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African bats in the collection of the National Museum, Prague (Chiroptera). II. Bats from Benin

Petr BENDA[1,2], Marek UVIZL[2,1], Peter VALLO[3] & Bruno Agossou DJOSSA[4,5]

[1] Department of Zoology, National Museum (Natural History), Václavské nám. 68, CZ–115 79 Praha 1, Czech Republic; petr.benda@nm.cz
[2] Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ–128 44 Praha 2, Czech Republic
[3] Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, CZ–603 65 Brno, Czech Republic
[4] Laboratory of Applied Ecology, Faculty of Agronomic Sciences, University of Abomey-Calavi, 01 BP 526, Cotonou, Benin
[5] Forestry and Bioresource Conservation Research Unit (U/RFCBio), Porto Novo National Agriculture University, Porto-Novo, Benin

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Abstract. A list of 58 specimens of bats belonging to 16 species of six families originating from Benin, housed in the collection of the National Museum, Prague, Czech Republic, is presented in a systematic review. The specimens represent 24 new records (species vs. locality) of bats from Benin. The species lists are complemented by comments on distribution and morphometric data. The collection contains three species new for the Beninese fauna, *Hipposideros jonesi*, *H. abae*, and *H.* cf. *lamottei*, and the bat fauna of Benin now comprises 55 species in total. *Scotophilus nigrita* is documented from Benin for the second time, and for the first time from a specific record site in this country. Besides the majority of common bat species, considering their available records in Benin, the collection includes several other species rather uncommon in the country, such as *Rhinolophus fumigatus*, *Hipposideros* cf. *ruber*, *Pseudoromicia rendalli*, or *Scotophilus livingstonii*. In two of the latter group of species, the molecular genetic analysis revealed new extents of distribution for particular mitochondrial lineages in Benin, like the D lineage of *H*. cf. *ruber* or *S. livingstonii* s.str. As complete as possible check-list of the Beninese bat fauna comprising all known record localities is included.

Key words. National Museum, collection, catalogue, bats, distribution, Afrotropics, West Africa, Gulf of Guinea, Dahomey.

INTRODUCTION

Benin is a rather small country of West Africa, occupying 114,763 square kilometres, dominated by extensive lowlands with only few hilly areas (the highest point being Mont Alédjo, 658 m a. s. l.). The country is covered by woodland savanna in a broad sense, its southern part belongs to the zone of forest-savanna mosaic, central belt to the zone of Guinean savanna, and the northern part of Benin is covered by the rather dry zone of Sudanian savanna; in the hilly western borderland, small patches of the Guinean forests are present (Burgess et al. 2004, Happold & Lock 2013). Benin (along with Togo and parts of Ghana and Nigeria) is situated

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in the Dahomey Gap, a band of relatively dry forest-savanna mosaic reaching from the north to the sea shore and interrupting the wide west-east running coastal belt of the Guinean rainforest (Salzmann & Hoelzmann 2005). Maybe because of the lack of tropical rainforests, the biota of Benin is less investigated than of those countries of West Africa where the rainforest represents a part of their environments.

In comparison with the faunas of other African countries or of West Africa as a whole, the bat fauna of Benin is relatively less known. This is apparent namely in comparison with three neighbouring countries, Togo, Burkina Faso, and Nigeria, where the bat fauna was thoroughly and repeatedly studied (De Vree et al. 1969, 1970, De Vree & Van Der Straeten 1971, Koopman et al. 1978, Robbins 1980, Happold 1987, Koch-Weser 1984, Kangoyé et al. 2015, Amori et al. 2016, 2022, Tanshi et al. 2018, 2021, etc.). The first report on the bat fauna of Benin was published by Robbins (1980) as a result of the African Mammal Project held by the National Museum of Natural History, Washington (USNM). Before this report was published, only five papers mentioning five single records of four bat species from Benin appeared (Dobson 1878, Theodor 1956, De Vree 1971, Poché 1975, Robbins 1978). In this first faunal review, Robbins (1980) reported 86 records of bats belonging to 32 species and this collection housed in the USNM represents the largest bat series from Benin till now (Van Cakenberghe & Seamark 2022). For a long time, this was the last significant effort in the bat research in the country, since Bergmans (2002) reported 34 species and Capo-Chichi et al. (2004) 35 species of bats in Benin, i.e. only three additional species after more than twenty years (despite a lot of new records they brought). However, the latter authors overlooked three papers, mentioning several new bats records from the country (Green 1983, Verschuren 1988, Haquart & Rombaut 1995).

Nevertheless, at the same time, Beninese students started to investigate the country's bat fauna, see the theses by Djossa (2003, 2007) and Voglozin (2003, 2005). Their activities resulted in several faunal reports (Djossa et al. 2008b, 2010, Djossa & Sinsin 2010, Voglozin & Sinsin 2007) and continued in a series of ecological and environmental studies on Beninese bats (Djossa et al. 2008a, 2012, 2015, Weber et al. 2009, Dougnon et al. 2012, Stechert et al. 2014). As a result of this stage, a new review of bat fauna of Benin was published by Djossa & Sinsin (2010), finally bringing data on 53 species of bats from the country. Although Djossa et al. (2010) discovered two additional species, several bat species mentioned to occur in Benin were based on doubtful or insufficient evidence (see Appendix 1), therefore, the bat fauna of Benin eventually comprises 52 species of bats. All species currently known from the country and their records (species vs. locality; 409 at minimum) are reviewed here in Appendix 1.

The museum specimens of bats from Benin are not scattered over many collections, Van Cakenberghe & Seamark (2022) reported altogether 1,164 specimens from nine museums. However, 86% of these bats, 1,002 specimens, are hosted by the USNM collection (see above). The remaining specimens are housed in the museum collections of Amsterdam (55 specimens), Leiden (44), Paris (32), Toronto (14), Harvard University, Cambridge (7), Tervuren (7), London (2), and Berlin (1).

A small collection of bats from Benin is also housed in the National Museum, Prague (NMP). The collection comprises the specimens gathered during a short research trip that followed the 10th African Small Mammal Symposium held at the University Abomey-Calavi, Benin, in August 2007. The NMP series of Beninese bats contains 58 specimens belonging to 16 species of six families. These bats originate from seven localities covering the central part of the country (Fig. 1) and represent 24 records (species vs. locality), i.e. about 6% of the available country's amount of bat records (Appendix 1). Thus, concerning the information potential, such a collec-

tion could have a certain value. In this catalogue, we describe the NMP collection of Beninese bats in the context of the knowledge of bat faunas of the country and West Africa as well. We intend this contribution as the second part of a catalogue series of African bats housed in the NMP collection (see Benda et al. 2022).

METHODS

The lists of specimens from the collection of the National Museum, Prague (NMP), are arranged in alphabetical order (according to the collection locality name) and then, in chronological order (according to collection date), for each species. The lists include, for each item, the following information: (1) indication of sex, (2) NMP collection ID, (3) preparation type (see Abbreviations below), (4) name of the locality (primarily listed by the name of the closest settlement or notable physical feature), (5) date of collection, and (6) collector name/s. For names of the first-level administrative divisions and geographic coordinates of the localities see gazetteer (Appendix 2; in alphabetical order). The lists of specimens of particular species are complemented by a list of references reporting the particular specimen/s or the finding/s, i.e., additional data concerning the specimens.

Basic biometric data taken from the NMP specimens are presented in Tables 1–5. The specimens were measured in a standard way with the use of mechanical calliper. Horizontal dental dimensions were taken on cingulum margins.

Molecular genetic examinations

For details concerning DNA sequencing of bats of the genera *Rhinolophus*, *Hipposideros*, and *Scotophilus* see Vallo et al. (2008, 2013, 2015) and Benda & Vallo (2012). The following methods were used for the genera *Chaerephon*, *Mops*, and *Pseudoromicia.*

The genomic DNA was extracted from alcohol-preserved tissue of the specimens using Geneaid Genomic DNA Mini Kit. We targeted the complete mitochondrial gene for NADH dehydrogenase subunit 1 (ND1). When we were not able to obtain any sequence for this marker, we targeted the mitochondrial gene for 16S rRNA (16S). These markers were used in previous studies dealing with African bats (Hoofer & Van Den Bussche 2003, Goodman et al. 2012, Benda et al. 2022). The genes were amplified with the primers ER65 (5'-CCTCGATGTTGGATCAGG-3') and ER66 (5'-GTATGGGCCCGATAGCTT-3; Dietz et al. 2016) for ND1, and 16SL1 (5'-CGCCTGTTTAACAAAAACAT-3') and 16SH1 (5'-CCGGTCTGAACTCAGATCACGT-3'; Palumbi et al. 1991) for 16S. The PCR amplifications were

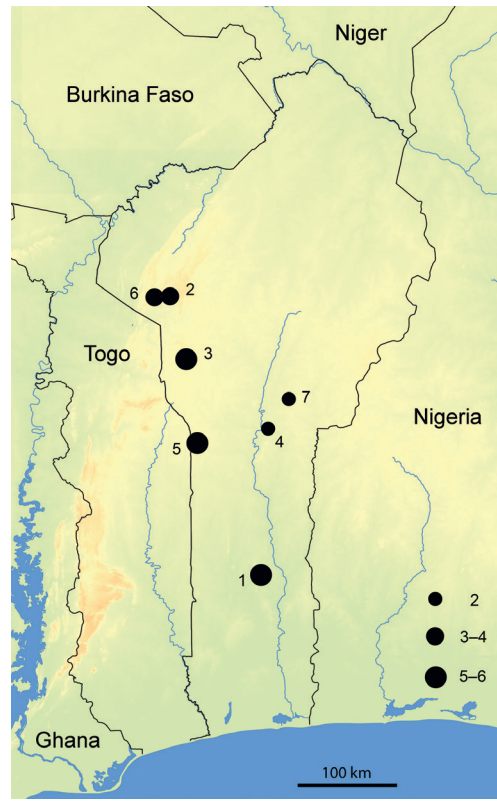


Fig. 1. Map of Benin showing the localities of recorded bat specimens housed in the collection of the National Museum, Prague, Czech Republic; the size of circle corresponds with the number of species collected (see legend in right bottom corner of the map). Localities: 1 – Awaya, 2 – Chute de Kota, 3 – Djougou, 4 – Koko, 5 – Manigri, 6 – Tagayé, 7 – Tourou.

treated as in Kocher et al. (1989) and Dietz et al. (2016), respectively. The PCR products were Sanger-sequenced from both sides using the PCR primers by Macrogen, Inc. (Amsterdam, the Netherlands).

