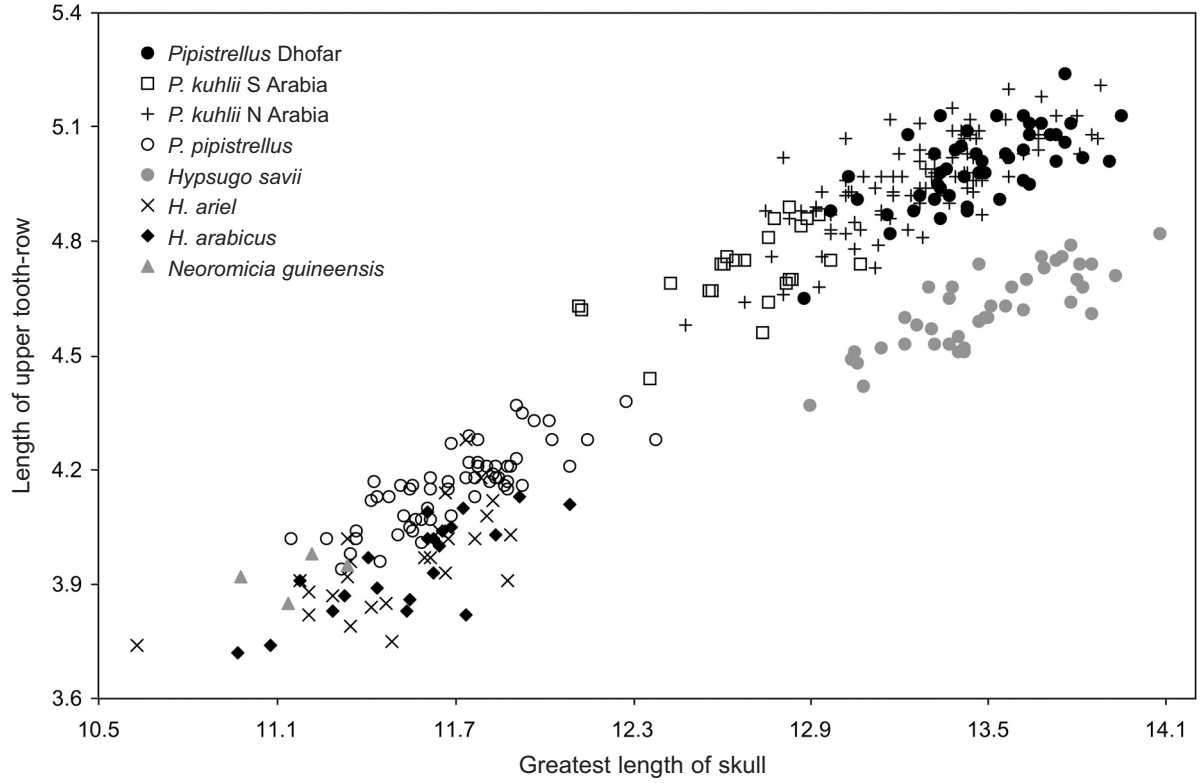

Fig. 1. Bivariate plot of skull dimensions of Arabian pipistrelle bats: greatest length of skull (LCr) against length of upper tooth-row (CM^3)

TABLE 1. External and cranial dimensions (in mm) of the examined sample sets of pipistrelle bats from Arabia. See Materials and Methods for variable abbreviations, and Appendix I for the specimens examined

Variable	*n*	**M**	min	max	SD	*n*	**M**	min	max	SD	*n*	**M**	min	max	SD
		Pipistrellus Dhofar					*Pipistrellus kuhlii* S Arabia					*Pipistrellus kuhlii* N Arabia			
LC	66	**51.0**	46	57	2.307	28	**47.1**	43	53	2.276	96	**49.6**	41	56	2.868
LCd	66	**38.3**	31	42	2.081	28	**40.6**	37	45	2.392	96	**41.1**	34	46	2.141
LAt	66	**35.48**	33.5	38.4	0.990	28	**33.38**	31.4	35.5	1.064	97	**34.65**	32.1	36.5	0.943
LAu	65	**14.04**	13.0	15.3	0.564	28	**14.12**	13.2	15.2	0.577	96	**13.39**	11.6	15.6	0.866
LTr	66	**5.53**	4.8	6.6	0.370	28	**5.83**	5.1	6.7	0.443	96	**5.96**	5.1	7.2	0.445
LCr	49	**13.46**	12.88	13.95	0.237	24	**12.68**	12.12	13.07	0.239	97	**13.26**	12.48	13.88	0.281
LCb	49	**13.00**	12.53	13.48	0.227	24	**12.25**	11.59	12.61	0.258	97	**12.84**	12.13	13.37	0.282
LaZ	46	**9.00**	8.45	9.56	0.210	21	**8.28**	7.97	8.57	0.180	85	**8.62**	8.07	9.24	0.210
LaI	49	**3.65**	3.39	3.84	0.104	24	**3.18**	2.93	3.51	0.132	97	**3.32**	3.05	3.53	0.095
LaInf	49	**4.30**	3.93	4.68	0.149	24	**3.82**	3.48	4.12	0.180	95	**3.94**	3.54	4.18	0.125
LaN	49	**6.92**	6.64	7.16	0.123	24	**6.35**	6.02	6.82	0.185	97	**6.60**	6.22	6.88	0.151
LaM	49	**7.74**	7.38	8.04	0.165	24	**7.23**	6.89	7.75	0.194	95	**7.69**	7.24	8.16	0.179
ANc	49	**5.10**	4.84	5.42	0.145	24	**4.49**	4.32	4.84	0.127	97	**4.71**	4.35	5.16	0.155
LBT	49	**2.99**	2.61	3.34	0.142	23	**2.90**	2.64	3.20	0.147	94	**3.02**	2.75	3.28	0.116
CC	47	**4.49**	4.19	4.79	0.118	24	**4.04**	3.79	4.25	0.106	96	**4.22**	3.96	4.55	0.134
M^3M^3	49	**6.16**	5.80	6.56	0.153	24	**5.50**	5.11	5.77	0.138	97	**5.65**	5.22	5.99	0.174
CM^3	49	**5.00**	4.65	5.24	0.103	24	**4.72**	4.44	4.89	0.105	96	**4.96**	4.58	5.21	0.123
LMd	49	**9.92**	9.38	10.36	0.213	24	**9.19**	8.73	9.46	0.196	97	**9.60**	8.54	10.27	0.257
ACo	49	**3.12**	2.89	3.34	0.106	24	**2.82**	2.62	2.97	0.093	97	**3.00**	2.74	3.31	0.125
CM_3	49	**5.34**	4.93	5.58	0.116	24	**5.04**	4.76	5.33	0.131	96	**5.27**	2.93	5.59	0.275
		Pipistrellus pipistrellus					*Hypsugo savii*					*Hypsugo arabicus*			
LC	66	**43.0**	36	48	2.953	40	**50.0**	45	58	3.599	26	**43.3**	40	48	1.668
LCd	65	**34.4**	27	39	2.404	40	**38.9**	34	45	2.517	26	**40.3**	37	44	2.205
LAt	67	**30.60**	28.6	32.5	0.904	41	**33.89**	32.1	36.5	0.998	26	**31.63**	28.9	34.3	1.054
LAu	65	**11.74**	10.0	13.5	0.951	40	**13.73**	12.0	15.8	0.899	26	**12.40**	11.2	13.5	0.445
LTr	65	**4.93**	3.9	6.0	0.436	39	**5.00**	3.8	6.1	0.570	26	**5.12**	4.7	5.8	0.272
LCr	59	**11.71**	11.15	12.38	0.245	41	**13.49**	12.90	14.08	0.279	22	**11.55**	10.97	12.09	0.266
LCb	59	**11.26**	10.73	11.78	0.234	40	**13.13**	12.49	13.67	0.294	22	**10.93**	10.47	11.26	0.247
LaZ	43	**7.45**	7.04	8.35	0.227	40	**8.73**	8.30	9.27	0.230	19	**7.29**	6.93	7.56	0.200
LaI	59	**3.11**	2.84	3.42	0.127	41	**3.46**	3.21	3.65	0.100	22	**2.90**	2.69	3.15	0.113
LaInf	59	**3.47**	3.28	3.83	0.115	40	**4.46**	4.14	4.84	0.168	22	**3.29**	3.07	3.56	0.132
LaN	59	**6.03**	5.67	6.41	0.152	41	**6.71**	6.44	6.98	0.134	22	**5.78**	5.59	6.02	0.128
LaM	59	**6.61**	6.32	7.24	0.147	40	**7.37**	6.98	7.81	0.173	22	**6.25**	5.97	6.48	0.143
ANc	59	**4.26**	3.93	6.77	0.353	41	**4.58**	4.20	6.74	0.374	22	**4.02**	3.76	4.22	0.105
LBT	59	**2.82**	2.53	3.26	0.132	40	**3.13**	2.88	3.45	0.129	22	**2.71**	2.52	2.97	0.138
CC	56	**3.51**	3.31	3.77	0.095	41	**4.29**	3.98	4.50	0.136	22	**3.31**	3.01	3.62	0.147
M^3M^3	58	**4.82**	4.47	5.21	0.136	41	**5.79**	5.54	6.13	0.147	21	**4.66**	4.39	5.09	0.150
CM^3	59	**4.16**	3.94	4.38	0.102	41	**4.62**	4.37	4.82	0.106	21	**3.95**	3.72	4.13	0.123
LMd	57	**8.16**	7.64	8.56	0.180	41	**9.49**	8.97	9.89	0.224	22	**7.79**	7.38	8.15	0.225
ACo	56	**2.36**	2.14	2.67	0.095	41	**2.83**	2.58	3.06	0.108	22	**2.30**	2.19	2.47	0.085
CM_3	56	**4.39**	4.06	4.62	0.110	41	**4.93**	4.58	5.13	0.120	22	**4.19**	3.93	4.48	0.129

TABLE 1. Continued

Variable	*n*	**M**	min	max	SD	*n*	**M**	min	max	SD	*n*	**M**	min	max	SD
		Hypsugo ariel S Arabia					*Hypsugo ariel* N Arabia					*Neoromicia guineensis*			
LC	20	**39.70**	35.00	45.00	2.758	10	**40.10**	37.00	42	1.595	5	**40.8**	39	42	1.095
LCd	20	**37.40**	32.00	44.00	3.251	9	**39.30**	37.00	44	2.000	5	**31.6**	29	35	2.191
LAt	20	**30.08**	28.10	32.10	0.984	11	**30.40**	28.90	33.7	1.235	5	**25.78**	25.2	26.9	0.665
LAu	20	**13.08**	12.20	14.10	0.563	10	**13.22**	12.50	14.0	0.473	5	**11.80**	10.8	12.7	0.696
LTr	20	**4.94**	4.10	5.60	0.422	10	**4.94**	4.40	5.6	0.401	5	**5.06**	4.2	5.7	0.647
LCr	16	**11.54**	10.63	11.84	0.308	10	**11.51**	11.18	11.89	0.279	4	**11.17**	10.98	11.34	0.151
LCb	16	**11.07**	10.19	11.50	0.358	10	**11.00**	10.67	11.51	0.261	4	**10.79**	10.65	10.96	0.130
LaZ	14	**7.08**	6.68	7.39	0.211	10	**6.93**	6.41	7.18	0.208	2	**7.04**	6.95	7.13	0.127
LaI	16	**2.63**	2.44	2.78	0.087	10	**2.64**	2.46	2.76	0.091	4	**2.80**	2.71	2.86	0.067
LaInf	16	**3.65**	3.34	3.92	0.142	10	**3.51**	3.26	3.86	0.185	4	**3.26**	3.21	3.34	0.062
LaN	16	**5.52**	5.34	5.75	0.116	10	**5.60**	5.33	5.76	0.120	4	**5.69**	5.62	5.75	0.070
LaM	16	**6.10**	5.87	6.32	0.144	10	**6.09**	5.82	6.31	0.137	4	**6.45**	6.43	6.49	0.029
ANc	16	**3.98**	3.73	4.17	0.113	10	**3.92**	3.79	4.02	0.084	4	**3.90**	3.67	4.02	0.163
LBT	15	**2.70**	2.44	2.92	0.142	10	**2.62**	2.28	2.93	0.204	4	**2.62**	2.52	2.75	0.097
CC	16	**3.47**	3.27	3.78	0.145	10	**3.40**	3.25	3.59	0.110	4	**3.32**	3.21	3.41	0.083
M^3M^3	15	**4.74**	4.47	5.18	0.185	10	**4.65**	4.42	4.87	0.144	4	**4.63**	4.49	4.89	0.182
CM^3	15	**3.99**	3.74	4.28	0.152	10	**3.92**	3.75	4.08	0.095	4	**3.93**	3.85	3.98	0.056
LMd	16	**7.87**	7.42	8.16	0.209	10	**7.77**	7.46	8.17	0.230	4	**7.84**	7.73	7.98	0.104
ACo	16	**2.34**	2.16	2.46	0.078	10	**2.37**	2.24	2.57	0.092	4	**2.47**	2.41	2.58	0.078
CM_3	13	**4.24**	4.02	4.47	0.150	10	**4.10**	3.87	4.29	0.134	4	**4.27**	4.21	4.37	0.076

parts (for comparison see Benda *et al*., 2006: 182, 191, 208; 2008: 33; 2010: 268, 274; 2011*a*: 40; 2012: 399, 404, 414–416, 436; 2014*a*: 48). Similarly as in other pipistrelle bats, the hairs of the Dhofar bats are bicoloured, larger proximal parts are dark brown, distal parts are paler, possessing one of the two colour tinges (very pale brown or greyish-ochre in the ventral hairs).

The skull of the Dhofar bats is robust, most massive among the south-Arabian pipistrelles (Table 2). The rostrum is relatively high and long in the Dhofar bats, much longer than in the Arabian species of the genera *Hypsugo* and *Neoromicia*, and on average also longer than in *P. pipistrellus*, but in length similar to Arabian *P. kuhlii* (Fig. 3A and Table 2). On the other hand, the rostrum is broad in the Dhofar bats, relatively much broader than in two other Arabian *Pipistrellus* species, in *H. arabicus* and in *N. guineensis*, but similarly broad as in *H. savii* and partially also as in *H. ariel* (Table 2). The braincase of the Dhofar bats is very high and rather broad (Fig. 3B), on average relatively highest among the Arabian pipistrelles (Table 2); it is similarly broad as in north-Arabian *P. pipistrellus*. The tympanic bulla of the Dhofar bats is relatively small, on average the smallest among the Arabian pipistrelles (Table 2). The combination of these few skull characters shows the Dhofar bats as a unique skull morphotype among the Arabian pipistrelle bats (Table 2 and Figs. 3–4). On the other hand, the robust nature of the skull in the Dhofar bats is similar to that in some Oriental representatives of the genus *Pipistrellus*, e.g., *P. ceylonicus* (Kelaart, 1852), *P. coromandra* (Gray, 1838), and/or *P. tenuis* (Temminck, 1840) — see Bates and Harrison (1997) and Benda and Gaisler (2015).

The dentition of the Dhofar bats is of the *Pipistrellus* formula, two upper premolars were present in all examined specimens. Both upper incisors are markedly bicuspid, the second incisor (I^3) is rather high, the I^3 crown reaches some 70–80% of the first incisor (I^2) height; the second cusp is in both incisors lower than the first (mesial) one, reaching some 60–80% of the mesial cusp (Fig. 5). The small upper premolar (P^2) is positioned palatally from the tooth-row, from side almost invisible, hidden by the canine and the large upper premolar (P^4), these two teeth are not in a direct mesio-distal contact, but very close to it (Fig. 5). This combination of characters distinguishes the Dhofar bats from all other Arabian pipistrelle bats. The small upper premolar is absent in *N. guineensis* and also in the majority of the examined specimens of the *Hypsugo* species. In

FIG. 2. Pelage colouration examples of *Pipistrellus dhofarensis* sp. n., above the dorsal aspect, below the ventral aspect. Ain Tabruq, Dhofar, Oman; males, holotype and paratypes (from right to left): NMP 92740, 92741 (holotype), 92747, 92748. Photos by A. Reiter

all Arabian pipistrelle bats other than the Dhofar bats, the second upper incisor (I^3) is unicuspid, and so is the first one (I^2) in *P. kuhlii*, in the latter species and in *V. rueppellii*, the I^3 crown is very small, reaching some 1/3 of the I^2 crown height (or even less). For further comparison see also Harrison and Bates (1991: 88–93) and/or Benda *et al*. (2006: 186; 2008: 39; 2015: 427).

The baculum of the Dhofar bats is a typical baculum of the genus *Pipistrellus* s.str. (see Hill and Harrison, 1987), it is a narrow and long bone, round on section, sligthly curved dorsally in its distal third in some individuals and with short bifurcations at both epiphyses (Fig. 6). Its total length is 3.55–3.95 mm (M 3.77 mm; $n = 7$), depth of the proximal bifurcation 0.58–0.76 mm, and depth of the distal bifurcation 0.34–0.47 mm. Generally, this shape is similar to bacula of *P. pipistrellus* and *P. kuhlii*, but these bones are much smaller (reaching only ca. 1/2 of the Dhofar bat baculum length), and *V. rueppellii*, but this bone is much larger (ca. twice longer than the Dhofar bat baculum), and all of them are more

markedly curved (Fig. 6 — see also Hill and Harrison, 1987: 285, 288, 293; Benda *et al*., 2006: 193). Bacula of other genera (*Hypsugo*, *Neoromicia*) show completely different shapes and sizes (Fig. 6; Hill and Harrison, 1987; Benda *et al*., 2006, 2011*a*, 2012). On the other hand, bacula of the Dhofar bats are similar in size and shape to those of several Indian *Pipistrellus* species, *P. ceylonicus*, *P. tenuis*, and *P. coromandra* — see Hill and Harrison (1987) and Bates and Harrison (1997).

The molecular genetic analysis of 32 individuals of the Dhofar bats (i.e., almost half of the number of available specimens) showed eight different haplotypes (Appendix II), differing in one to seven substitutions (distance range 0.14–0.97%). While half of the number of haplotypes were found only in one individual and two haplotypes (Dhofar 2 and Dhofar 6) in two individuals each, two remaining haplotypes were much more common, the haplotype Dhofar 1 was documented from 17 bats and the haplotype Dhofar 8 from seven bats (Fig. 7). Both latter haplotypes were found to be widespread across the whole Dhofar region, between Hawf in Yemen and Wadi Hannah in the eastern part of the Omani Dhofar, inclusive.

The comparison of a partial sequence of the mitochondrial cyt *b* gene (641 bp) with sequences from a selection of pipistrelle bats of various genera from the Palaearctic, Afro-tropic and the Oriental regions (i.e. from all three biogeographic regions surrounding the Dhofar area), grouped the Dhofar bats as a well supported separate lineage within a group of Oriental species of the genus *Pipistrellus* (Fig. 8). The Dhofar bat lineage belongs to a well supported cluster of three lineages, comprising also *P. abramus* and *P. javanicus*; on the other hand, the Dhofar bats are distant from these taxa rather deeply, by 13.7–16.1% and 13.6–14.0%, respectively, of the uncorrected genetic distance (Table 3). All other known Arabian taxa of pipistrelle bats were shown to cluster within different and far distant clades representing different genera or species groups of vespertilionine bats (Fig. 8) and the topology of branches generally conforms to the known phylogenetic patterns in this group (see e.g., Roehrs *et al*., 2010).

Basic characteristics of echolocation calls of the Dhofar bats from particular sites of the Omani part of Dhofar are presented in Table 4. A comparison of statistical values of these calls with the echolocation characteristics of three other pipistrelle bats from southern Arabia (Oman) are given in Table 5.

TABLE 2. Skull shape indices of the examined sample sets of pipistrelle bats from Arabia. See Abbreviations in the Materials and Methods for abbreviations of measurements taken

Index	*n*	M	min	max	SD	*n*	M	min	max	SD	*n*	M	min	max	SD
		Pipistrellus Dhofar					*Pipistrellus kuhlii* S Arabia					*Pipistrellus kuhlii* N Arabia			
CM^3/LCr	49	**0.371**	0.360	0.385	0.006	24	**0.372**	0.358	0.382	0.007	96	**0.374**	0.361	0.392	0.006
LaInf/LCr	49	**0.319**	0.305	0.343	0.008	24	**0.301**	0.271	0.322	0.013	94	**0.297**	0.277	0.320	0.032
CC/CM^3	47	**0.899**	0.852	0.943	0.018	24	**0.856**	0.808	0.895	0.019	96	**0.852**	0.813	0.897	0.021
LaN/LCr	49	**0.514**	0.495	0.536	0.008	24	**0.501**	0.469	0.523	0.014	97	**0.498**	0.470	0.521	0.010
ANc/LaN	49	**0.737**	0.710	0.776	0.015	24	**0.707**	0.666	0.737	0.018	97	**0.714**	0.664	0.759	0.021
LBT/LCr	49	**0.222**	0.203	0.242	0.009	23	**0.229**	0.211	0.247	0.012	94	**0.228**	0.213	0.247	0.008
		Pipistrellus pipistrellus					*Hypsugo savii*					*Hypsugo arabicus*			
CM^3/LCr	59	**0.355**	0.346	0.367	0.005	41	**0.343**	0.333	0.352	0.004	21	**0.342**	0.325	0.352	0.007
LaInf/LCr	59	**0.296**	0.277	0.317	0.008	40	**0.330**	0.309	0.349	0.010	22	**0.285**	0.270	0.301	0.007
CC/CM^3	56	**0.843**	0.801	0.881	0.019	41	**0.929**	0.855	0.972	0.026	21	**0.838**	0.770	0.895	0.029
LaN/LCr	59	**0.515**	0.490	0.543	0.012	41	**0.498**	0.474	0.515	0.009	22	**0.501**	0.481	0.522	0.010
ANc/LaN	59	**0.706**	0.662	1.087	0.053	41	**0.682**	0.626	1.004	0.056	22	**0.696**	0.667	0.728	0.016
LBT/LCr	59	**0.241**	0.222	0.270	0.010	40	**0.232**	0.215	0.247	0.009	22	**0.234**	0.217	0.257	0.011
		Hypsugo ariel S Arabia					*Hypsugo ariel* N Arabia					*Neoromicia guineensis*			
CM^3/LCr	15	**0.346**	0.334	0.365	0.008	10	**0.340**	0.326	0.350	0.008	4	**0.351**	0.346	0.357	0.005
LaInf/LCr	16	**0.317**	0.298	0.331	0.011	10	**0.305**	0.284	0.330	0.017	4	**0.292**	0.283	0.300	0.007
CC/CM^3	15	**0.864**	0.833	0.916	0.024	10	**0.868**	0.823	0.912	0.023	4	**0.847**	0.819	0.886	0.028
LaN/LCr	16	**0.479**	0.461	0.509	0.012	10	**0.487**	0.470	0.510	0.015	4	**0.509**	0.505	0.512	0.004
ANc/LaN	16	**0.722**	0.689	0.766	0.021	10	**0.700**	0.667	0.754	0.027	4	**0.686**	0.653	0.714	0.026
LBT/LCr	15	**0.235**	0.213	0.248	0.011	10	**0.228**	0.198	0.251	0.016	4	**0.234**	0.226	0.243	0.007