Sequences were edited and aligned using the MAFFT plugin (Katoh & Standley 2013) in Geneious 11.0.5 (https://www.geneious.com), and subsequently manually edited. Sequences of protein-coding markers were translated to amino acids to check for the presence of stop codons, which would indicate pseudogenes have been amplified. Basic Local Alignment Search Tool (BLAST; Altschul et al. 1990) was used to search for the most related sequences and therefore to identify the species of some samples that were difficult to identify by morphological examination. The GenBank Accession Numbers of the newly defined haplotypes are listed in Appendix 3, comparative haplotypes were extracted from the studies by Hoofer & Van Den Bussche (2003) and Goodman et al. (2012).

Abbreviations

Dimensions. **External**: LC = head and body length; – LCd = tail length; – LAt = forearm length; – LA = ear (auricle) length; – LT = tragus length; – LaFE = horseshoe width. – **Cranial**: LCr = greatest length of skull (including praemaxilla); – LOc = occipitocanine length; – LCb = condylobasal length; – LCc = condylocanine length; – LaZ = zygomatic width; – LaI = width of interorbital constriction; – LaP = width of postorbital constriction; – LaInf = infraorbital width; – LaN = neurocranium width; – LaM = mastoidal width; – ANc = neurocranium height; – LBT = largest horizontal length of tympanic bulla; – CC = rostral width between labial margins of canines; – M^2M^2 = rostral width between labial margins of second upper molars; – M^3M^3 = rostral width between labial margins of third upper molars; – CM^2 = length of upper tooth-row between mesial margin of canine and distal margin of second molar; – CM^3 = length of upper tooth-row between mesial margin of canine and distal margin of third molar; – LMd = condylar length of mandible; – ACo = height of coronoid process; – CM_3 = length of lower tooth-row between mesial margin of canine and distal margin of third molar.
Collections. MNHN = National Museum of Natural History, Paris, France; – NMP = National Museum (Natural History), Prague, Czech Republic; – USNM = National Museum of Natural History, Smithsonian Institution, Washington DC, United States of America; – ZMA = Zoological Museum, Amsterdam, the Netherlands.
Others. A = alcohol specimen; – leg. = legit [presented, bequeathed, sent]; – M = mean; – max., min. = dimension range margins; – S = skull; – SD = standard deviation.

ANNOTATED LIST OF SPECIMENS

Pteropodidae

Eidolon helvum (Kerr, 1792)

Material (1). 1 ♂ (NMP 91887 [S+A]), Manigri, 6 km SE of Bassila, 2 September 2007, leg. P. Benda.

Eidolon helvum is the most widespread fruit bat species of sub-Saharan Africa, it was recorded in all habitats and regions between the Cape Verde Islands, Mauritania, and Senegal in the west, to the Sudan, Ethiopia and Kenya in the east, and South Africa and Mozambique in the south (Hayman & Hill 1971, Bergmans 1990, Jiménez & Hazevoet 2010, Thomas & Henry 2013a). It is a very abundant bat in the whole forest and savanna zones of West Africa (Rosevear 1965), northern marginal records are available from the Sahel zone of Mauritania, Niger, and the Sudan (Thomas 1903, Dekeyser 1950, Cosson et al. 1996).

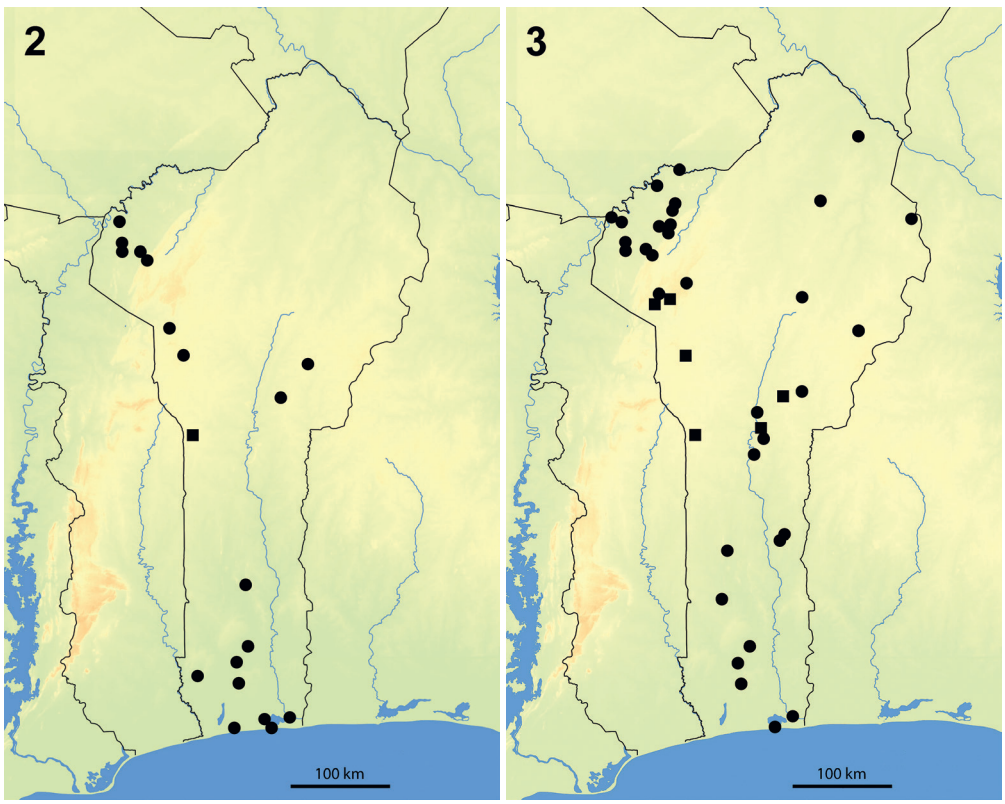
In Benin, *E. helvum* represents one of the most common bats in general, it is the third most common fruit bat species of the country (Appendix 1), and it is similarly abundant also in the neighbouring countries (Kock 1978, Happold 1987, Kangoyé et al. 2015, Amori et al. 2016). At least 19 occurrence sites of this bat were reported from Benin, they are spread over majority

of the country area with the exception of its north-eastern part (Fig. 2; Dobson 1878, Robbins 1980, Verschuren 1988, Bergmans 1990, 2002, Haquart & Rombaut 1995, Djossa 2007, Djossa et al. 2008a, b, 2010). This gap in distribution is interesting, since in the neighbouring countries, the records are available also from the northern areas (Happold 1987, Kangoyé et al. 2015).

The collection locality of the NMP specimen of *E. helvum* here reported falls to the centre of Beninese range of this bat (Fig. 2). The single collected specimen of *E. helvum* from Benin is rather surprising considering the wide and abundant occurrence of this bat in the country. The dimensions of this specimen are shown in Table 1.

Epomophorus gambianus (Ogilby, 1835)

Material (4). 1 ♀ (NMP 91881 [S+A]), Chute de Kota, 5 km S of Kota Monogou, 1 September 2007, leg. P. Benda;



Figs. 2, 3. Distribution of bats in Benin; circles – published records (see Appendix 1), squares – new records. 2 – *Eidolon helvum*. 3 – *Epomophorus gambianus*.

Table 1. Basic biometric data on the NMP specimens of Pteropodidae bats from Benin (only adult specimens are included). The values are in millimetres, for dimension abbreviations see Methods

dimension	*Eidolon helvum*	*Epomophorus gambianus*			*Epomophorus pusillus*	
	91887 ♂	91856 ♂	91855 ♀	91881 ♀	91882 ♂	91888 ♀
LC	179	165	155	142	91	90
LAt	118.7	89.6	84.7	86.6	52.2	52.7
LA	29.0	23.8	21.5	23.0	15.8	16.5
LCr	54.34	57.90	51.85	48.02	29.18	28.08
LCb	53.36	58.14	51.67	48.07	28.25	27.38
LaZ	32.63	28.21	26.54	25.59	18.31	18.41
LaI	9.33	8.04	7.48	7.73	5.36	5.24
LaP	10.34	10.68	9.47	9.64	9.42	9.26
LaInf	12.16	12.28	11.37	11.63	7.07	7.27
LaN	21.20	18.65	17.16	16.93	12.55	12.97
LaM	20.04	19.29	18.63	18.08	12.95	12.45
ANc	15.68	11.37	11.17	10.42	9.25	8.98
LBT	5.27	4.96	4.88	4.92	3.18	3.20
CC	10.24	10.41	9.47	9.37	5.99	6.17
M^2M^2	–	14.42	13.54	–	9.56	9.51
CM^2	20.69	21.23	18.81	18.58	8.74	8.53
LMd	43.11	46.88	40.14	39.26	22.36	21.84
ACo	17.74	18.93	15.64	15.27	8.23	8.27
CM_3	23.45	22.89	19.28	20.15	10.14	9.75

1 ♂, 1 ♀ (NMP 91855, 91856 [S+A]; Fig. 4), Koko, 11 km NW of Alafiarou, 27 August 2007, leg. P. Benda, A. Konečný & R. Šumbera;
1 ♂ (NMP 91852 [A]), Tourou, 10 km W of Parakou, 26 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

Epomophorus gambianus is a very common fruit bat in the belt of the Sudanese and Guinean savannas, stretching from Senegal to western Ethiopia (Hayman & Hill 1971, Bergmans 1988, Burgin et al. 2020). It is very common in the whole open woodland zone of West Africa (Rosevear 1965), where it seems to be the commonest non-colonial species of fruit bats (cf. Happold 1987). This bat represents also a very abundant faunal element in two neighbouring countries of Benin, around 45 sites are known from Togo, and about 55 from Burkina Faso (Kangoyé et al. 2015, Amori et al. 2016). In both Togo and Burkina Faso, *E. gambianus* is the most common bat species, similarly as in Benin (Appendix 1); at least 33 localities have been reported from the latter country, scattered across its whole territory (Fig. 3; Robbins 1980, Green 1983, Haquart & Rombaut 1995, Bergmans 2002, Djossa 2007, Djossa et al. 2008a, b, Djossa et al. 2010, Van Cakenberghe & Seamark 2022). Within a research survey in the Pendjari National Park, NW Benin, the catch of *E. gambianus* represented 49.6% (604 inds.) of the netted fruit bats of eight species (Djossa et al. 2008a).