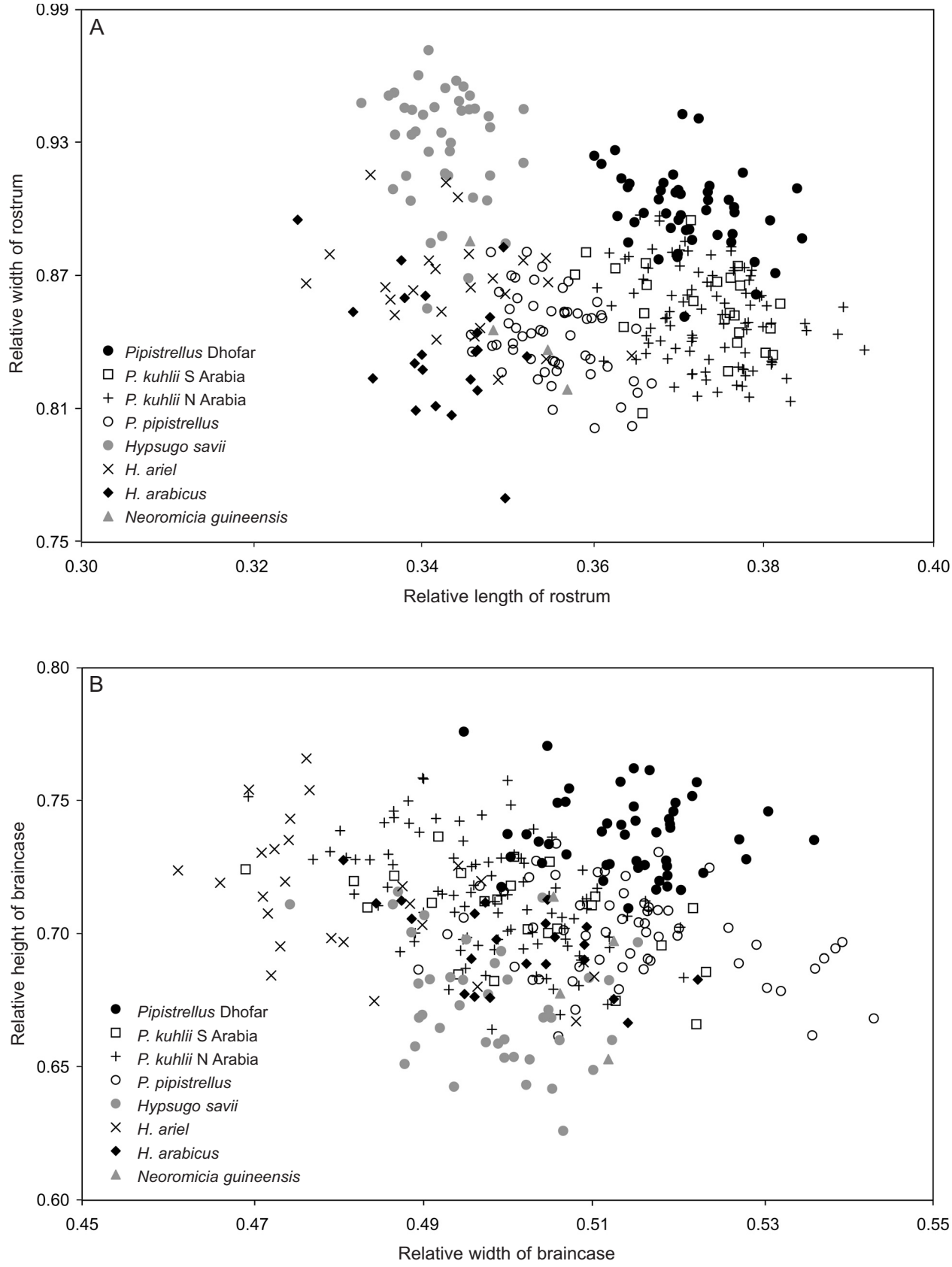

FIG. 3. Bivariate plot of skull dimensions of Arabian pipistrelle bats: A — relative length of rostrum (CM^3/greatest length of skull) against relative width of rostrum (rostrum width across upper canines/CM^3) and B — relative width of braincase (braincase width/greatest length of skull) against relative height of braincase (braincase height/braincase width)

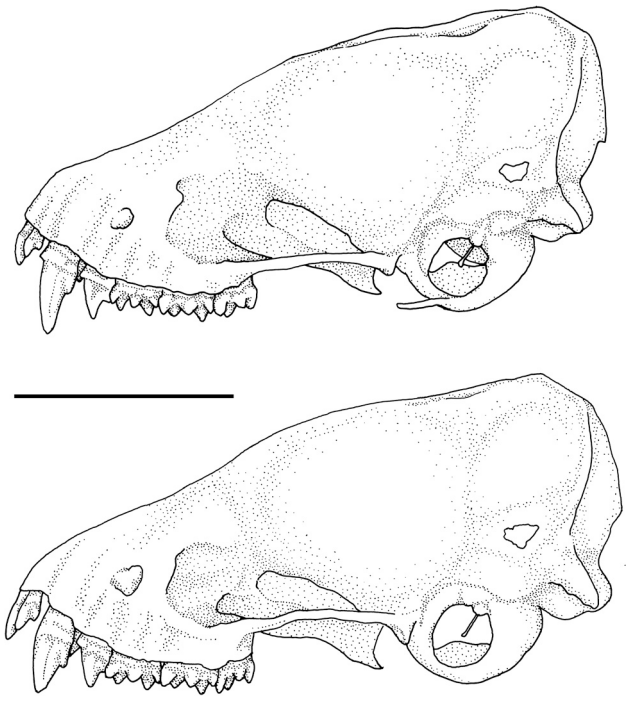

FIG. 4. Lateral views of the holotype and paratype skulls of *P. dhofarensis* sp. n. from Ain Tabruq, Oman; above — NMP 92741 (holotype); below — NMP 92740 (paratype). Scale bar 5 mm

DISCUSSION

The above summarised results of morphologic and molecular genetic comparisons showed the Dhofar pipistrelle bats to represent a distinct morphotype and lineage, which differs from all other Arabian pipistrelles. On the other hand, the morphologic analysis of cranial and bacular characters as well as the genetic analysis showed these bats to be phylogenetically positioned closely to the Oriental representatives of the genus *Pipistrellus*. Although similar and related to the Oriental pipistrelles, the Dhofar bats apparently represent a separate species and this separation is clear both from the genetic distinctness (at least from the three available species examined) and from morphological characters (comp. Bates and Harrison, 1997). The morphologically closest species seem to be *P. javanicus* and *P. ceylonicus*, from which the Dhofar bats differ markedly in body and skull size (*P. javanicus* is smaller, with the forearm length up to 30 mm, while *P. ceylonicus* is larger, with forearm length up to 42 mm) and particularly in the dental traits, namely in the shape of upper incisors; in *P. javanicus* the first upper incisor (I^2) is more compressed with its distal cusp being often only indistinctly separated (so, frequently I^2 appears as unicuspid in this bat), while in *P. ceylonicus* the secondary cusp on the second upper incisor (I^3) is relativelly low and medially orientated, but present. From *P. javanicus* the Dhofar bats markedly differ also in the form and size of baculum.

The Dhofar bats represent the westernmost offshoot of the Oriental vespertilionid bat fauna, isolated by more than 1,500 km across the Indian Ocean and/or the deserts of the Middle East from the area of continuous distribution of this fauna in the Indian Subcontinent (see Corbet and Hill, 1992; Bates and Harrison, 1997). The Dhofar bats, the only (phylogenetically) Oriental vespertilionid bat of the Afrotropics, seem to comprise a similar biogeographical element as the flying foxes of the genus *Pteropus* Brisson, 1762, similarly common bats in the Oriental region as the pipistrelles. These megabats reach the Afro-tropical region only in its easternmost margins (Seychelles, Comoros, Zanzibar

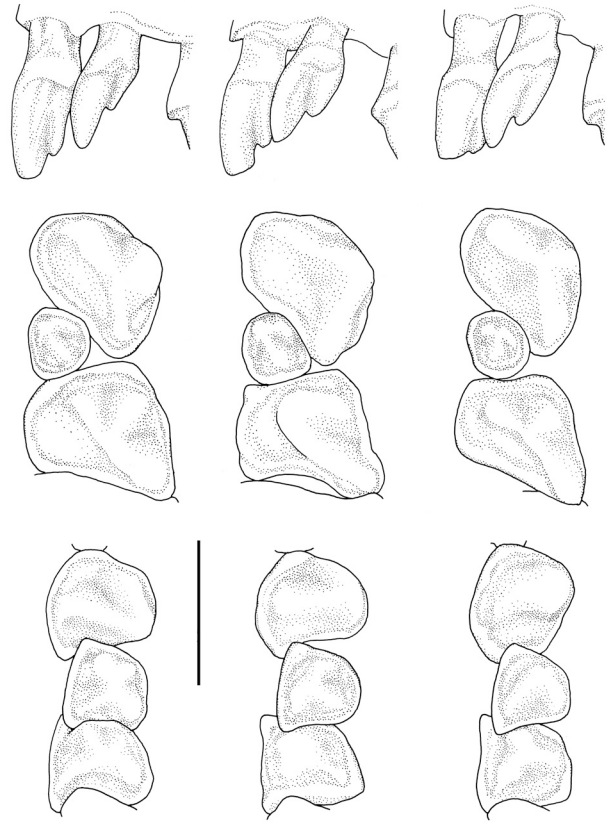

FIG. 5. Views of the tooth-rows of *P. dhofarensis* sp. n.; top row — antero-lateral views on left upper incisors; middle row — occlusal views of the upper unicuspid teeth, below row — occlusal views of the lower unicuspid teeth; left column — NMP 92741 (holotype), Ain Tabruq, Oman; middle column — NMP 92740 (paratype), Ain Tabruq, Oman; right column — NMP 94014, Difa, Oman. Scale bar 1 mm

Archipelago, Madagascar, Mascarenes) and do not occur in the African continent per se (Bergmans, 1990; Almeida *et al*., 2014). However, whether this biogeographical similarity of the Oriental mega- and microbats in the Afro-tropics follows also similar histories, remains a task for more profound analyses. At least two scenarios of the origin of the Dhofar pipistrelle populations could be taken in consideration; the populations descend from an isolate that resulted from the strong aridisation of the Middle East at the Miocene-Pliocene transition, or the populations originate from stray individuals that were brought to Dhofar by monsoons from the Indian subcontinent. Anyway, considering the relatively rich genetic variation within the Dhofar bat populations, their colonisation of Dhofar certainly does not seem to represent a recent event.

The Dhofar bat represents the fourth bat species endemic to southern Arabia, along with *Rhinopoma hadramauticum* Benda, 2009, *Triaenops parvus* Benda and Vallo, 2009 and *Asellia arabica* Benda, Vallo and Reiter, 2011 (see Benda and Vallo, 2009; Benda *et al*., 2009, 2011*b*). However, only the Dhofar pipistrelle bat is restricted by its distribution range to the relatively humid savannah part of

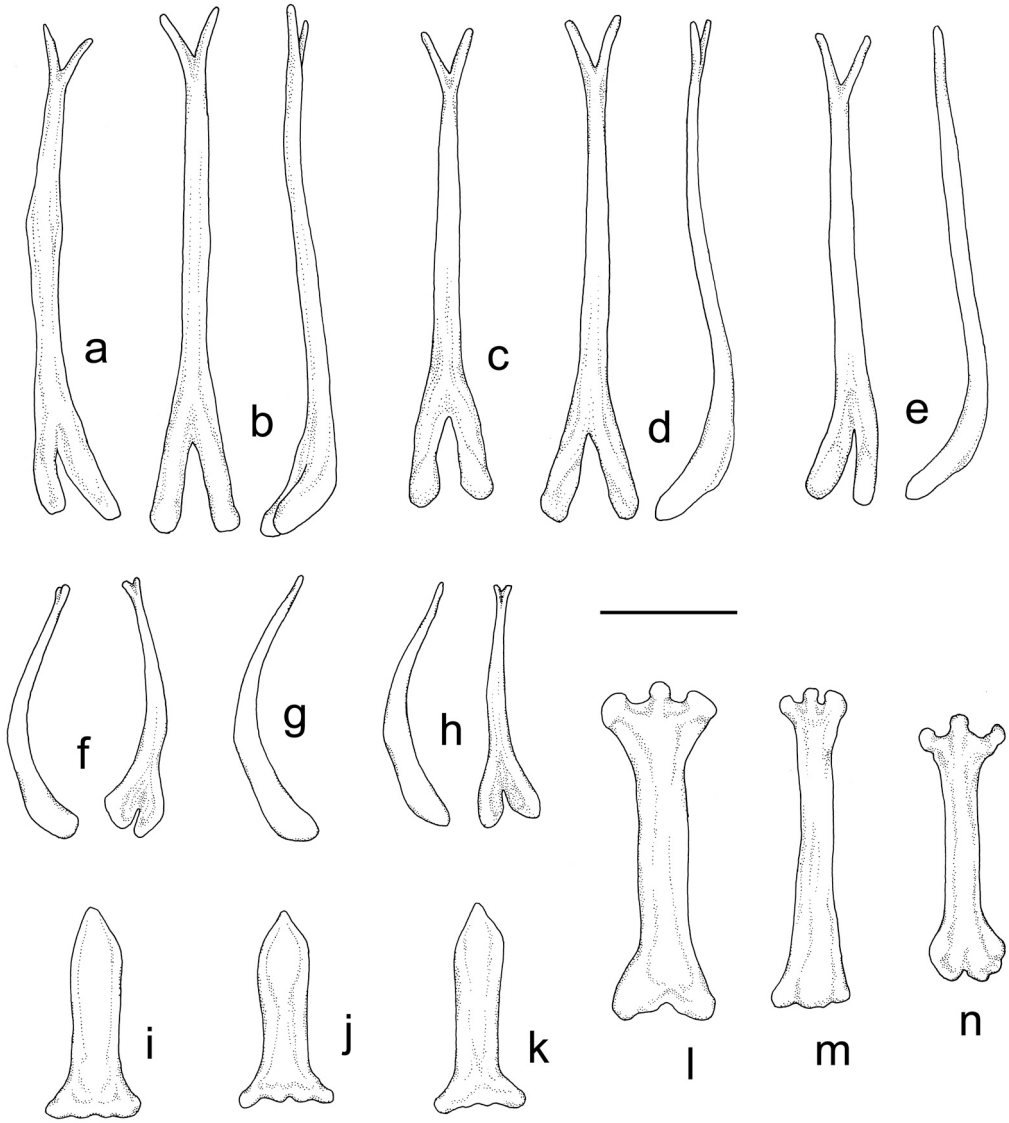

FIG. 6. Bacula of pipistrelle bats from southern Arabia: a–e — *P. dhofarensis* sp. n., f–h — *P. kuhlii*, i–k — *H. ariel*, l–n — *H. arabicus*; a — NMP 95634, Hawf, Yemen; b — NMP 95646, Hawf, Yemen; c — NMP 95633, Hawf, Yemen; d — NMP 92707, Hagarir, Oman; e — NMP 94010, Difa, Oman; f — NMP pb3639, Assala, Yemen; g — NMP 92618, Nakhl, Oman; h — NMP 93816, Shinas, Oman; i — NMP pb3029, Hawf, Yemen; j — NMP pb3052, Damqawt, Yemen; k — NMP 94075, Rima, Wadi Gharah, Oman; l — NMP 93740, Al Aqor, Wadi Tiwi, Oman; m — NMP 92783, Mansaft, Oman; n — NMP 48415, Pir Sohrab, Iran. Scale bar 1 mm

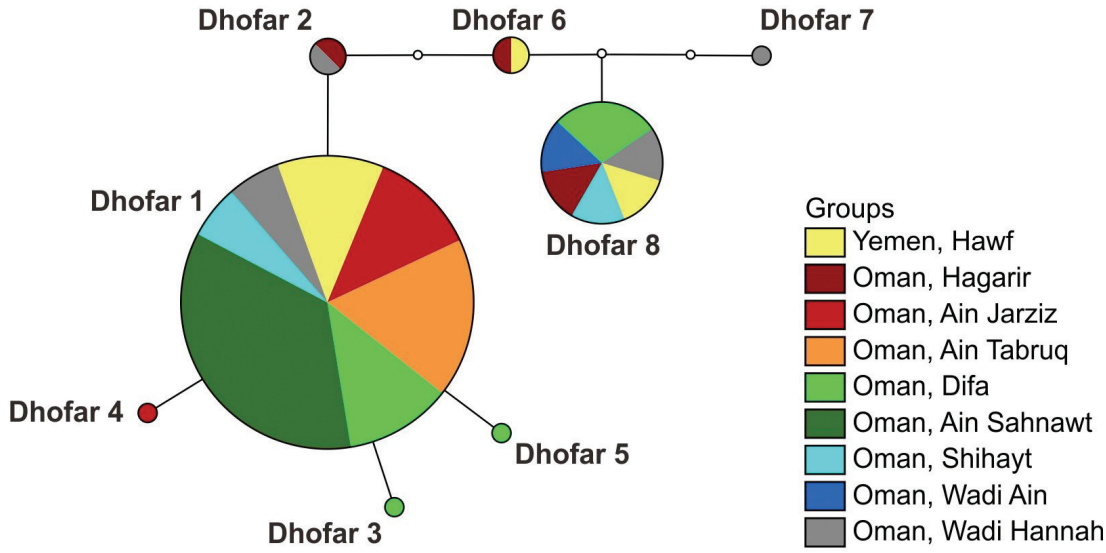

FIG. 7. Median-joining haplotype network of *P. dhofarensis* sp. n. based on 721 bp of the cytochrome *b* gene. Circle sizes are proportional to the number of individuals with the particular haplotype. Mutation steps are shown as small empty circles

Dhofar, while other two species live also in more arid regions at the coast of the Hadramaut province of Yemen and *R. hadramauticum* is known from a single locality just in coastal Hadramaut. These four species, members of four different families, represent 28.6% of the local bat fauna. Such a large percentage of endemism is not known in other mammalian groups of the broader Dhofar region and, at the same time, this is the only zone of a significant bat endemism in the whole Middle East. Although the Dhofar biota represents the easternmost ofshoot of the Afro-tropic region, the Dhofar bat endemics show relations to the faunas living east and north of Dhofar, and the Dhofar pipistrelle bat is the most extreme example of this.

TAXONOMIC DESCRIPTION

Pipistrellus dhofarensis sp. n.

Type material

Holotype: Adult male (NMP 92741, alcoholic specimen with extracted skull), Ain Tabruq, 28 October 2009, leg. P. Benda, A. Reiter and M. Uhrin.

Paratypes: 6 ♂♂, 6 ♀♀ (NMP 92740, 92742, 92743, 92747–92750 [S+A], 92744–92746, 92751, 92752 [A]), site, date and collectors as in the holotype.

Type locality

Sultanate of Oman, Dhofar Province, Ain Tabruq spring; 17°06'N, 54°20'E, 115 m a.s.l.

Description

Pipistrellus dhofarensis sp. n. is a small bat and a medium-sized to large representative of the genus *Pipistrellus* (Fig. 9), on average the largest form of the genus occurring in Arabia (Table 2): forearm length 33–39 mm, greatest length of skull 12.8–14.0 mm, length of the upper tooth-row 4.6–5.3 mm. The ears are short and massive (leathery), of a nearly triangular shape, with obtuse angles, 13.0–15.3 mm long, and the tragus is short and broad, curved anteriorly, 4.8–6.6 mm long (Fig. 9). For external and most of the cranial dimensions of *P. dhofarensis* sp. n. see Table 1, the additional dimensions of unicuspid and molar tooth-rows, respectively, are as follows (n = 49): M^1M^3 3.16–3.55 mm (M 3.41 mm), CP^4 1.97–2.38 mm (M 2.22 mm), M_1M_3 3.24–3.92 mm (M 3.69 mm), CP_4 1.81–2.00 mm (M 1.92 mm). The dorsal pelage colouration of *P. dhofarensis* sp. n. has two basic colour morphs (Fig. 2), greyish-brown with a slight silverish tinge and reddish-brown; the ventral pelage is markedly paler than the dorsal one (Fig. 2). The hairs are bicoloured, larger proximal parts are dark brown, distal parts are paler, possessing one of the two colour tinges (see Figs. 2 and 9). The wing membranes, ears and face are dark greyish-brown, the membrane parts along bones are slightly paler (Fig. 2). The proximal part of the uropatagial membrane (ca. 10 mm along the body) is in some individuals covered by sparse hairs, in some individuals bald. The size of epiblema is variable, in some individuals is about 2 mm wide, rounded, with a well visible keel,

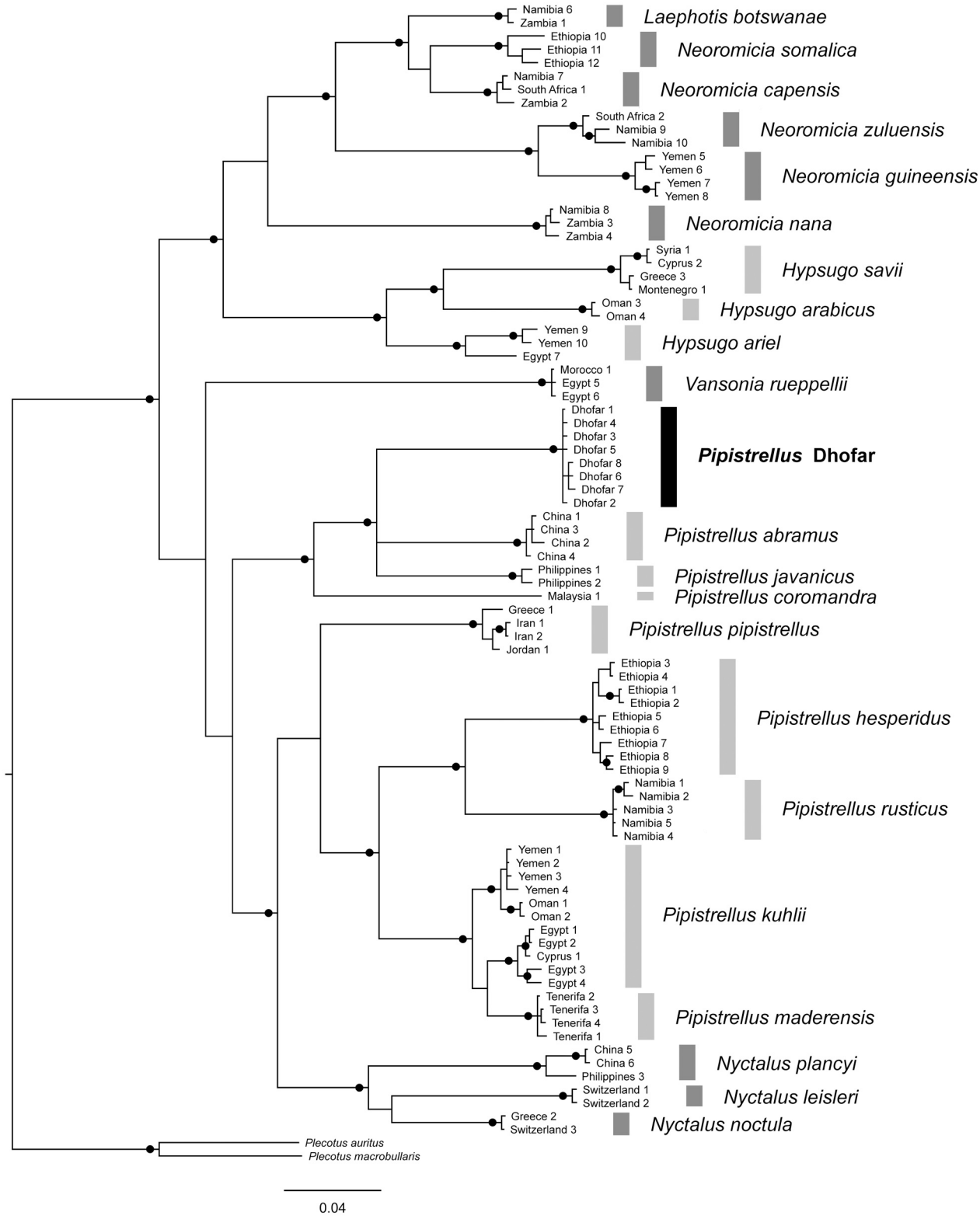

FIG. 8. Bayesian consensus tree representing the phylogenetic relationships among haplotypes of Arabian pipistrelle bats and haplotypes from a selection of Old World pipistrelles based on sequences (641 bp) of the mitochondrial cytochrome *b* gene. A dot associated with a node indicates a support by more than 95% posterior probability (BI reconstructions) and 70% bootstrap (ML reconstructions)

TABLE 3. Percent pairwise uncorrected genetic distances among haplotypes of the compared pipistrelle bats (641 bp of the cytochrome *b* gene); above diagonal — mean, below diagonal — range