The localities of the NMP specimens as well as the additional recorded sites (see Note below) enrich the number of localities by 18.2% to 39–40 (see Appendix 1), all six new sites come from the west-central part of Benin (Fig. 3). Despite the highest number of localities for a bat species

that was documented for *E. gambianus* in Benin, this number is still low in comparison with the situation in the neighbouring Togo, a half-area country compared to Benin, however, with still a higher number of records of this fruit bat than those available from Benin (see Amori et al. 2016). This difference well demonstrates the relatively low level of bat research in Benin. The dimensions of the adult NMP specimens of *E. gambianus* from Benin are shown in Table 1.

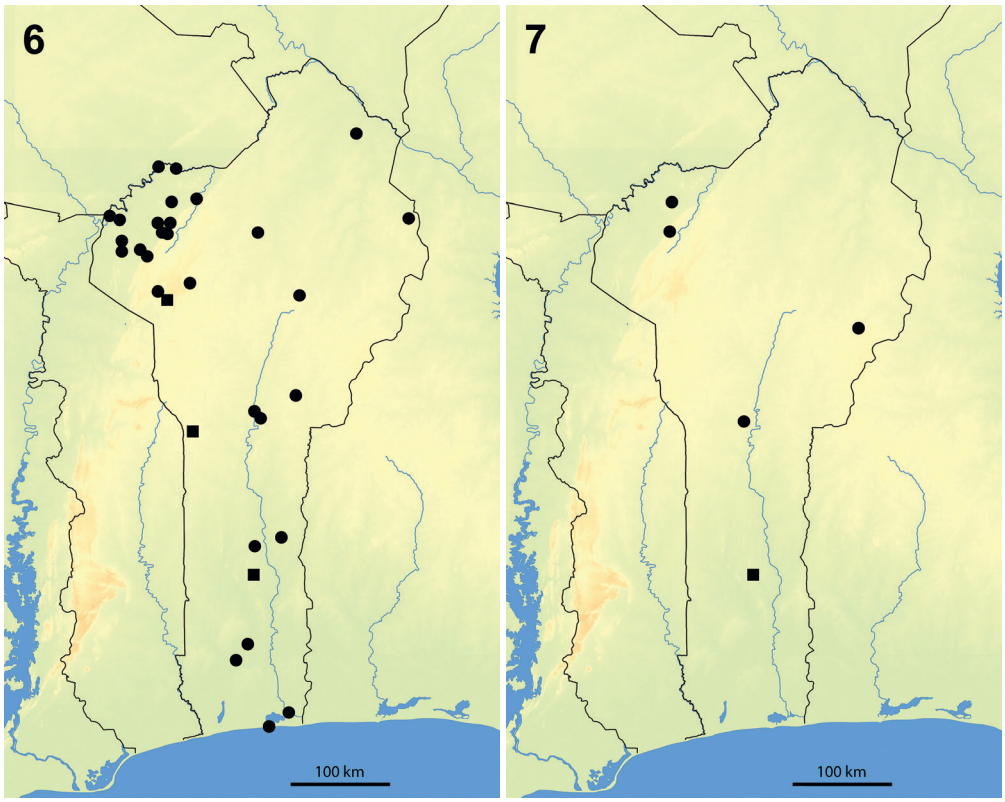
Note. Individuals of *Epomophorus gambianus* were netted additionally at three sites (all bats were released after their identification and measuring): 2 ♀♀ at Djougou, NW margin of the town, 28 August 2007; 1 ♂, 7 ♀♀ at Manigri, 6 km SE of Bassila, 2 September 2007; and 1 ♀ at Tagayé, 15 km SW of Natitingou, 30 August 2007.

Epomophorus pusillus Peters, 1867

Material (4). 1 ♀ (NMP 91833 [A]), Awaya, 10 km E of Dassa, 25 August 2007, leg. P. Benda, A. Konečný & R. Šumbera;
1 ♂, 1 ♀ (NMP 91882 [S+A], 91883 [A]; Fig. 5), Chute de Kota, 5 km S of Kota Monogou, 1 September 2007, leg. P. Benda;
1 ♀ (NMP 91888 [S+A]), Manigri, 6 km SE of Bassila, 2 September 2007, leg. P. Benda.

Epomophorus pusillus is a fruit bat distributed widely in woodland savanna and forest zones of West and Central Africa from Senegal in the west to South Sudan and Ethiopia in the east, and to Angola, Zambia, and Tanzania in the south (Rosevear 1965, Hayman & Hill 1971, Monadjem et al. 2020). It is a very common bat of Benin, the second most frequently observed bat species (Appendix 1), and it is similarly common in the neighbouring countries (Happold 1987, Kangoyé et al. 2015, Amori et al. 2016). At least 30 localities of *E. pusillus* have been reported from Benin, scattered across the whole country area (Fig. 6; Robbins 1980, Green

Figs. 4, 5. Portraits of fruit bat males from Benin. 4 – *Epomophorus gambianus* from Koko. 5 – *Epomophorus pusillus* from Chute de Kota near Kota Monogou. All photos by Petr Benda or Zdeňka Bendová.



Figs. 6, 7. Distribution of bats in Benin; circles – published records (see Appendix 1), squares – new records. 6 – *Epomophorus pusillus*. 7 – *Rhinolophus fumigatus*.

1983, Bergmans 1989, 2002, Haquart & Rombaut 1995, Djossa 2007, Djossa et al. 2010, Van Cakenberghe & Seamark 2022). Interestingly, in northern Benin, this bat reaches the northern limits of its distribution range in the broader region of the Dahomey Gap (see Bergmans 1989, Thomas & Henry 2013b), although to the west and east of northern Benin, the range of *E. pusillus* reaches more northwards (Happold 1987, Kangoyé et al. 2015). The USNM specimen from Guéné in north-eastern Benin (Robbins 1980) represents the northernmost record in this range part, situated at the border between the zones of the Sudanese and Sahel savannas (Happold & Lock 2013).

The NMP specimens come from localities that do not represent a significant enlargement of the range in Benin, they only make the picture of distribution more accurate (Fig. 6). The final number of 33–34 records of *E. pusillus* from Benin aligns the knowledge of this bat from this country with the surrounding countries, viz. Togo (37 records; Amori et al. 2016), Burkina Faso (~30 records; Kangoyé et al. 2015), and/or Nigeria (27 records; Happold 1987). The dimensions of the adult NMP specimens of *E. pusillus* from Benin are shown in Table 1.

Rhinolophidae

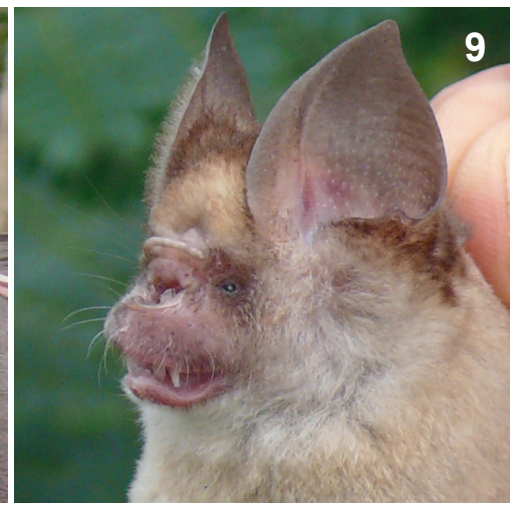
***Rhinolophus fumigatus* Rüppell, 1842**

Material (5). 3 ♂♂, 2 ♀♀ (NMP 91838–91841 [S+A], 91837 [A]; Fig. 8), Awaya, 10 km E of Dassa, 25 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

References. Benda & Vallo (2012), Demos et al. (2019), Benda (2021), Van Cakenberghe & Seamark (2022).

The distribution range of *Rhinolophus fumigatus* under its current taxonomic conception is very wide but patchy in the whole sub-Saharan Africa; it stretches across the savanna zones from Senegal to Eritrea and South Africa (Hayman & Hill 1971, Csorba et al. 2003, Cotterill & Happold 2013, Burgin et al. 2020). In West Africa, this bat is considered rather infrequent (Rosevear 1965, Happold 1987), it is more common in the Sudanese savanna zone of the inland countries than in more humid areas of the offshore countries. For instance, only one locality of *R. fumigatus* is available from Ghana (Grubb et al. 1998), three from Togo (Amori et al. 2016), and four from Benin (Robbins 1980, Djossa & Sinsin 2010), while roughly 13 localities are known from Burkina Faso (Kangoyé et al. 2015) and the same number of sites is available from Nigeria (Happold 1987). The majority of sites of this bat in the latter country lie in the relatively dry areas north of 9°10'N (Van Cakenberghe & Seamark 2022), in the zones of Guinean and Sudanese savannas (Happold & Lock 2013).

Although Robbins (1980) reported two sites and Djossa & Sinsin (2010) three additional localities of *R. fumigatus* from Benin, four records is the final number (Fig. 7). The USNM specimen from Bimbereke, referred to this bat by Robbins (1980) was re-identified as *R.* [cf.] *darlingi*, see Djossa (2007) and Van Cakenberghe & Seamark (2022). The NMP series of



Figs. 8, 9. Portraits of two bat species from Awaya near Dassa, Benin. 8 – *Rhinolophus fumigatus*. 9 – *Hipposideros abae*.