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	*Pipistrellus* Dhofar	–	14.55	13.85	16.46	18.17	20.04	18.50	17.10	17.39	18.85	18.06	21.03
2	*P. abramus*	13.7–16.1	–	14.12	16.46	17.42	18.97	17.95	17.37	17.90	16.45	16.43	18.72
3	*P. javanicus*	13.6–14.0	13.4–15.3	–	16.69	18.32	18.43	19.78	16.08	16.77	16.23	16.55	19.32
4	*P. coromandra*	16.1–16.9	16.1–16.9	16.5–16.8	–	18.04	18.53	18.97	19.37	19.54	17.49	17.02	19.66
5	*P. pipistrellus*	17.1–18.6	16.7–18.7	17.6–18.9	17.9–18.1	–	15.66	16.57	14.00	13.99	15.76	16.53	16.71
6	*P. hesperidus*	19.5–20.3	18.4–19.5	17.6–19.2	18.1–18.7	15.2–16.2	–	13.03	14.70	14.68	16.58	17.86	18.07
7	*P. rusticus*	18.1–18.9	17.8–18.6	19.3–20.3	18.6–19.5	16.0–17.5	12.3–13.7	–	14.84	14.69	17.10	15.90	18.82
8	*P. kuhlii*	16.4–17.9	16.1–18.9	15.3–16.8	18.7–20.3	13.4–14.9	13.9–15.4	14.4–15.4	–	5.62	16.76	16.44	18.39
9	*P. maderensis*	17.0–17.6	17.3–18.9	16.5–17.0	19.3–19.7	13.7–14.2	14.0–15.3	14.4–15.0	4.8–6.4	–	17.21	17.14	17.56
10	*Nyctalus noctula*	18.6–19.0	16.2–16.9	16.1–16.4	17.5	15.4–16.2	16.1–16.9	16.9–17.3	16.2–17.7	17.0–17.5	–	13.18	14.96
11	*N. leisleri*	17.1–18.7	15.6–17.6	16.1–17.0	16.7–17.3	15.9–17.1	17.4–18.4	15.5–16.4	15.5–17.2	16.9–17.3	12.8–13.6	–	16.23
12	*N. plancyi*	20.8–21.4	18.1–19.0	19.0–19.5	19.5–19.8	16.5–17.0	17.6–18.6	18.3–19.5	17.6–19.0	17.3–17.9	14.7–15.1	15.6–17.2	–
13	*Vansonia rueppellii*	19.7–20.3	18.7–20.1	18.9–19.5	19.0–19.2	17.9–19.0	18.9–19.7	18.7–19.7	17.6–18.3	17.2–17.5	17.3–17.8	17.4–18.4	22.0–22.2
14	*Neoromicia nana*	18.6–20.1	18.1–19.6	18.1–18.4	20.0–20.6	16.7–17.9	19.0–20.1	18.1–19.0	16.2–18.4	17.6–18.6	19.2–19.5	18.9–19.5	21.1–21.8
15	*N. somalica*	17.8–18.8	17.0–19.0	17.0–18.4	16.8–18.0	16.5–18.1	19.0–20.4	18.6–20.3	17.5–19.5	18.4–19.1	17.3–18.6	18.6–19.8	20.4–22.2
16	*N. capensis*	18.1–18.4	16.7–18.6	15.4–16.2	16.2–16.5	15.3–16.5	17.9–19.8	19.2–20.1	15.9–17.8	17.6–18.6	16.6–17.8	17.8–18.1	19.5–20.1
17	*N. zuluensis*	17.9–19.0	17.2–18.7	17.9–19.5	20.0–20.4	18.3–19.1	17.8–19.7	19.5–20.9	17.3–19.7	17.6–18.9	18.6–19.0	19.7–20.3	18.4–20.3
18	*N. guineensis*	19.0–19.7	18.3–19.3	17.9–19.5	20.3–20.4	18.4–19.0	18.6–20.3	19.3–20.6	16.8–18.7	16.5–17.8	19.2–20.0	19.2–20.9	20.0–20.7
19	*Laephotis botswanae*	18.1–18.7	18.6–19.3	17.8–18.3	18.6–18.9	16.2–17.2	18.4–19.2	19.7–20.7	18.3–19.8	19.3–19.5	18.1–18.3	19.1–19.7	19.7–20.3
20	*Hypsugo savii*	18.7–19.7	16.4–17.9	17.9–19.0	18.9–19.5	18.3–19.3	18.1–19.5	19.2–20.0	18.7–20.4	18.7–20.0	19.5–20.0	21.1–22.3	20.1–20.6
21	*H. ariel*	18.6–20.1	17.6–18.6	16.8–19.3	19.2–19.5	16.8–19.2	20.1–21.5	19.8–21.4	17.3–19.3	17.3–18.6	18.3–19.2	18.1–20.3	18.6–20.0
22	*H. arabicus*	18.4–18.9	20.9–21.4	17.9–18.4	20.7	18.4–19.1	19.8–21.1	20.1–21.7	17.8–19.3	18.1–18.7	18.6–18.9	19.1–19.7	21.2–22.3
23	*Plecotus* sp.	20.6–21.2	19.3–20.9	18.7–20.4	19.0–20.6	20.6–21.8	16.5–19.8	18.9–20.1	18.4–20.0	17.8–19.0	20.7–21.5	18.8–20.0	20.9–22.5

TABLE 3. Extended

No.	Species	13	14	15	16	17	18	19	20	21	22	23
1	*Pipistrellus* Dhofar	19.98	19.36	18.35	18.32	18.60	19.31	18.51	19.17	19.39	18.64	20.89
2	*P. abramus*	19.25	18.76	17.95	17.45	17.97	18.68	18.84	17.43	18.06	21.10	20.05
3	*P. javanicus*	19.21	18.25	17.72	15.81	18.80	18.76	18.02	18.56	18.41	18.17	19.73
4	*P. coromandra*	19.14	20.23	17.27	16.38	20.18	20.32	18.72	19.19	18.98	20.75	19.81
5	*P. pipistrellus*	18.37	17.13	17.40	15.83	18.55	18.66	16.71	18.77	18.08	18.87	21.14
6	*P. hesperidus*	19.34	19.57	19.89	18.60	18.83	19.33	18.77	18.74	20.88	20.32	18.03
7	*P. rusticus*	19.08	18.47	19.28	19.57	20.05	19.92	20.03	19.58	20.72	20.69	19.52
8	*P. kuhlii*	17.89	17.42	18.50	16.85	18.68	17.70	19.06	19.71	18.41	18.54	19.24
9	*P. maderensis*	17.30	18.12	18.72	18.15	18.37	17.16	19.46	19.34	17.97	18.41	18.41
10	*Nyctalus noctula*	17.54	19.36	17.86	17.07	18.84	19.71	18.19	19.75	18.79	18.74	21.08
11	*N. leisleri*	17.85	19.21	19.12	17.93	19.97	20.12	19.37	21.72	19.34	19.37	19.37
12	*N. plancyi*	22.05	21.44	21.07	19.86	19.50	20.33	20.05	20.41	19.41	21.63	21.58
13	*Vansonia rueppellii*	–	18.41	18.42	17.89	20.12	19.72	18.85	19.11	20.49	20.02	20.28
14	*Neoromicia nana*	18.3–18.6	–	16.01	16.28	17.78	19.51	16.51	18.28	18.93	18.51	19.92
15	*N. somalica*	18.3–18.7	15.5–16.4	–	9.00	15.56	16.48	10.15	19.33	17.29	17.09	20.21
16	*N. capensis*	17.5–18.1	15.8–16.8	8.6–9.2	–	15.57	16.64	9.15	18.98	16.76	17.86	18.95
17	*N. zuluensis*	19.8–20.4	16.8–18.6	15.1–16.1	15.0–16.1	–	8.79	16.22	18.72	18.58	18.95	21.42
18	*N. guineensis*	19.0–20.1	19.0–20.0	16.1–16.8	16.1–17.0	7.6–9.8	–	15.99	18.88	19.15	18.06	20.10
19	*Laephotis botswanae*	18.7–19.0	16.2–16.8	10.0–10.6	8.7–9.7	15.9–16.4	15.6–16.5	–	19.50	16.95	17.39	19.89
20	*Hypsugo savii*	18.7–19.5	17.8–18.7	18.6–20.0	18.6–19.3	18.3–19.5	18.1–19.7	18.9–20.0	–	14.14	14.20	19.15
21	*H. ariel*	19.3–21.2	18.6–19.3	16.5–18.0	15.9–17.6	18.1–19.0	18.7–19.5	16.5–17.3	13.6–14.5	–	13.60	19.27
22	*H. arabicus*	20.0–20.1	18.1–18.9	16.9–17.3	17.5–18.3	18.7–19.5	17.8–18.4	17.2–17.6	13.7–14.7	13.4–13.9	–	19.89
23	*Plecotus* sp.	20.1–20.4	19.5–20.3	19.8–20.6	18.4–20.0	20.9–21.8	19.3–21.7	19.5–20.3	18.9–19.5	18.3–20.1	19.8–20.0	–

TABLE 4. Mean values of particular components of echolocation calls of *P. dhofarensis* sp. n. from particular sites in Dhofar, Oman (data are presented separately for the foraging and the hand-released bats). Explanations: *n* calls = number of particular calls analysed; *n* seq = number of sequences recorded and analysed; PD = pulse duration [ms]; Fmax = frequency of maximum energy (peak frequency) [kHz]; SF = start frequency [kHz]; EF = end frequency [kHz]; IPI = inter-pulse interval [ms]

Site	Date	*n* calls	*n* seq	PD	Fmax	SF	EF	IPI
Foraging bats								
Mudhai	24 October 2009	23	5	5.80	46.13	49.25	44.98	107.59
Hagarir	25 October 2009	5	1	4.50	45.74	52.22	44.72	89.58
Ain Jarziz	27 October 2009	7	1	8.25	38.74	53.53	37.44	106.58
Ain Tabruq	28 October 2009	19	3	7.76	41.13	58.81	39.40	69.31
Difa	26 March 2012	3	1	3.50	45.63	49.17	44.30	107.25
Shihayt	28 March 2012	4	1	7.30	41.38	50.93	40.48	68.57
Total foraging bats		61	12	6.57	43.30	53.32	42.00	91.21
Hand-released bats								
Hagarir	25 October 2009	8	1	5.26	39.99	56.67	37.57	79.53
Ain Jarziz	27 October 2009	8	2	5.84	41.84	62.87	38.33	72.38
Total hand-released bats		16	3	5.37	41.25	59.53	37.99	73.60

in some individuals it is a narrow structure resembling a thickened margin of the calcareal spur only.

The skull of *P. dhofarensis* sp. n. is robust (Fig. 4), the dorsal skull profile is only slightly convex in the frontal region, its highest point is near to the lambda; a low sagittal crest is present in some specimens. The rostrum is high, long and broad, both relatively and absolutely, the braincase is broad and very high, the zygomatic arches are very narrow and fine. The horizontal length of tympanic bulla represents 20–24% of the greatest skull length. The dental formula is 2123/3123, both upper incisors are markedly bicuspid (Fig. 5), the second incisor (I^3) is rather high, the I^3 crown reaches some 70–80% of the first one (I^2) height; in both incisors, the second cusp is markedly lower than the first (mesial) one, reaching some 50–80% of the first cusp. The small upper premolar (P^2) is positioned palatally from the tooth-row, almost invisible in the lateral view, hidden by the canine and the large upper premolar (P^4), the latter two teeth are positioned very close to each other, but not in a direct mesio-distal contact. P^4 bears a moderately developed cusp on the mesio-palatal margin of the cingulum. The medio-distal length of P^2 (0.45–0.53 mm) represents 20.6–25.0% of the upper unicuspid tooth-row (CP^4). The lower incisors are tricuspid. Size of the crown area of the first lower premolar (P_2) is very variable, but it is mostly very close to that of the second lower premolar (P_4) — the medio-distal length of P_2 (0.45–0.69 mm) represents 24.4–37.6% (mean 32.8%) of the upper unicuspid tooth-row (CP_4). The molars are massive, typical of the genus *Pipistrellus*, in the upper molars, metalophs in M^1 and M^2 are heavilly developed, while paralophs are rather weak, metaconules are high, and paraconules are

TABLE 5. Comparison of echolocation parameters of pipistrelle bats from southern Arabia. For explanations see Table 4

Parameter	PD	Fmax	SF	EF	IPI
		Pipistrellus Dhofar (*n* seq = 15, *n* calls = 60–73)			
M	6.30	42.88	54.41	41.09	87.39
SD	1.71	3.09	6.40	3.25	37.23
min–max	2.94–9.54	37.80–48.60	46.80–76.70	36.10–46.20	26.50–247.80
		Pipistrellus kuhlii (*n* seq = 6, *n* calls = 13–28)			
M	5.27	40.02	47.22	38.68	140.20
SD	1.33	1.32	4.98	1.72	57.58
min–max	3.57–6.80	37.30–42.00	40.70–55.40	35.40–41.70	84.60–286.00
		Hypsugo ariel (*n* seq = 3, *n* calls = 14–17)			
M	4.54	44.62	55.77	43.41	78.61
SD	0.52	1.93	8.99	1.62	9.83
min–max	3.72–5.29	41.70–47.20	44.50–75.80	41.00–45.50	57.60–91.40
		Hypsugo arabicus (*n* seq = 2, *n* calls = 4–19)			
M	7.87	34.18	41.76	32.07	103.60
SD	1.07	1.49	4.21	1.55	5.31
min–max	6.60–8.80	31.90–36.50	36.10–48.50	30.00–34.40	96.70–108.60

FIG. 9. Left — portrait of *P. dhofarensis* sp. n. from Hagarir, Oman. Right — penis of *P. dhofarensis* sp. n. from Ain Jarziz, Dhofar, Oman (NMP 92726). Photos by A. Reiter

in all three molars only slightly developed; nyctalodoncy is in all three lower molars very distinctly evident.

The penis of *P. dhofarensis* sp. n. has the shape typical of the genus *Pipistrellus* (Fig. 9), the glans penis has a very distinct medial stripe on the dorsal side of praeputium and is covered by very pale hairs. The body of penis is almost naked, with a fine 'collar' of short hairs in the middle of its length. The skin of the whole penis is pale greyish-brown. The baculum of *P. dhofarensis* sp. n. is a narrow and long change to bone, round on section in its central part, with relatively short bifurcations at both epiphyses, straight or slightly curved dorsally in the distal third of its length (Fig. 6a–e). The baculum dimensions are as follows ($n = 7$): baculum length 3.55–3.95 mm (M 3.77 mm), maximum width of the proximal epiphysis 0.55–1.29 mm (M 0.81 mm), maximum width of the distal epiphysis 0.37–0.47 mm (M 0.43 mm), diaphysis width at proximal bifurcation 0.20–0.34 mm (M 0.25 mm), diaphysis width at distal bifurcation 0.11–0.16 mm (M 0.13 mm), depth of the proximal bifurcation 0.58–0.76 mm (M 0.65 mm), depth of the distal bifurcation 0.34–0.47 mm (0.38 mm).

Dimensions of the holotype (in mm): LC 54; LCd 36; LAt 35.3; Lau 13.8; LTr 5.7; LCr 13.54; LCb 12.83; LaZ 9.12; LaI 3.65; LaInf 4.33; LaN 6.92; LaM 7.71; ANc 5.11; LBT 2.91; CC 4.55; M^3M^3 6.15; CM^3 4.91; M^1M^3 3.42; CP^4 2.14; P^2 0.50; LMd 9.78; ACo 3.32; CM_3 5.34; M_1M_3 3.79; CP_4 1.90; P_2 0.66.

Echolocation

The search phase calls of foraging individuals of *P. dhofarensis* sp. n. show the following parameters (see Table 5 for complete statistics of the data): pulse duration 2.9–9.6 ms, frequency of maximum energy (peak frequency) 37.8–48.6 kHz (mean 42.88 kHz; $n = 73$), start frequency at 46.8–76.7 kHz, end frequency at 36.1–46.2 kHz.

Genetics

Pipistrellus dhofarensis sp. n. showed unique base positions in the 641 bp partial sequence of the mitochondrial gene for cytochrome *b* at 28 sites (4.4% of the sequence) within the group of the closely related Oriental pipistrelles examined (*P. dhofarensis* sp. n., *P. abramus*, *P. javanicus*, and *P. coromandra*): 426, 510, 525, 702, 738, 816, 873, 933 (A→G); 432, 483, 579, 729, 958, 981 (C/T→A); 478, 507, 756, 963, 993, 1057 (C→T); 480 (T→A); 501 (G→A); 543, 698, 759 (T→C); 666 (A/C→G); 741 (A/C→T); 792 (C→A). Moreover, eight sites were unique within all compared *Pipistrellus* species included in this study: 432, 579 (C/T→A); 478 (C→T); 480 (C/G/T→A); 666 (A/C/T→G); 698 (T→C); 702, 738 (A→G);

792, and 981 (C/T→A). Unique site position numbers correspond to positions of the complete cytochrome *b* gene (1140 bp).

Mitochondrial sequence of holotype and two examined paratypes (NMP 92741, 92748, 92751) — partial sequence (721 bp) of the cytochrome *b* gene (GenBank Accession Number KX375141; haplotype Dhofar 1, see Appendix II), 5' end: ttt ctg agg ggc cac agt aat tac caa tct cct ctc cgc cat ccc tta tat tgg aac aga ctt agt aga atg aat ctg agg tgg att ttc tgt gga caa agc cac ttt gac tcg att ctt tgc ctt cca ctt cct ctt acc att tat cat ttc agc cct agt aat ggt cca ttt act att cct aca cga aac agg atc taa caa ccc aac agg cat ccc ctc tgs cat aga tat aat ccc ctt cca tcc gta cta tac aat caa aga tat cct agg act ttc tgt gat aat ctt agc cct att atc cct agt act att ctc gcc tga cat att agg aga tcc cga taa tta tac acc agc aaa ccc act caa tac acc ccc tca tat taa acc tga atg gta ttt cct att tgc ata tgc aat cct acg atc aat tcc caa taa act agg agg agt gct agc cct agt cct ctc aat tct cat cct cat cat tat ccc cct cct cca cac ttc caa gca acg aag cat gac ttt tcg acc cat tag tca atg cct att ctg act att aac agc aga tct ttt aac cct gac atg aat cgg agg aca acc agt cga aca tcc cta cgt aat tat cgg aca att agc ctc tat cct ata ctt tat aat tat cat tgt aat aat acc act agc cag tct tat aga aaa cca cct att aaa atg a.

Distribution

Pipistrellus dhofarensis sp. n. occurs in a very limited territory, in a belt of relatively humid savannah habitats of coastal Arabia between easternmost Yemen and south-western Oman, less than 200 km long and only few km wide. This distribution range represents one of the smallest ranges among continentally distributed bats. The westernmost and most elevated known locality is Hawf, Yemen (16°39'N, 53°03'E, 735 m a.s.l.), the easternmost and lowest site is Wadi Ain, 13 km east of Mirbat, Oman (17°01'N, 54°47'E, 59 m a.s.l.).

Etymology

The name *dhofarensis* refers to Dhofar, a small and fertile region on the Omani-Yemeni transition in the central part of the south-Arabian coastal zone, famous for its frankincense production. The proposed English vernacular name of *Pipistrellus dhofarensis* sp. n. is Dhofar pipistrelle.

Differential diagnosis

For a detailed comparison and the differential diagnosis of *P. dhofarensis* sp. n. see Comparisons and Tables 1 and 2 as well as Discussion. For a brief review of comparison of particular morphological characters of *P. dhofarensis* sp. n. see Table 6.

TABLE 6. State of morphological characters in the pipistrelle bats of Arabia, north-eastern Africa and India as compared to that in *P. dhofarensis* sp. n. [R] — relative value of the character

Species	Body size	Pelage colouration	Rostrum shape [R]	Braincase shape [R]	I^2	I^3	P^3 [R]	Baculum	
								shape	size
Pipistrellus pipistrellus	much smaller	similar	narrower & shorter	lower	bicuspid	unicuspid	smaller	similar	much smaller
P. kuhlii N Arabia	similar	paler	narrower	narrower	unicuspid	unicuspid, smaller	smaller	similar	smaller
P. kuhlii S Arabia	smaller	paler	narrower	narrower	unicuspid	unicuspid, smaller	smaller	similar	smaller
P. hesperidus	smaller	similar	similar to narrower	lower	unicuspid	unicuspid, smaller	smaller	similar	smaller
P. rusticus	much smaller	similar	shorter	similar	unicuspid	unicuspid, smaller	smaller	similar	much smaller
P. abramus	smaller	similar	similar	similar	bicuspid	bicuspid	similar	similar	much larger
P. javanicus	smaller	similar	similar	similar	uni- to bicuspid	bicuspid	similar	similar	much larger
P. coromandra	much smaller	similar	narrower & shorter	lower	uni- to bicuspid	bicuspid bicuspid,	smaller	similar	smaller
P. ceylonicus	larger	similar	similar	similar	bicuspid	second cusp smaller	similar	similar	similar
P. tenuis	much smaller	similar	shorter	lower	bicuspid	smaller unicuspid,	smaller	similar	smaller
Vansonia rueppellii	smaller	paler	shorter	similar	bicuspid	much smaller	similar mostly	similar	much larger
Hypsugo savii	similar	paler	shorter	lower	bicuspid	uni- to bicuspid	absent	different	smaller
H. ariel	much smaller	paler	narrower & shorter	narrower	uni- to bicuspid	unicuspid	smaller	different	much smaller
H. arabicus	much smaller	paler	narrower & shorter	lower	bicuspid	unicuspid	smaller mostly	different	much smaller
Neoromicia capensis	smaller	similar	narrower & shorter	lower & narrower	uni- to bicuspid	unicuspid, smaller	unicuspid, absent mostly	different	smaller
N. somalica	much smaller	similar	shorter	lower & broader	uni- to bicuspid	much smaller	absent	different	smaller
N. guineensis	much smaller	similar	narrower & shorter	lower	bicuspid	unicuspid, smaller	absent	different	much smaller
N. nana	much smaller	similar	shorter	lower	bicuspid	similar	similar	different	much smaller

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Appendix I

List of the specimens examined in morphological analysis

Pipistrellus dhofarensis sp. n. — **Oman**: 5 ♂♂, 3 ♀♀ (NMP 92725–92728, 92730, 92731 [S+A], 92729, 92732 [A]), Ain Jarziz (Dhofar Prov.), 27 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 3 ♂♂, 3 ♀♀ (NMP 94032–94035 [S+A], 94031, 94036 [A]), Ain Sahnawt (Dhofar Prov.), 27 March 2012, leg. P. Benda, A. Reiter and M. Uhrin; – 7 ♂♂, 6 ♀♀ (NMP 92740–92743, 92747–92750 [S+A], 92744–92746, 92751, 92752 [A]), Ain Tabruq (Dhofar Prov.), 28 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 5 ♂♂, 2 ♀♀ (NMP 94009–94014 [S+A], 94008 [A]), Difa (Dhofar Prov.), 26 March 2012, leg. P. Benda, A. Reiter and M. Uhrin; – 3 ♂♂, 5 ♀♀ (NMP 92706, 92707, 92709–92712 [S+A], 92708, 92713 [A]), Hagarir (Dhofar Prov.), 25 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 4 ♂♂ (NMP 94061, 94062 [S+A]), Shihayt, Wadi Darbat (Dhofar Prov.), 28 March 2012, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂ (NMP 94063 [A]), Wadi Ain, 13 km E of Mirbat (Dhofar Prov.), 29 March 2012, leg. P. Benda, A. Reiter and M. Uhrin; – 3 ♂♂, 2 ♀♀ (NMP 94067–94070 [S+A], 94066 [A]), Wadi Hannah (Dhofar Prov.), 30 March 2012, leg. P. Benda, A. Reiter and M. Uhrin. – **Yemen**: 9 ♂♂, 7 ♀♀ (NMP 95632–95635, 95637, 95638, 95641–95645 [S+A], 95636, 95639, 95640, 95646, 95647 [A]), Hawf (Al Mahra Prov.), 12 and 14 October 2005, leg. P. Benda.

Pipistrellus pipistrellus (Schreber, 1774) — **Jordan**: 1 ♂, 5 ♀♀ (NMP 92827–92831 [S+A], 92832 [A]), 'Arjan, 12 July 2010, leg. P. Benda and A. Reiter; – 2 ♀♀ (NMP 92807, 92808 [S+A]), Al Maqar'iyya, 7 July 2010, leg. P. Benda and A. Reiter; – 1 ♀ (NMP 92815 [S+A]), As Salihiyyah, 8 July 2010, leg. P. Benda and A. Reiter; – 1 ♂, 3 ♀♀ (NMP 92458–92460 [S+A], 92461 [A]), Jebel Masuda, Ain Amshit, 15 May 2009, leg. P. Benda, J. Obuch and A. Reiter; – 1 ♂, 1 ♀ (NMP 92378, 92379 [S+A]), Tall Numeira, 17 October 2008, leg. P. Benda and J. Obuch; – 1 ♀ (NMP 92427 [S+A]), Wadi Ghuweir, Khirbet Feynan, 13 May 2009, leg. P. Benda, J. Obuch and A. Reiter. – **Lebanon**: 3 ♀♀ (NMP 93534, 93535 [S+A], 93536 [A]), Adonis, Nahr Ibrahim, 1 June 2010, leg. P. Benda and M.