Table 2. Basic biometric data on the NMP specimens of *Rhinolophus fumigatus* and *Hipposideros jonesi* from Benin; data on the external dimensions of *H. jonesi* include also those of two specimens kept in the University of Abomey-Calavi, Benin. The values are in millimetres, for dimension abbreviations see Methods

dimension	*Rhinolophus fumigatus*					*Hipposideros jonesi*				
	n	**M**	min	max	SD	*n*	**M**	min	max	SD
LC	*5*	**63.4**	62	65	1.140	*8*	**52.9**	50	55	1.885
LCd	*5*	**26.6**	25	29	1.673	*8*	**21.8**	19	24	1.753
LAt	*5*	**49.04**	48.5	49.8	0.503	*8*	**46.68**	45.2	47.3	0.748
LA	*5*	**23.60**	23.1	24.3	0.447	*8*	**24.95**	23.2	25.8	0.907
LaFE	*5*	**9.08**	8.7	9.5	0.286	*8*	**7.34**	6.7	8.4	0.515
LCr	*4*	**21.70**	21.45	21.98	0.222	*4*	**18.04**	17.88	18.21	0.169
LCO	*4*	**20.89**	20.75	21.02	0.112	*5*	**17.67**	17.48	17.78	0.127
LCc	*4*	**18.27**	18.18	18.38	0.102	*5*	**15.50**	15.43	15.57	0.059
LaZ	*4*	**11.09**	10.95	11.14	0.095	*5*	**8.47**	8.42	8.51	0.034
LaI	*4*	**2.38**	2.20	2.48	0.125	*5*	**2.66**	2.54	2.82	0.113
LaInf	*4*	**5.59**	5.41	5.67	0.124	*5*	**4.78**	4.68	4.91	0.092
LaN	*4*	**8.80**	8.68	8.96	0.122	*5*	**8.15**	8.02	8.31	0.124
LaM	*4*	**9.94**	9.83	10.13	0.133	*5*	**9.78**	9.74	9.87	0.059
ANc	*4*	**6.75**	6.56	6.84	0.132	*5*	**5.38**	5.19	5.47	0.114
LBT	*4*	**3.50**	3.42	3.71	0.140	*5*	**3.19**	3.07	3.27	0.086
CC	*4*	**5.73**	5.65	5.77	0.055	*5*	**3.69**	3.59	3.78	0.077
M^3M^3	*4*	**8.03**	7.82	8.29	0.201	*5*	**5.74**	5.67	5.83	0.065
CM^3	*4*	**7.61**	7.44	7.72	0.131	*5*	**5.80**	5.74	5.84	0.043
LMd	*4*	**14.14**	13.98	14.26	0.118	*4*	**10.33**	10.17	10.38	0.105
ACo	*4*	**3.33**	3.23	3.44	0.101	*4*	**2.18**	2.11	2.23	0.049
CM_3	*4*	**8.22**	8.05	8.44	0.163	*4*	**6.14**	6.07	6.22	0.062

specimens of *R. fumigatus* from Awaya situated at the latitude of 7°47'N in the southern part of Benin thus represents the fifth record from the country and the southernmost record of this bat in the region of the Dahomey Gap (Fig. 7; see Cotterill & Happold 2013).

The dimensions of the NMP specimens of *R. fumigatus* from Benin are shown in Table 2. These specimens represent a unique morphotype, with extremely small body and skull size, on average smaller compared to the published data for this bat species (see Rosevear 1965, Koopman 1975, Bergmans 1977, Csorba et al. 2003, Thorn & Kerbis Peterhans 2009, Kangoyé et al. 2015, Cotterill & Happold 2013, etc.). Most of their dimensions lie on the lower margins of the published ranges or even beyond those given for *R. fumigatus* from West Africa and/or other parts of the distribution range. On the other hand, the available sequences of the mitochondrial gene for cytochrome *b* from the NMP specimens (Benda & Vallo 2012) are an integral part of the diversified *fumigatus/eloquens* lineage (composed of five to eight sublineages), the Beninese samples cluster closest with the sequences from the Central African Republic and Kenya (Demos et al. 2019).

This incongruity in morphometric and genetic variations shows, at least, a morphologic plasticity in *R. fumigatus* that is not reflected in the phylogenetic relationships of populations. However, the variation in various traits that suggests a hidden taxonomic diversity in this bat is

reported repeatedly (cf. Rosevear 1965, Csorba et al. 2003, Kangoyé et al. 2015, Demos et al. 2019) and still remains unresolved concerning the number of taxa (subspecies or even species), since the available evidence does not show any clear solution. A number of authors stressed a high level of variability in *R. fumigatus*, which is incomparable to other similar *Rhinolophus* species and requires a revision. We can only agree with such a view.

Hipposideridae

Hipposideros jonesi Hayman, 1947

Material (6). 5 ♂♂, 1 ♀ (NMP 91842–91844, 91846, 91847 [S+A], 91845 [A]), Awaya, 10 km E of Dassa, 25 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

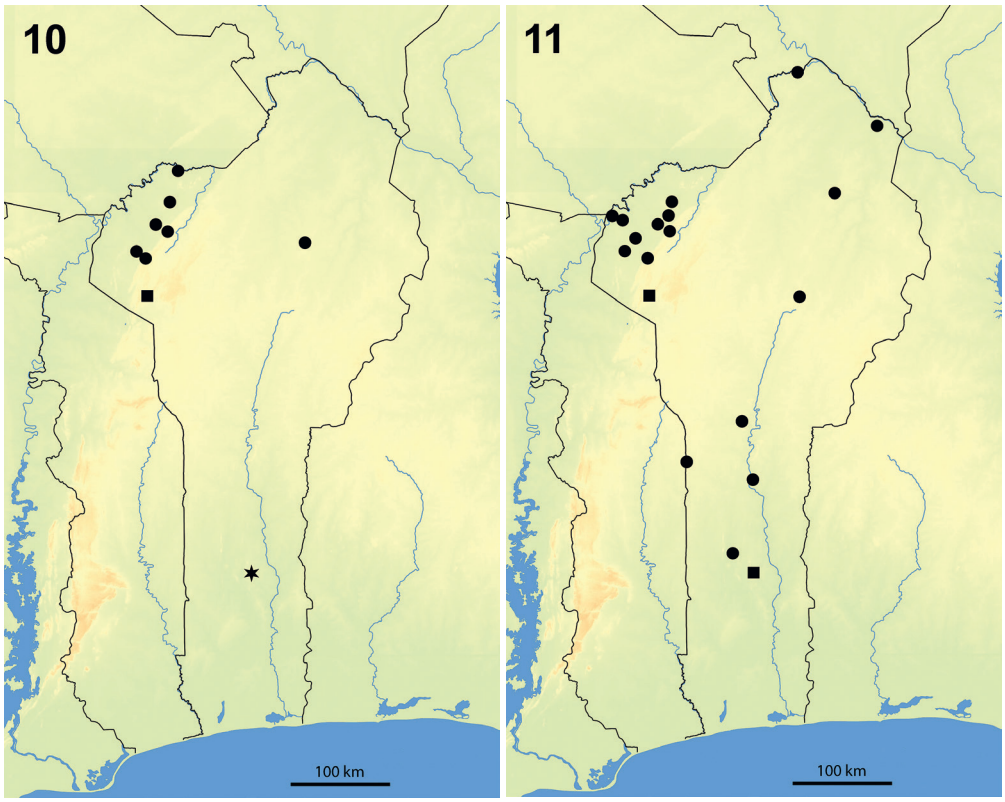
References. Vallo (2008), Vallo et al. (2008), Djossa & Sinsin (2010), Granjon & Birnbaum (2010), Monadjem et al. (2013), Patterson et al. (2020), Baldwin et al. (2021), Benda (2021), Van Cakenberghe & Seamark (2022).

Hipposideros jonesi is an endemic of West Africa, it is known from a limited number of localities in a wide belt of forest and savanna zones stretching from Senegal to Cameroon (Fahr 2013a, Burgin et al. 2020). In most of the countries of this belt, this bat is a rare species, known just from 1–2 records; only from Guinea, Ghana, and Burkina Faso, *H. jonesi* was reported from a higher number of sites (see Kangoyé et al. 2015, Nkrumah et al. 2021, Van Cakenberghe & Seamark 2022), while in Togo this bat remains unknown (Amori et al. 2016). The NMP series of specimens represents the first record of *H. jonesi* from Benin (see also Djossa & Sinsin 2010).

Within its whole range, *H. jonesi* was recorded most abundantly in the Sudanese savanna zone of southern Burkina Faso close to the northern border of Benin (nine localities, see Kangoyé et al. 2015). However, the only Beninese record does not come from the northern part of the country, adjacent to Burkina Faso, but from the border of the Guinean savanna and forest-savanna mosaic zones in the southern part of Benin (Fig. 10). Nevertheless, the closest record from Nigeria, from Idere (7°29'N, 3°15'E, Happold 1987; ca. 110 km E of Awaya) also originates from this transition between two biotic zones, similarly as the Beninese record (Happold & Lock 2013).

Kangoyé et al. (2015) reported one individual of *H. jonesi* from Burkina Faso with an orange-yellow colouration, while the other captured bats of this species were presumably of the typical greyish-brown colour phase as it is common in this bat (Rosevear 1965). All NMP specimens collected in Benin were of the latter colouration phase (pale greyish-brown), no orange-yellow bat was found.

The dimensions of the NMP specimens of *H. jonesi* from Benin are shown in Table 2. (The collected series was composed of eight bats, two males were deposited in the collection of the University of Abomey-Calavi, Benin. The NMP series thus comprises six remaining bats, while the external dimensions for Table 2 were taken from the complete series.) Fahr & Ebigbo (2003) discussed causality of the significant morphometric variation of *H. jonesi* documented across its distribution range (cf. Eisentraut & Knorr 1957, Hayman 1964, Koch-Weser 1984) and suggested environmental factors like seasonality or habitat humidity as possible drives of the size differences among populations. In this respect, the dimensions of the Beninese samples correspond to those reported in this bat from Burkina Faso by Kangoyé et al. (2015) and indicate the Beninese populations to represent a small- to medium-sized morphotype considering the dimension ranges of *H. jonesi* from its whole distribution range (Fahr 2013a).



Figs. 10, 11. Distribution of bats in Benin. 10 – *Hipposideros* spp.: circles – published data on *H.* cf. *ruber* (see Appendix 1), square – new record of *H.* cf. *ruber*, asterisk – locality of the first Beninese records of *H. jonesi*, *H. abae*, and *H.* cf. *lamottei*. 11 – *Nycteris macrotis*: circles – published records (see Appendix 1), squares – new records.

Hipposideros abae Allen, 1917

Material (2). 2 ♂♂ (NMP 91850, 91851 [S+A]; Fig. 9), Awaya, 10 km E of Dassa, 25 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

References. Vallo (2008), Vallo et al. (2008), Granjon & Birnbaum (2010), Monadjem et al. (2013), Baldwin et al. (2014), Weber et al. (2019), Patterson et al. (2020), Benda (2021), Liang et al. (2021), Rossoni et al. (2021), Benda et al. (2022), Van Cakenberghe & Seamark (2022).