Appendix I. Continued

Uhrin; – 4 ♂♂, 1 ♀ (NMP le102, le103, 91896 [S+A], le105, 91895 [A]), Afqa Cave, 26 June 2006, leg. R. Lučan, I. Horáček and P. Hulva, 17 January 2008, leg. P. Benda, R. Lučan, I. Horáček and M. Uhrin; – 3 ♂♂, 2 ♀♀ (NMP 93528, 93529, 93531, 93532 [S+A], 93530 [A]), Balaa, 31 May 2010, leg. P. Benda and M. Uhrin; – 1 ♂ (NMP le101 [S+A]), Er Rouais Cave, 26 June 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 2 ♂♂, 2 ♀♀ (NMP 93545, 93547, 93548 [S+A], 93546 [A]), Faraya El Mzar, 2 June 2010, leg. P. Benda and M. Uhrin; – 1 ♂ (NMP 93524 [S+A]), Frat, Nahr Ibrahim, 29 May 2010, leg. P. Benda and M. Uhrin; – 1 ♂, 1 ♀ (NMP 91902, 91903 [S+A]), Haqel Al Azime, Achou Cave, 18 January 2008, leg. P. Benda, R. Lučan, I. Horáček and M. Uhrin; – 1 ♀ (NMP 93572 [S+A]), Jenta, 8 June 2010, leg. P. Benda and M. Uhrin; – 6 ♂♂, 1 ♀ (NMP le19–le24 [S+A], le26 [A]), Jezzine, Pont El Khalass, 23 June 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 2 ♂♂ (NMP 93565, 93566 [S+A]), Majdal Tarchich, 7 June 2010, leg. P. Benda and M. Uhrin; – 2 inds. (NMP le12, le13 [S+A]), Nahr Es Safa, 22 June 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 1 ♂ (NMP le118 [S+A]), Qadisha Cave, 27 June 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 2 ♂♂, 2 ♀♀ (NMP le169, le193, le212, 93693 [S+A]), Ras El Assi, 29 June 2006, leg. R. Lučan, I. Horáček and P. Hulva, 17 March 2009, leg. T. Bartonička, P. Benda, R. Lučan and I. Horáček. – **Syria**: 1 ♀ (NMP 48902 [S+A]), Baniyas, 31 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 4 ♂♂ (NMP 48981–48984 [S+A]), Maalula, 30 April 2001, leg. P. Muncinger and P. Nová; – 2 ♀♀ (NMP 48084, 48085 [S+A]), Rabi'ah, 1 July 1998, leg. M. Andreas, P. Benda and M. Uhrin; – 1 ♂, 1 ♀ (NMP 48871, 48872 [S+A]), Sarghaya, 28 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂ (NMP 48060, 48061, 48063 [S+A]), Slinfeh, 29 June 1998, leg. M. Andreas, P. Benda and M. Uhrin.

Pipistrellus kuhlii (Kuhl, 1817) — **Jordan**: 3 ♀♀ (NMP 92818, 92819 [S+A], 92820 [A]), As Salihiyyah, 8 July 2010, leg. P. Benda and A. Reiter; – 4 ♂♂, 2 ♀♀ (NMP 92368–92372, 92822 [S+A]), Azraq, 13 October 2008, leg. P. Benda and J. Obuch, 9 July 2010, leg. P. Benda and A. Reiter; – 1 ♂ (NMP 92367 [S+A]), Hammam As Sarh, 13 October 2008, leg. P. Benda and J. Obuch; – 1 ♂, 1 ♀ (NMP 92840, 92841 [S+A]), Jufat Al Qafrayn, 15 July 2010, leg. P. Benda and A. Reiter; – 2 ♂♂, 1 ♀ (NMP 92559–92561 [S+A]), Milka, 27 May 2009, leg. Z. Amr, P. Benda and A. Reiter; – 1 ♂ (NMP 92833 [S+A]), Nahla, 13 July 2010, leg. P. Benda and A. Reiter; – 1 ♂ (NMP 92365 [S+A]), Qasr Kharana, 12 October 2008, leg. P. Benda and J. Obuch; – 1 ♀ (NMP 92823 [S+A]), Shawmari Reserve, 10 July 2010, leg. P. Benda and A. Reiter. – **Lebanon**: 1 ♂ (NMP le213 [S+A]), El Fidar, 2 July 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 1 ♂, 2 ♀♀ (NMP le202–le204 [S+A]), Ras El Assi, 29 June 2006, leg. R. Lučan, I. Horáček and P. Hulva. – **Oman**: 1 ♂, 1 ♀ (NMP 92639, 92640 [S+A]), Ar Rustaq, 19 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂ (NMP 93728 [S+A]), Jaalan Bani Bu Hassan, 2 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂ (NMP 94003 [S+A]), Khassab, 18 March 2012, leg. P. Benda, A. Reiter and M. Uhrin; – 3 ♂♂ (NMP 92618, 92619 [S+A], 92617 [A]), Nakhl, 17 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♂♂, 1 ♀ (NMP 93815–93817 [S+A]), Shinas, 13 April 2011, leg. P. Benda, A. Reiter and M. Uhrin. – **Syria**: 4 ♀♀ (NMP 48808, 48810, 48811 [S+A], 48809[S+B]), Abu Kemal, 16 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♀♀ (NMP 48824, 48825 [S+A]), Ain Diwar, 18 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 2 ♀♀ (NMP 48844–48847 [S+A]), Al Tawani, 21 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 2 ♀♀ (NMP 48831, 48832, 48835, 48836 [S+A]), Ayyash, 19 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂, 3 ♀♀ (NMP 48903–48906, 48908 [S+A], 48907 [S+B]), Baniyas, 31 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 5 ♂♂ (NMP 48028, 48029, 48966–48968 [S+A]), Halabiyyeh, 17 June 1998, leg. M. Andreas, P. Benda and M. Uhrin, and 15 April 2001, leg. P. Munclinger and P. Nová; – 2 ♂♂ (NMP 48820, 48821 [S+A]), Khazneh, 17 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 49988 [S+A]), Qala'at Al Hosn, 10 May 2001, leg. R. Lučan; – 1 ♂ (NMP 48814 [S+A]), Qala'at Ar Rahba, 17 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂ (NMP 48767–48769 [S+A]), Qala'at Ja'abar, 12 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 48758 [S+A]), Qala'at Najm, 10 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♀♀ (NMP 48888–48890 [S+A]), Qantara, 30 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 48891 [S+A]), Qasr Ibn Wardan, 31 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 1 ♀ (NMP 48929–48931 [S+A]), Qatura, 2 June 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂, 1 ♀ (NMP 49987, 48947 [S+A]), Ras Al Bassit, 29 April 2001, leg. R. Lučan, 3 June 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 13 ♂♂, 3 ♀♀ (NMP 47993–47999, 48948, 48949, 48951, 48952, 48784–48786, 48789, 48790 [S+A]), Rasafah, 16 June 1998, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin, 13 April 2001, leg. P. Munclinger and P. Nová, 13 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 2 ♀♀ (NMP 48884–48887 [S+A]), Safita, 29 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♂♂ (NMP 48800–48802 [S+A]), Sbeikhan, 15 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 2 ♂♂, 4 ♀♀ (NMP 48837–48842 [S+A]), Tadmor, 20 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 3 ♀♀ (NMP 48862–48864 [S+A]), Talsh'hab, 25 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂, 1 ♀ (NMP 48034 [S+A], 48036 [S+B]), Tell Sheikh Hamad, 19 June 1998, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin. – **Yemen**: 3 ♂♂, 1 ♀ (NMP pb3743, pb3745, pb3746 [S+A], pb3744 [A]), Arus, 1 November 2007, leg. P. Benda and A. Reiter; – 2 ♂♂ (NMP pb3638, pb3639 [S+A]), Assala, 26 October 2007, leg. P. Benda and A. Reiter; – 1 ♀ (NMP pb3105 [S+A]), Hammam Ali, 27 October 2005, leg. P. Benda; – 7 ♂♂, 4 ♀♀ (NMP pb3094–pb3098, pb3101–pb3104 [S+A], pb3099, pb3100 [A]), Wadi Maytam, 26 October 2005, leg. P. Benda.

Hypsugo savii (Bonaparte, 1837) — **Lebanon**: 4 ♂♂, 1 ♀, 1 ind. (NMP 90900, 91783, 91784, le106, le108, le197 [S+A]), Afqa Cave, 26 June 2006, leg. R. Lučan, I. Horáček and P. Hulva, 15 July 2006, leg. P. Benda, 22 January 2007, leg. P. Benda, R. Černý, R. Lučan and I. Horáček; – 1 ♂ (NMP 93561 [S+A]), Arnoun, 6 June 2010, leg. P. Benda and M. Uhrin; – 1 ♂ (NMP 93527 [S+A]), Balaa, 31 May 2010, leg. P. Benda and M. Uhrin; – 2 ♂♂ (NMP le99, le100 [S+A]), El Aaqoura, Er Rouais Cave, 26 June 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 6 ♂♂ (NMP le27, le29–le33 [S+A]), Jezzine, Pont El Khalass, 23 June 2006, leg. R. Lučan, I. Horáček and P. Hulva; – 3 ♂♂

Appendix I. Continued

(NMP le205–le207 [S+A]), Ras El Assi, Deir Mar Maroun Monastery, 29 June 2006, leg. R. Lučan, I. Horáček and P. Hulva. – **Syria**: 2 ♀♀ (NMP 48868 [S+B], 48869 [S+A]), Barqash, 26 May 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 5 ♂♂ (NMP 48919–48923 [S+A]), Hayalien, 1 June 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 1 ♂ (NMP 48980 [S+A]), Maalula, 30 April 2001, leg. P. Munclinger and P. Nová; – 1 ♀ (NMP 48076 [S+A]), Qala'at Sheisar, 1 July 1998, leg. M. Andreas, P. Benda and M. Uhrin; – 3 ♀♀ (NMP 48932–48934 [S+A]), Qatura, 2 June 2001, leg. M. Andreas, P. Benda, A. Reiter and D. Weinfurtová; – 9 ♂♂ (NMP 48064–48068, 48070–48072 [S+A], 48069 [S+B]), Slinfeh, 29 June 1998, leg. M. Andreas, P. Benda and M. Uhrin; – 1 ♂ (NMP 48048 [S+A]), Yabroud, 27 June 1998, leg. M. Andreas, P. Benda and M. Uhrin.

Hypsugo arabicus (Harrison, 1979) — **Oman**: 1 ♂ (NMP 92624 [S+A]), Al Aqar, 2 km S of Wakan, 17 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♂♂, 2 ♀♀ (NMP 93739–93741 [S+A], 93742 [A]), Al Aqor, Wadi Tiwi, 4 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♂♂ (NMP 92665, 92666 [S+A]), Al Nakhar, 22 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♀♀ (NMP 93822, 93823 [S+A]), Al Zihaymi, 14 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂ (NMP 92779 [S+AR), Dibab, 2 November 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♀♀ (NMP 93760, 93761 [S+A]), Ghab, Wadi Al Hawasina, 7 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♂♂, 1 ♀ (NMP 92782, 92783 [S+A], 92784 [A]), Mansaft, 3 November 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂, 2 ♀♀ (NMP 93785, 93786 [S+A], 93787 [A]), Misfat Al Khawater, 9 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♀ (NMP 92774 [S+A]), Muqal, 1 November 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂ (NMP 93997 [S+A]), Sal Alah, 15 March 2012, leg. P. Benda, A. Reiter and M. Uhrin; – 3 ♀♀ (NMP 93812, 93813 [S+A], 93814 [A]), Subakh, Hatta Pools, 12 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 2 ♀♀ (NMP 93733, 93734 [S+A]), Wadd, 3 April 2011, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♀ (NMP 94001 [S+A]), Wadi Banah, 16 March 2012, leg. P. Benda, A. Reiter and M. Uhrin.

Hypsugo ariel (Thomas, 1904) — **Jordan**: 7 ♂♂, 1 ♀ (NMP 92488–92494 [S+A], 92487 [A]), Al Ghal, 17 May 2009, leg. P. Benda and A. Reiter; – 1 ♀ (NMP 92380 [S+A]), Tall Numeira, 17 October 2008, leg. P. Benda and J. Obuch; – 1 ♀ (NMP 92804 [S+A]), Wadi Al Hassa, 5 July 2010, leg. P. Benda and A. Reiter; – 1 ♂ (NMP 92095 [S+A]), Wadi Rum, 24 October 2004, leg. R. Lučan. – **Oman**: 1 ♂ (NMP 92754 [S+A]), Jufa, 29 October 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 3 ♂♂, 1 ♀ (NMP 94074–94076 [S+A], 94073 [A]), Rima, Wadi Gharah, 2 April 2012, leg. P. Benda, A. Reiter and M. Uhrin. – **Yemen**: 1 ♂ (NMP pb3058 [S+A]), Al Nueimah, 20 October 2005, leg. P. Benda; – 2 ♂♂, 1 ♀ (NMP pb3050, pb3051 [S+A], pb3052 [A]), Damqawt, 16 October 2005, leg. P. Benda; – 5 ♂♂, 4 ♀♀ (NMP pb3022–3025, 3027–3030 [S+A], pb3026 [A]), Hawf, 14 October 2005, leg. P. Benda; – 1 ♂, 1 ♀ (NMP pb3054 [S+A], pb3055 [A]), 25 km WSW of Sayhut, 17 October 2005, leg. P. Benda.