Hipposideros abae is a rather rare bat with a wide distribution range that stretches across the forest and savanna zones from Guinea-Bissau and Sierra Leone in the west to north-western Ethiopia and northern Uganda in the east (Rosevear 1965, Hayman & Hill 1971, Kruskop et al. 2016). In most of the countries in this range, this species is an uncommon bat known from just a few (1–2) sites, and in Guinea, Liberia, Mali, and Niger, *H. abae* remains unknown

(Rainho & Franco 2001, Thorn & Kerbis Peterhans 2009, Happold 2013a, Van Cakenberghe & Seamark 2022). Only from Sierra Leone, Ghana, Nigeria, Central African Republic, and the Democratic Republic of the Congo, this bat is reported from five or more sites (Van Cakenberghe & Seamark 2022), and even nine localities are available from Burkina Faso (Kangoyé et al. 2015), the highest number per country.

The two NMP specimens reported here represent the first record of *H. abae* from Benin. In the region of the Dahomey Gap, *H. abae* is a rare bat with only two additional records available; one from southern Togo (Amousskopé; Amori et al. 2016) and one from south-eastern Ghana (Pinkwae Forest; Decher et al. 1997). All these localities lie in the zone of the forest-savanna mosaic (Happold & Lock 2013), the Beninese site being the northernmost one.

Two colour phases, greyish-brown and orange-yellow, are known in this bat species, similarly as in other rhinolophoid bats (Rosevear 1965). The pelage of the NMP specimens of *H. abae* from Benin is pale brown (Fig. 9), this colour tinge is closer to the fawn greyish-brown phase (usually being slightly darker) than to the orange-yellow phase, reported as the only colouration of this bat observed in Burkina Faso by Kangoyé et al. (2015). The dimensions of the NMP specimens are shown in Table 3.

Table 3. Basic biometric data on the NMP specimens of *Hipposideros abae*, *H.* cf. *lamottei*, *H.* cf. *ruber*, and *Nycteris macrotis* from Benin. The values are in millimetres, for dimension abbreviations see Methods

	Hipposideros abae		*Hipposideros* cf. *lamottei*		*Hipposideros* cf. *ruber*	*Nycteris macrotis*				
	♂	♀	♂	♀	♀					
	91850	91851	91849	91848	91879	*n*	**M**	min	max	SD
LC	71	71	55	57	59	*5*	**64.8**	62	67	1.924
LCd	34	31	35	33	23	*5*	**61.2**	56	65	3.271
LAt	60.5	60.5	54.3	52.5	50.5	*5*	**49.92**	48.3	51.6	1.268
LA	21.8	23.4	18.0	17.7	18.2	*5*	**33.88**	32.8	35.2	0.988
LT	–	–	–	–	–	*5*	**7.66**	7.5	8.0	0.230
LaFE	7.1	7.0	6.9	6.3	6.6	–	–	–	–	–
LCr	22.81	23.26	19.39	19.07	19.75	*4*	**21.47**	20.97	21.75	0.352
LCO	23.18	23.56	19.17	18.76	19.35	*4*	**21.63**	21.13	22.15	0.454
LCc	20.12	20.08	16.52	16.16	16.82	*4*	**19.05**	18.82	19.25	0.188
LaZ	13.67	13.67	10.48	10.25	11.11	*4*	**12.74**	12.31	13.21	0.369
LaI	3.15	2.98	2.98	2.97	3.21	*4*	**6.17**	5.92	6.47	0.230
LaP	–	–	–	–	–	*4*	**4.47**	4.08	4.77	0.306
LaInf	5.95	6.05	5.15	5.17	5.21	*4*	**5.76**	5.62	6.03	0.189
LaN	10.34	10.23	8.87	8.89	8.87	*4*	**9.20**	8.92	9.39	0.211
LaM	11.77	11.55	10.19	10.09	10.51	*4*	**9.27**	9.02	9.64	0.268
ANc	7.44	7.13	5.97	6.01	6.02	*4*	**7.62**	7.33	8.16	0.372
LBT	3.94	3.86	3.36	3.42	3.43	*4*	**3.67**	3.31	3.98	0.279
CC	6.17	6.37	4.55	4.62	5.17	*4*	**5.94**	5.77	6.02	0.118
M^3M^3	8.84	9.22	6.92	6.94	7.52	*4*	**8.36**	8.18	8.60	0.180
CM^3	8.78	8.86	6.74	6.67	7.24	*4*	**7.77**	7.67	7.86	0.078
LMd	15.58	15.58	12.23	11.76	12.73	*4*	**14.29**	13.88	14.74	0.368
ACo	4.39	4.02	2.96	2.87	3.03	*4*	**5.21**	4.90	5.43	0.223
CM_3	9.68	9.74	7.26	7.18	7.62	*4*	**8.32**	8.08	8.46	0.176

Hipposideros cf. *lamottei* Brosset, 1985

Material (2). 1 ♂, 1 ♀ (NMP 91848, 91849 [S+A]; Figs. 12, 13), Awaya, 10 km E of Dassa, 25 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

References. Vallo (2008), Vallo et al. (2008), Granjon & Birnbaum (2010), Monadjem et al. (2013), Baldwin et al. (2014, 2021), Weber et al. (2019), Arai & Yanagihara (2020), Patterson et al. (2020), Benda (2021), Benda et al. (2022), Van Cakenberghe & Seamark (2022).

The NMP specimens here mentioned as *Hipposideros* cf. *lamottei* are referred to this name by Patterson et al. (2020) and Baldwin et al. (2021), while other authors mentioned them as (the B1 sublineage of) *H. ruber* or *H.* aff. *ruber* (Vallo et al. 2008, Granjon & Birnbaum 2010, Monadjem et al. 2013, Baldwin et al. 2014, Weber et al. 2019, Arai & Yanagihara 2020, Benda 2021, Benda et al. 2022, Van Cakenberghe & Seamark 2022). These specimens represent the first and only confirmed record of the B1 sublineage of bats of the *Hipposideros caffer* group in Benin. Although the specimens most probably belong to a separate species, its phylogenetic position as well as its naming remain problematic and unresolved.

Vallo et al. (2008) first demonstrated the genetic variation in the *caffer* group, they analysed sequences of the mitochondrial gene for cytochrome *b* and found seven clades (lineages and sublineages) that potentially represent separate species, i.e. seven instead of two traditionally recognised in the group, *H. caffer* and *H. ruber*. However, only two clades could be coidentified with proper species, the A1 sublineage with *H. caffer* (Sundevall, 1846) and A2 sublineage with *H. tephrus* Cabrera, 1906, while the taxonomic affiliations of the other clades remained unclear.

According to Vallo et al. (2008), the bats belonging to the B1 sublineage are distributed only in West Africa – two samples/haplotypes were identified in Benin, one sample in southern Senegal – and genetically they are sufficiently distant from the other lineages to be considered a separate species (K2P distance): >8.4% from the other lineages (A, C, D) and 5.1–7.0% from the B2 sublineage detected in East Africa. Monadjem et al. (2013), who first employed sequences of *H. lamottei* (from Mount Nimba in Guinea, the type locality of this species), showed the B lineage to be the closest related to *H. lamottei* s.str. They reported the following K2P distances of this species: 5.2–6.4% from the B2 sublineage, 6.0–6.4% from the B1 sublineage, and >9.0% from other lineages. Although the species status and extent of distribution range of *H. lamottei* were discussed or even questioned several times (see Koopman 1989, Koopman et al. 1995, Grubb et al. 1998, Fahr & Ebigbo 2003, Decher & Fahr 2007, Fahr 2013b), the results by Monadjem et al. (2013) supported it to be regarded a species of its own. The former relativisations of the full species status of *H. lamottei* consisted in the unclear morphologic definition of the species sensu Brosset (1985) and thus, its easy confusion with *H. ruber* s.l. and/or *H. fuliginosus* (Temminck, 1853).

The B lineage sensu Vallo et al. (2008) combines the bats characterised traditionally as *H. ruber* s.l. (Benin, Malawi) and *H. caffer* s.l. (Senegal, Kenya, Zanzibar) based on their morphometry, similarly as the C lineage, while the D lineage conformed only to *H. ruber* s.l. (and the A lineage to *H. caffer* s.l., see above). Since the B lineage was demonstrated to be closely positioned to *H. lamottei* in genetic characters, Monadjem et al. (2013) added the morphologic differences and diagnostic traits allowing to distinguish between *H. lamottei* and *H. ruber* s.l., i.e. the bats belonging to the lineages B, C, and D, sensu Vallo et al. (2008). Monadjem et al. (2013: 349–350) wrote as follows: "What distinguishes this species [= *H. lamottei*] is the combination of the following features: large forearm length (generally >55 mm), large mastoid

breadth (generally >10.0 mm), and delicate molars leading to a narrow M^3–M^3 breadth (generally 6.5–6.9 mm). […] The B1 specimens (from Benin) appear to have similar cranial dimensions ([LCc]: 16.2–16.5 mm, and [LaZ]: 10.3–10.5 mm, compared with those of *H. lamottei* […], however, the forearm lengths of the Benin bats are significantly shorter (52.5–54.3 mm; Vallo *et al*., 2008) compared with those of *H. lamottei* from Mount Nimba ([mean]=56.0 mm[, range 54.5–56.8 mm] and SD=0.88 mm, *n*=9)." Fahr (2013b: 390) defined the differences between *H. lamottei* (*Hl*) and *H. ruber* s.l. (*Hr*) as follows: body size larger in *Hl*, smaller in *Hr*, LAt 55–57 mm, mean 55.8 mm in *Hl*, 47–55 mm, mean 51.1 mm in *Hr*; skull relatively smaller in *Hl* than in *Hr*, LCO 18.9–19.6 mm, mean 19.2 mm, 34–35% of LAt in *Hl*, 17.8–20.3 mm, mean 19.1 mm, 35–41% of LAt in *Hr*; zygomatic width smaller than mastoid width in *Hl*, larger in *Hr*; dentition weak in *Hl*, strong in *Hr*.

The dimensions of the NMP specimens of *H*. cf. *lamottei* from Benin are shown in Table 3. Considering the above list of metric characters by Monadjem et al. (2013) and Fahr (2013b), two ratios have to be added to the available plain values in Table 3 concerning the two NMP bats: LCO/LAt 35.3% and 35.7%; and LaZ/LaM 101.6% and 102.8%. Regarding the diagnostic characters by the above authors, the morphometric data show the Beninese NMP bats to represent a morphological transition between *H. ruber* s.l. and *H. lamottei*, rather than one of these morphotypes. Their clear identification based on the morphometric comparison is not possible, moreover, considering certain shift in values caused by a different way of measuring by different authors. Although additional differences between *H. lamottei* and *H. ruber* s.l. were found in echolocation call parameters in Guinea (Monadjem et al. 2013), such evidence is not available from Benin. The pelage colouration of the Beninese specimens is dark brown (Figs. 12, 13), similar to that reported for *H. lamottei* (Fahr 2013b).