Neoromicia guineensis (de Bocage, 1889) — **Yemen**: 2 ♂♂ (NMP pb3124, pb3125 [S+A]), Jebel Bura, 30 October 2005, leg. P. Benda; – 3 ♂♂ (NMP pb3663, pb3664 [S+A], pb3662 [A]), Ash Shukayrah, Wadi Bani Khawlan, 27 October 2007, leg. P. Benda and A. Reiter.

Appendix II

List of the specimens examined in genetic analysis

Species	Haplotype	GBAN	Country	Locality	Vaucher/Reference
Pipistrellus sp. n.	Dhofar 1	KX375141	Oman	Ain Jarziz	NMP 92727
P. sp. n.	Dhofar 1	–	Oman	Ain Jarziz	NMP 92732
P. sp. n.	Dhofar 1	–	Oman	Ain Tabruq	NMP 92741
P. sp. n.	Dhofar 1	–	Oman	Ain Tabruq	NMP 92748
P. sp. n.	Dhofar 1	–	Oman	Ain Tabruq	NMP 92751
P. sp. n.	Dhofar 1	–	Oman	Difa	NMP 94008
P. sp. n.	Dhofar 1	–	Oman	Difa	NMP 94013
P. sp. n.	Dhofar 1	–	Oman	Ain Sahnawt	NMP 94031
P. sp. n.	Dhofar 1	–	Oman	Ain Sahnawt	NMP 94032
P. sp. n.	Dhofar 1	–	Oman	Ain Sahnawt	NMP 94033
P. sp. n.	Dhofar 1	–	Oman	Ain Sahnawt	NMP 94034
P. sp. n.	Dhofar 1	–	Oman	Ain Sahnawt	NMP 94035
P. sp. n.	Dhofar 1	–	Oman	Ain Sahnawt	NMP 94036
P. sp. n.	Dhofar 1	–	Oman	Shihayt, Wadi Darbat	NMP 94061
P. sp. n.	Dhofar 1	–	Oman	Wadi Hannah	NMP 94068
P. sp. n.	Dhofar 1	–	Yemen	Hawf	NMP 95633
P. sp. n.	Dhofar 1	–	Yemen	Hawf	NMP 95640
P. sp. n.	Dhofar 2	KX375142	Oman	Hagarir	NMP 92708
P. sp. n.	Dhofar 2	–	Oman	Wadi Hannah	NMP 94070
P. sp. n.	Dhofar 3	KX375143	Oman	Difa	NMP 94012
P. sp. n.	Dhofar 4	KX375144	Oman	Ain Jarziz	NMP 92725
P. sp. n.	Dhofar 5	KX375145	Oman	Difa	NMP 94014
P. sp. n.	Dhofar 6	KX375146	Oman	Hagarir	NMP 92710

Appendix II. Continued

Species	Haplotype	GBAN	Country	Locality	Vaucher/Reference
P. sp. n.	Dhofar 6	–	Yemen	Hawf	NMP 95645
P. sp. n.	Dhofar 7	KX375147	Oman	Wadi Hannah	NMP 94066
P. sp. n.	Dhofar 8	KX375148	Oman	Hagarir	NMP 92706
P. sp. n.	Dhofar 8	–	Oman	Difa	NMP 94009
P. sp. n.	Dhofar 8	–	Oman	Difa	NMP 94010
P. sp. n.	Dhofar 8	–	Oman	Shihayt, Wadi Darbat	NMP 94062
P. sp. n.	Dhofar 8	–	Oman	Wadi Ain, E of Mirbat	NMP 94063
P. sp. n.	Dhofar 8	–	Oman	Wadi Hannah	NMP 94069
P. sp. n.	Dhofar 8	–	Yemen	Hawf	NMP 95647
Pipistrellus abramus	China 1	KF782167	China	–	Dong *et al.* (2014)
P. abramus	China 2	GQ332528	China	–	Wei *et al.* (2010)
P. abramus	China 3	GQ332494	China	–	Wei *et al.* (2010)
P. abramus	China 4	KF051952	China	–	Dong *et al.* (unpubl.)
Pipistrellus coromandra	Malaysia 1	KP688404	Malaysia	–	Rahman *et al.* (2016)
Pipistrellus hesperidus	Ethiopia 1	KX375149	Ethiopia	Menagesha Forest	NMP pb5482
P. hesperidus	Ethiopia 2	KX375150	Ethiopia	Menagesha Forest	NMP pb5476
P. hesperidus	Ethiopia 3	KX375151	Ethiopia	Harrena Forest	NMP 94998
P. hesperidus	Ethiopia 4	KX375152	Ethiopia	Metu	NMP 92210
P. hesperidus	Ethiopia 5	KX375153	Ethiopia	Goba	NMP 92117
P. hesperidus	Ethiopia 6	KX375154	Ethiopia	Metu	NMP 92213
P. hesperidus	Ethiopia 7	KX375155	Ethiopia	Korem	NMP pb5487
P. hesperidus	Ethiopia 8	KX375156	Ethiopia	Desea Forest	NMP pb5498
P. hesperidus	Ethiopia 9	KX375157	Ethiopia	Simien National Park	NMP pb5519
Pipistrellus javanicus	Philippines 1	JX570908	Philippines	–	Heaney *et al.* (2012)
P. javanicus	Philippines 2	JX570909	Philippines	–	Heaney *et al.* (2012)
Pipistrellus kuhlii	Yemen 1	KX375158	Yemen	Mashgab	NMP pb3638
P. kuhlii	Yemen 2	KX375159	Yemen	Shibam	NMP pb3746
P. kuhlii	Yemen 3	KX375160	Yemen	Shibam	NMP pb3743
P. kuhlii	Yemen 4	KX375161	Yemen	Shibam	NMP pb3745
P. kuhlii	Oman 1	KP455382	Oman	–	Benda *et al*. (2014*b*)
P. kuhlii	Oman 2	KP455383	Oman	–	Benda *et al*. (2014*b*)
P. kuhlii	Egypt 1	KP455372	Egypt	–	Benda *et al*. (2014*b*)
P. kuhlii	Egypt 2	KP455371	Egypt	–	Benda *et al*. (2014*b*)
P. kuhlii	Egypt 3	KP455345	Egypt	–	Benda *et al*. (2014*b*)
P. kuhlii	Egypt 4	KP455339	Egypt	–	Benda *et al*. (2014*b*)
P. kuhlii	Cyprus 1	KP455370	Cyprus	–	Benda *et al*. (2014*b*)
Pipistrellus maderensis	Tenerifa 1	KP455376	Tenerifa	–	Benda *et al*. (2014*b*)
P. maderensis	Tenerifa 2	KP455373	Tenerifa	–	Benda *et al*. (2014*b*)
P. maderensis	Tenerifa 3	KP455374	Tenerifa	–	Benda *et al*. (2014*b*)
P. maderensis	Tenerifa 4	KP455375	Tenerifa	–	Benda *et al*. (2014*b*)
P. pipistrellus	Jordan 1	KX375162	Jordan	Tall Numeira	NMP 92378
P. pipistrellus	Greece 1	AJ504443	Greece	–	Stadelmann *et al*. (2004*a*)
P. pipistrellus	Iran 1	KF874520	Iran	–	Benda *et al*. (2012)
P. pipistrellus	Iran 2	KF874519	Iran	–	Benda *et al*. (2012)
Pipistrellus rusticus	Namibia 1	KX375163	Namibia	Nyangana	NMP pb5215
P. rusticus	Namibia 2	KX375164	Namibia	Diyogha	NMP pb5324
P. rusticus	Namibia 3	KX375165	Namibia	Nyangana	NMP pb5214
P. rusticus	Namibia 4	KX375166	Namibia	Diyogha	NMP pb5323
P. rusticus	Namibia 5	KX375167	Namibia	Gcangcu	NMP pb5149
Nyctalus leisleri	Switzerland 1	JX570901	Switzerland	–	Heaney *et al.* (2012)
N. leisleri	Switzerland 2	AF376832	Switzerland	–	Ruedi and Mayer (2001)
Nyctalus noctula	Greece 2	JX570902	Greece	–	Heaney *et al.* (2012)
N. noctula	Switzerland 3	AJ841967	Switzerland	–	Stadelmann *et al.* (2004*b*)
Nyctalus plancyi	China 5	KP273590	China	–	Qian *et al*. (2015)
N. plancyi	Philippines 3	JX570905	Philippines	–	Heaney *et al.* (2012)
N. plancyi	China 6	DQ435073	China	–	Thabah *et al.* (2007)
Vansonia rueppellii	Morocco 1	KX375168	Morocco	Cascades Bou Mazouz	NMP 90080
V. rueppellii	Egypt 5	KX375169	Egypt	Al Baharyia, Bawiti	NMP 94970
V. rueppellii	Egypt 6	KX375170	Egypt	Al Baharyia, Bawiti	NMP 94967
Laephotis botswanae	Namibia 6	KX375171	Namibia	Eenhana	NMP pb5928

Appendix II. Continued

Species	Haplotype	GBAN	Country	Locality	Vaucher/Reference
L.botswanae	Zambia 1	KX375172	Zambia	Sioma Bush Camp	NMP RS966
Neoromicia capensis	Namibia 7	KX375173	Namibia	Ghaub Farm	NMP pb5880
N. capensis	South Africa 1	KX375174	South Africa	Lesetlheng	NMP 95667
N. capensis	Zambia 2	KX375175	Zambia	Sioma Bush Camp	NMP RS986
Neoromicia guineensis	Yemen 5	KX375176	Yemen	Ash Shuqayrah	NMP pb3662
N. guineensis	Yemen 6	KX375177	Yemen	Ash Shuqayrah	NMP pb3664
N. guineensis	Yemen 7	KX375178	Yemen	Riqab, Jebel Bura	NMP pb3124
N. guineensis	Yemen 8	KX375179	Yemen	Riqab, Jebel Bura	NMP pb3125
Neoromicia nana	Namibia 8	KX375180	Namibia	Okashana	NMP pb5909
N. nana	Zambia 3	KX375181	Zambia	Livingstone	NMP RS992
N. nana	Zambia 4	KX375182	Zambia	North Luangwa	NMP RS1235
Neoromicia somalica	Ethiopia 10	KX375183	Ethiopia	Menagesha Forest	NMP pb5484
N. somalica	Ethiopia 11	KX375184	Ethiopia	Harle	NMP pb5486
N. somalica	Ethiopia 12	KX375185	Ethiopia	Sorobo	NMP pb5655
Neoromicia zuluensis	South Africa 2	KX375186	South Africa	Mahagala	NMP 95658
N. zuluensis	Namibia 9	KX375187	Namibia	Otjitotongwe Farm	NMP pb6039
N. zuluensis	Namibia 10	KX375188	Namibia	Sesfontein	NMP pb5802
Hypsugo arabicus	Oman 3	KX375189	Oman	Al Nakhar	NMP 92665
H. arabicus	Oman 4	KX375190	Oman	Subakh, Hatta Pools	NMP 93814
Hypsugo ariel	Yemen 9	KX375191	Yemen	Hawf	NMP pb3026
H. ariel	Yemen 10	KX375192	Yemen	Damqawt	NMP pb3051
H. ariel	Egypt 7	KX375193	Egypt	El A'aqab	NMP 92597
Hypsugo savii	Syria 1	KX375194	Syria	Hayalien	NMP 48920
H. savii	Greece 3	KX375195	Greece	Anthiro	NMP 49029
H. savii	Montenegro 1	KX375196	Montenegro	Gurec	NMP 90223
H. savii	Cyprus 2	KX375197	Cyprus	Troodos Forest	NMP 90410
Plecotus auritus	–	AY665169	–	–	Tsytsulina *et al*. (2012)
Plecotus macrobullaris	–	KR134407	–	–	Alberdi *et al*. (2015)