Considering solely the phylogenetic position of the B1 sublineage, Patterson et al. (2020) labelled it *H.* cf. *lamottei*, apparently stressing its sister position to *H. lamottei* s.str., however,

Figs. 12, 13. Portraits of *Hipposideros* cf. *lamottei* from Awaya near Dassa, Benin.

without any explanation or additional discussion. Baldwin et al. (2021), who found the B1 sublineage in bats from central Ghana, also used this assignation for it. However, these authors added as follows (p. 10): "Labeling the forest clades of West Africa as cf. *lamottei* also may not be appropriate given that *H. lamottei* is a unique species located in the montane savannah habitats of Mt. Nimba and is morphologically distinct from populations represented by the phylogenetically related B sublineages of West and East Africa […]."

Although we do not consider the morphological differences between the B1 sublineage / *H.* cf. *lamottei* from Benin and *H. lamottei* to be sufficiently distinct to be taken into account, as both morphotypes are almost identical (see above), the mutual phylogenetic position of these two clades is not yet resolved (the known genetic distances between the limited samples support rather their species statuses, see above). Thus, the real taxonomic affiliation of the B1 sublineage remains open and additional sampling with a larger geographic coverage is necessary to define its morphologic and genetic limits. Thus, we suggest to use the term *H*. cf. *lamottei* just as a technical assignation of the taxon representing a peculiar clade, that is either a part of the species *H. lamottei* (as a subspecies or just a group of populations) or belongs to a yet undescribed species of its own.

Hipposideros cf. *ruber* (Noack, 1893)

Material (1). 1 ♀ (NMP 91879 [S+A]), Tagayé, 15 km SW of Natitingou, 30 August 2007, leg. P. Benda, B. Djossa, A. Konečný & R. Šumbera.

References. Vallo (2008), Vallo et al. (2008, 2011a), Granjon & Birnbaum (2010), Opoku (2016), Baldwin et al. (2021), Benda (2021), Mamba et al. (2021), Benda et al. (2022), Van Cakenberghe & Seamark (2022).

Hipposideros cf. *ruber* is a parataxon comprising several separate species possessing the *ruber* morphotype of the *H. caffer* group sensu Koopman (1975), defined as the large-sized bats of the group with the condylocanine length of skull larger than 15.5 mm (see also Vallo et al. 2008). At least two of these species occur in West Africa in sympatry, besides the third one, *H*. cf. *lamottei* discussed above (see there and Vallo et al. 2008, 2011a, Baldwin et al. 2021, Mamba et al. 2021).

The bats conforming to the *ruber* morphotype are distributed broadly across the forest and woodland savanna zones of sub-Saharan Africa, from the Gambia and Sierra Leone to Ethiopia, Angola, and Mozambique (Hayman & Hill 1971, Happold 2013b). Despite the broad and common occurrence in other countries of West Africa, in Benin this bat has remained unknown for a long time; Bergmans (2002) and Capo-Chichi et al. (2004) did not report any record from the country (although one record was available at that time, Green (1983) described a finding of a large colony in the Pendjari Hotel, Pendjari NP, under the name *H. caffer guineensis*).

Until now, seven sites of occurrence of *H.* cf. *ruber* were published from Benin (Green 1983, Djossa 2007, Van Cakenberghe & Seamark 2022), all situated in the north-western part of the country adjacent to the Pendjari protected areas (Fig. 10). The NMP specimen of this parataxon comes from the southernmost site in Benin, although not far from other locations (Fig. 10). However, only the NMP specimen was examined with the help of molecular genetic methods and it was found to pertain to the D lineage by Vallo et al. (2008). It is thus the only genetic lineage known from the country, although also other clades comprising the *ruber* morphotype could be distributed in northern Benin, e.g. the C1 sublineage known from Burkina Faso (Kangoyé et al. 2015).

The D lineage comprises only the bats of the *ruber* morphotype and besides Benin, it was detected also in Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, and Burkina Faso (Vallo et al. 2008, 2011a, Kangoyé et al. 2015, Weber et al. 2019, Patterson et al. 2020, Mamba et al. 2021). After some 15 years of investigation and examinations of hundreds of samples of the *caffer* group originating from throughout Africa (cf. Patterson et al. 2020, Baldwin et al. 2021), this lineage seems to be restricted to the western part of the forest and savanna zones of West Africa from Senegal to Benin, the Beninese locality being the eastern-most point of the known range.

No name is available for the bats of the *ruber* morphotype from this limited range (Allen 1939, Simmons 2005). The name *rubra* Noack, 1893 is based on a bat from East Africa and it is not clear whether this name could be assigned to any of the genetic lineages detected in West Africa, similarly as other names associated with this morphotype, *centralis* Andersen, 1906, *guineensis* Andersen, 1906, and *niapu* Allen, 1917 (see Simmons 2005, Vallo et al. 2008, Patterson et al. 2020). Only one name was created based on bats of the *caffer* group from West Africa, *Hipposideros braima* Monard, 1939, described from Guinea-Bissau (Monard 1939). However, this name is assigned to the *caffer* morphotype (Aellen 1956, Simmons 2005) and seems to be not applicable for naming of the D lineage. Although this topic still needs an additional research, the current level of knowledge indicates that this lineage could represent a well defined and undescribed taxon.

The dimensions of the NMP specimen of *H.* cf. *ruber* from Benin are shown in Table 3. The plain values and the additional ratios (LCO/LAt 38.3%; LaZ/LaM 105.7%) show this bat to pertain to a morphotype well corresponding with the definition of *H. ruber* s.l. by Monadjem et al. (2013) and Fahr (2013b), see under *H.* cf. *lamottei*. The pelage colouration of the NMP specimen of *H.* cf. *ruber* is bright orange.

N y c t e r i d a e

Nycteris macrotis Dobson, 1876

Material (5). 2 ♂♂, 1 ♀ (NMP 91834, 91835 [S+A], 91836 [A]; Figs. 14, 15), Awaya, 10 km E of Dassa, 25 August 2007, leg. P. Benda, A. Konečný & R. Šumbera;
1 ♂, 1 ♀ (NMP 91877, 91878 [S+A]), Tagayé, 15 km SW of Natitingou, 30 August 2007, leg. P. Benda, B. Djossa, A. Konečný & R. Šumbera.

Nycteris macrotis is a widely distributed slit-faced bat, its range covers a large part of sub-Saharan Africa in several extensive patches from Senegal in the west to the Sudan and Somaliland in the east, and Botswana and Mozambique in the south (Hayman & Hill 1971, Van Cakenberghe & De Vree 1985, Burgin et al. 2020). In West Africa, the continuous range of this bat stretches from the Gambia, Mauritania, and Sierra Leone to western Chad and Cameroon (Van Cakenberghe & De Vree 1985, Benda et al. 2011). In Benin, *N. macrotis* belongs to the most common bats, at least 18 localities are spread over most of the country area except the southern regions (Fig. 11; Robbins 1980, Van Cakenberghe & De Vree 1985, Haquart & Rombaut 1995, Bergmans 2002, Djossa 2007, Van Cakenberghe & Seamark 2022). It is similarly common in the neighbouring countries – in Togo, Burkina Faso, and Benin, *N. macrotis* is the most common slit-faced bat, while in Nigeria it is the second most common one (Happold 1987, Kangoyé et al. 2015, Amori et al. 2016). Two sites of origin of the NMP specimens increase the number of records of this bat in Benin to 20–21 localities (see Appendix 1). However, they

Figs. 14, 15. Portraits of *Nycteris macrotis* from Awaya near Dassa, Benin.

do not represent an important contribution to the distribution picture of *N. macrotis* (Fig. 11) that becomes the fifth most frequent bat species of the country.

The dimensions of the NMP specimens of *N. macrotis* from Benin are shown in Table 3. The pelage colouration slightly differed between specimens from the two localities, the Awaya bats were dark cinnamon brown (Figs. 14, 15) and the Tagayé bats were greyish-brown; no orange-yellow phase was observed (contra Kangoyé et al. 2015).

M o l o s s i d a e

***Chaerephon pumilus* (Cretzschmar, 1830)**

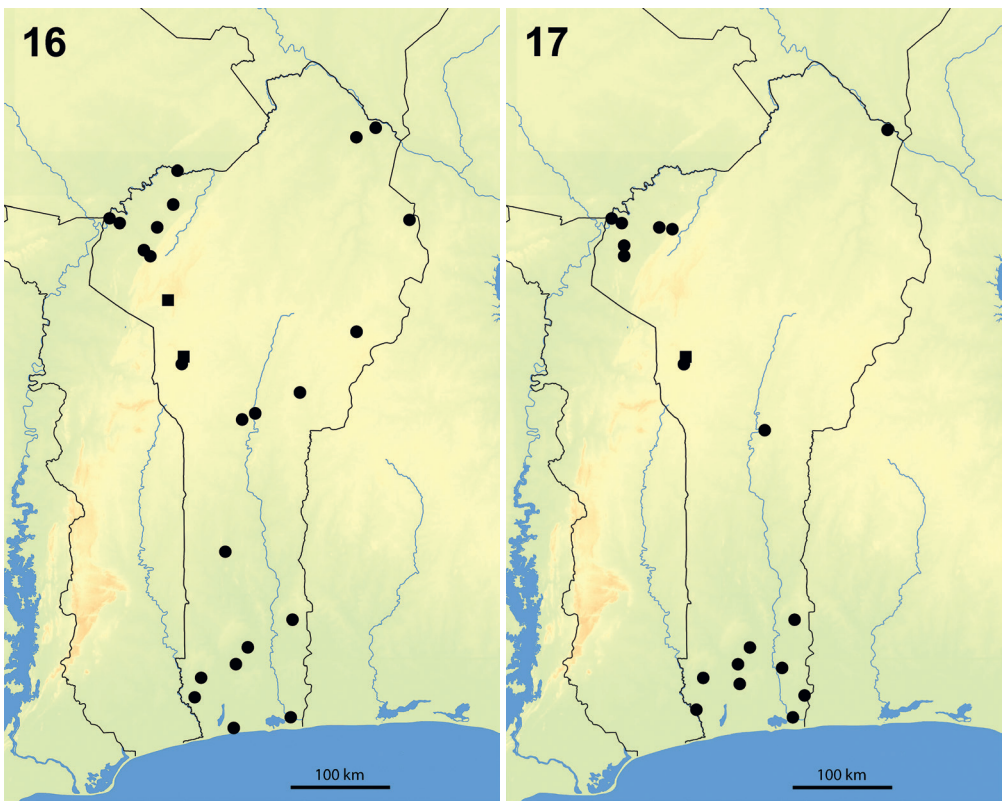
Material (9). 2 ♂♂, 1 ♀ (NMP 91885, 91886 [S+A], 91884 [A]), Chute de Kota, 5 km S of Kota Monogou, 1 September 2007, leg. P. Benda;
4 ♂♂, 2 ♀♀ (NMP 91867–91871 [S+A], 91872 [A]; Figs. 18, 19), Djougou, NW margin of the town, 28 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

Bats traditionally assigned to *Chaerephon pumilus* are currently considered a complex composed of several species (Goodman et al. 2010, Naidoo et al. 2016, Monadjem et al. 2020). However, the phylogenetic relations within the complex as well as its taxonomic arrangement still remain to be resolved. If the complex really comprises more species, there is a high probability that the name *C. pumilus* is not applicable for the populations from a big part of sub-Saharan Africa (Naidoo et al. 2016), although the status of West African populations has not been examined yet.

The morphotype of *C. pumilus* s.l. ranks among the most common and widespread bat forms in the Afrotropics except the southern Sahara and the arid regions of south-western Africa

(Hayman & Hill 1971, Bouchard 1998). In Benin, this bat is the most frequently recorded representative of the molossid family, it was reported from 23 sites scattered across the whole country (Fig. 16; De Vree 1971, Robbins 1980, Green 1983, Bergmans 2002, Bekker & Ekué 2004, Djossa 2007, Djossa et al. 2010, Van Cakenberghe & Seamark 2022). Similarly, *C. pumilus* s.l. is reported as the most common free-tailed bat in three neighbouring countries, Togo, Burkina Faso, and Nigeria (Happold 1987, Kangoyé et al. 2015, Amori et al. 2016). The localities of two NMP series of Beninese specimens are situated within the known range in the country and do not represent an important contribution to the distribution picture of this common bat (Fig. 16).

The dimensions of the NMP specimens of *C. pumilus* s.l. from Benin are shown in Table 4. A genetic analysis of the mitochondrial ND1 gene showed these specimens to be in agreement by 97.6–98.9% (mean 98.5%) with the haplotype referred to *C. pumilus* from Uganda (sensu Ammerman et al. 2012).



Figs. 16, 17. Distribution of bats in Benin; circles – published records (see Appendix 1), squares – new records. 16 – *Chaerephon pumilus*. 17 – *Mops condylurus*.


Figs. 18, 19. Portraits of *Chaerephon pumilus* from Djougou, Benin.

Mops condylurus (Smith, 1833)

Material (4). 2 ♂♂, 2 ♀♀ (NMP 91873, 91874, 91876 [S+A], 91875 [A]; Fig. 20), Djougou, NW margin of the town, 28 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

Mops condylurus represents one of the most common savanna bats of sub-Saharan Africa (Hayman & Hill 1971, Happold 2013c). The continuous range of *M. condylurus* in West Africa stretches from the Gambia and Guinea to northern Cameroon and western Central African Republic (Rosevear 1965, Bakwo Fils et al. 2014, Burgin et al. 2020). This bat is a very common species in the region of the Dahomey Gap and second most frequently found molossid bat of Togo and Nigeria (Happold 1987, Amori et al. 2016). In Benin, *M. condylurus* is similarly abundant, it is the second most common species of the family there and sixth most common bat species in general, at least 18 record sites are known to be spread across the whole country (Fig. 17; Robbins 1980, Bergmans 2002, Bekker & Ekué 2004, Djossa 2007, Djossa et al. 2010, Van Cakenberghe & Seamark 2022). The NMP specimens of *M. condylurus* originating from near Djougou in western Benin do not contribute significantly to a more precise picture of the species distribution (Fig. 17), since this bat was documented from this area already by Robbins (1980). The dimensions of the NMP specimens from Benin are shown in Table 4.

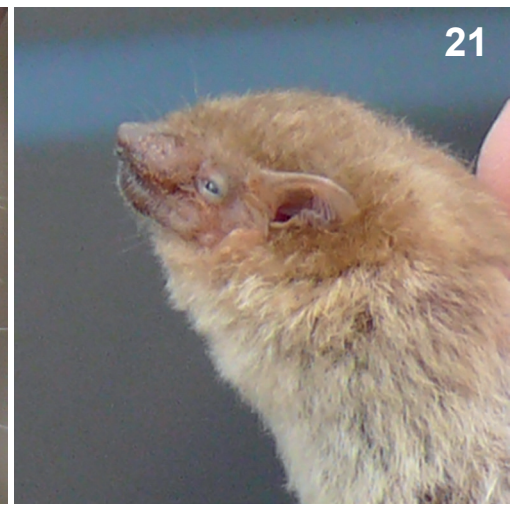
Vespertilionidae

Pseudoromicia rendalli (Thomas, 1889)

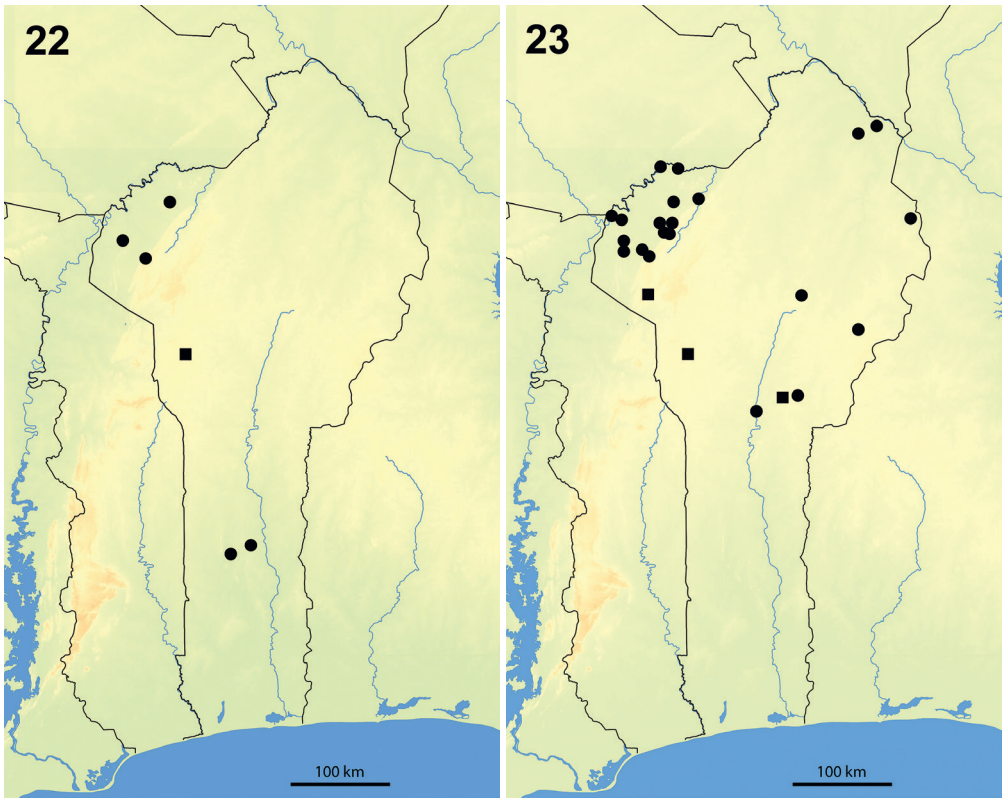
Material (1). 1 ♀ (NMP 91866 [S+A]; Fig. 21), Djougou, NW margin of the town, 28 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

Table 4. Basic biometric data on the NMP specimens of Molossidae bats from Benin. The values are in millimetres, for dimension abbreviations see Methods

dimension	*Chaerephon pumilus*					*Mops condylurus*				
	n	**M**	min	max	SD	*n*	**M**	min	max	SD
LC	*9*	**57.1**	55	60	1.537	*4*	**77.3**	75	79	1.708
LCd	*9*	**28.8**	27	31	1.394	*4*	**40.5**	38	43	2.082
LAt	*9*	**36.30**	34.5	37.6	1.072	*4*	**48.90**	47.2	50.8	1.865
LA	*9*	**17.93**	17.2	19.1	0.568	*4*	**21.50**	19.9	22.7	1.178
LT	*9*	**3.52**	2.9	4.1	0.349	*4*	**3.83**	3.2	4.4	0.665
LCr	*7*	**15.62**	15.26	16.01	0.301	*3*	**20.92**	20.74	21.12	0.191
LCb	*7*	**14.59**	14.16	14.98	0.267	*3*	**18.79**	18.65	18.98	0.171
LaZ	*7*	**9.72**	9.27	10.09	0.273	*3*	**13.41**	13.33	13.54	0.112
LaI	*7*	**3.52**	3.39	3.63	0.091	*3*	**4.58**	4.52	4.65	0.066
LaInf	*7*	**4.33**	4.00	4.57	0.176	*3*	**5.73**	4.99	6.11	0.638
LaN	*7*	**8.13**	7.82	8.40	0.206	*3*	**10.72**	10.56	10.93	0.190
LaM	*7*	**9.31**	9.09	9.56	0.157	*3*	**12.44**	12.33	12.53	0.103
ANc	*7*	**5.56**	5.32	5.81	0.157	*3*	**7.50**	7.41	7.66	0.137
LBT	*7*	**3.46**	3.32	3.61	0.111	*3*	**3.88**	3.81	3.91	0.058
CC	*7*	**4.35**	4.10	4.50	0.139	*3*	**6.12**	6.09	6.17	0.044
M^3M^3	*7*	**7.19**	6.84	7.43	0.204	*3*	**9.24**	9.14	9.33	0.095
CM^3	*7*	**5.91**	5.75	6.02	0.113	*3*	**7.82**	7.76	7.94	0.104
LMd	*7*	**10.19**	9.96	10.45	0.196	*3*	**14.19**	14.04	14.28	0.133
ACo	*7*	**2.79**	2.73	2.86	0.053	*3*	**3.94**	3.79	4.11	0.162
CM_3	*7*	**6.23**	5.94	6.47	0.168	*3*	**8.58**	8.53	8.61	0.044



Figs. 20, 21. Portraits of two bat species from Djougou, Benin. 20 – *Mops condylurus*. 21 – *Pseudoromicia rendalli*.



Figs. 22, 23. Distribution of bats in Benin; circles – published records (see Appendix 1), squares – new records. 22 – *Pseudoromicia rendalli*. 23 – *Scotophilus leucogaster*.

The recently described bat genus *Pseudoromicia* Monadjem, Patterson, Webala et Demos, 2021, endemic to tropical Africa, contains at least ten species (Monadjem et al. 2021, Grunwald et al. 2023, Juste et al. 2023) and among them, *P. rendalli* has the broadest distribution. Its range stretches across the savanna zones from the Gambia and Siera Leone in the west, to the Sudan in the east, and northern Botswana and eastern South Africa in the south (Rosevear 1965, Hayman & Hill 1971, Monadjem et al. 2020). It is widely distributed in the Dahomey Gap, several records are known from both Togo and Nigeria (Happold 1987, Amori et al. 2016, Van Cakenberghe & Seamark 2022), while it was documented only marginally in southern Burkina Faso, where just a single bat was found (Kangoyé et al. 2015). In the region of the Gap, most of the records are known from Benin, where five localities of *P. rendalli* are available from two separate areas, northern and southern (Fig. 22; Robbins 1980, Djossa 2007, Van Cakenberghe & Seamark 2022). The locality of the NMP specimen lies between these two regions, suggesting a continuous distribution all over the country or at least its whole western part (Fig. 22).

The dimensions of the NMP specimen of *P. rendalli* from Benin are shown in Table 5; the data correspond to those given for this species by Grunwald et al. (2023). A genetic analysis of the mitochondrial 16S gene showed the Beninese NMP specimen to be in agreement by 99.5% with the haplotype referred to *P. rendalli* from Kenya (sensu Hoofer & Van Den Bussche 2003).

Scotophilus nigrita (Schreber, 1774)

Material (1). 1 ♂ (NMP 91889 [S+A]), Manigri, 6 km SE of Bassila, 2 September 2007, leg. P. Benda.

References. Vallo et al. (2015), Demos et al. (2018), Van Cakenberghe & Seamark (2022).

Scotophilus nigrita is a broadly distributed bat known from the savanna zones of sub-Saharan Africa from Senegal to the Sudan and Mozambique (Rosevear 1965, Hayman & Hill 1971, Robbins et al. 1985). However, its records are very rare throughout this range, De Vree (1973) listed just nine localities from the continent, Robbins et al. (1985) 14 sites, and Bakwo Fils et al. (2012: 56) marked 23 sites of *S. nigrita* on their map of Africa. Most recently, Van Cakenberghe & Seamark (2022) listed 44 record localities of this bat in total, but spread over an enormous area of 21 countries. In West Africa, *S. nigrita* is known from nine countries in

Table 5. Basic biometric data on the NMP specimens of Vespertilionidae bats from Benin. The values are in millimetres, for dimension abbreviations see Methods

	Pseudoromicia rendallii	*Scotophilus nigrita*			*Scotophilus leucogaster*			*Scotophilus nigritellus*	*Scotophilus livingstonii*
	91866 ♀	91889 ♂	n	**M**	min	max	SD	91857 ♀	91890 ♂
LC	53	125	*11*	**77.0**	74	80	1.844	67	84
LCd	43	90	*11*	**55.5**	51	61	2.544	47	64
LAt	36.4	87.8	*11*	**52.23**	49.7	53.8	1.243	42.9	58.1
LA	13.6	25.8	*11*	**17.27**	16.8	17.8	0.323	16.0	21.4
LT	4.6	10.8	*11*	**8.10**	7.5	8.8	0.397	7.5	8.7
LCr	13.07	31.08	*7*	**18.81**	18.12	19.23	0.486	16.54	21.04
LCb	12.43	27.67	*7*	**17.66**	16.75	19.18	0.782	15.26	19.75
LaZ	8.78	21.04	*7*	**13.50**	13.09	13.87	0.272	11.91	15.24
LaI	3.74	6.75	*7*	**4.86**	4.69	5.03	0.133	4.18	4.92
LaInf	4.05	10.74	*7*	**6.69**	6.46	6.93	0.166	5.67	7.24
LaN	6.76	13.44	*7*	**9.27**	9.02	9.51	0.158	8.44	10.24
LaM	7.68	17.41	*7*	**11.99**	11.58	12.34	0.250	10.02	12.78
ANc	4.59	12.44	*7*	**8.26**	7.81	8.62	0.367	6.68	9.42
LBT	2.97	5.18	*7*	**4.00**	3.79	4.14	0.121	3.47	4.58
CC	4.09	10.68	*7*	**6.48**	6.26	6.69	0.153	5.51	7.55
M^3M^3	6.02	13.22	*7*	**8.43**	8.22	8.57	0.117	7.44	9.47
CM^3	4.68	11.52	*7*	**6.63**	6.27	6.89	0.204	5.87	7.18
LMd	9.55	28.04	*7*	**13.79**	13.48	14.13	0.261	12.06	15.84
ACo	3.07	9.66	*7*	**5.57**	5.33	5.75	0.136	4.73	6.43
CM^3	5.08	13.47	*7*	**7.61**	7.28	7.86	0.195	6.50	8.27

a belt from Senegal to Cameroon – it is a region with the most abundant evidence of this bat (Van Cakenberghe & Seamark 2022).

Bergmans (2002) and Capo-Chichi et al. (2004) did not report *S. nigrita* as a part of the fauna of Benin, although already Robbins et al. (1985: 71) mentioned one MNHN specimen from "Benin, no specific locality". As the former authors perhaps could expect an error in the country assignation, confusing the country of Benin with Benin City in Nigeria, and refused to mention the specimen, it remained overlooked. However, since Van Cakenberghe & Seamark (2022) reported the respective MNHN specimen as labelled to originate in Dahomey, an old name of the country of Benin, the Beninese occurrence of *S. nigrita* is clear, albeit not accurately located (although Djossa & Sinsin 2010 reported it erroneously to originate from Porto-Novo). However, the here presented NMP specimen from Manigri represents a clear and first exactly localised record of this bat species from Benin. The region of the Dahomey Gap is an area of a rather dense occurrence of *S. nigrita*, besides two Beninese specimens, two records were made in Togo (Amori et al. 2016), and three sites are available from south-western Nigeria (Happold 1987). On the other hand, no record of *S. nigrita* is known from Burkina Faso (Kangoyé et al. 2015). Anyway, the Dahomey Gap harbours more than ten percent of localities of this bat.

The dimensions of the NMP specimen of *S. nigrita* from Benin are shown in Table 5, some of them were published already by Vallo et al. (2015).

Scotophilus leucogaster (Cretzschmar, 1830)

Material (11). 5 ♂♂, 3 ♀♀ (NMP 91858–91861, 91864 [S+A], 91862, 91863, 91865 [A]), Djougou, NW margin of the town, 28 August 2007, leg. P. Benda, A. Konečný & R. Šumbera;
1 ♀ (NMP 91880 [S+A]), Tagayé, 15 km SW of Natitingou, 30 August 2007, leg. P. Benda, B. Djossa, A. Konečný & R. Šumbera;
2 ♂♂ (NMP 91853 [S+A], 91854 [A]; Figs. 24, 25), Tourou, 10 km W of Parakou, 26 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

References. Vallo et al. (2013), Demos et al. (2018), Van Cakenberghe & Seamark (2022).

Scotophilus leucogaster is one of the most common microbats of the dry savanna zones of the Afrotropics, where its distribution range comprises two separate patches (Robbins et al. 1985). The northern patch stretches across the savannas south of the Sahara from Mauritania and Sierra Leone to the Sudan, Yemen, and Kenya, the southern one comprises the savannas of the central part of southern Africa (Van Cakenberghe & Happold 2013a, Burgin et al. 2020). A continuous belt of abundant occurrence of *S. leucogaster* in West Africa was documented in the Guinean and Sudanese savanna zones (cf. Happold & Lock 2013) between northern Ghana and western Burkina Faso in the west and northern Cameroon and western Chad in the east (Van Cakenberghe & Seamark 2022). This bat is very common in the Dahomey Gap, in most of the countries it is one of the commonest bat species (see Happold 1987, Grubb et al. 1998, Amori et al. 2016) and in Burkina Faso, it is the most widespread and the second most frequently recorded bat in general (Kangoyé et al. 2015). In Benin, *S. leucogaster* is the third most common bat (Appendix 1), 23 record sites were reported from the relatively dry northern part of the country (Fig. 23; Robbins 1980, Haquart & Rombaut 1995, Djossa 2007, Van Cakenberghe & Seamark 2022), corresponding with the geographical extent of the Guinean and Sudanese savanna zones and north of the forest-savanna mosaic zone (Happold & Lock 2013). The three localities of here presented NMP specimens complete the picture of distribution of this bat in Benin (Fig. 23). The dimensions of the NMP Beninese specimens of this bat are shown in Table 5.

Figs. 24, 25. Portraits of *Scotophilus leucogaster* from Tourou near Tarakou, Benin.

Scotophilus nigritellus de Winton, 1899

Material (1). 1 ♀ (NMP 91857 [S+A]; Figs. 28, 29), Koko, 11 km NW of Alafiarou, 27 August 2007, leg. P. Benda, A. Konečný & R. Šumbera.

References. Vallo et al. (2013, 2019), Demos et al. (2018), Van Cakenberghe & Seamark (2022).

Scotophilus nigritellus is a species endemic to West Africa (Vallo & Van Cakenberghe 2017). However, formerly this species was regarded as a part of *S. viridis* (Peters, 1852), which used to be considered a broadly distributed African savanna bat (see e.g., Robbins et al. 1985, Happold 1987, Koopman 1993, Simmons 2005, Van Cakenberghe & Happold 2013b, Kangoyé et al. 2015, or Amori et al. 2016), merely as a synonym or at a level of subspecies (see Van Cakenberghe & Happold 2013b). Recently, with the help of the molecular genetic approaches, the species rank of *S. viridis* was split into three separate savanna species that live in allopatry, *S. viridis* s.str in southern and eastern Africa, *S. nigritellus* in West Africa, and *S. altilis* Allen, 1914 in north-eastern Africa (Trujillo et al. 2009, Vallo et al. 2013, 2019, Demos et al. 2018), although some authors regarded the species rank for *S. nigritellus* even earlier (see e.g., Koopman et al. 1978, Robbins 1980, or Grubb et al. 1998).

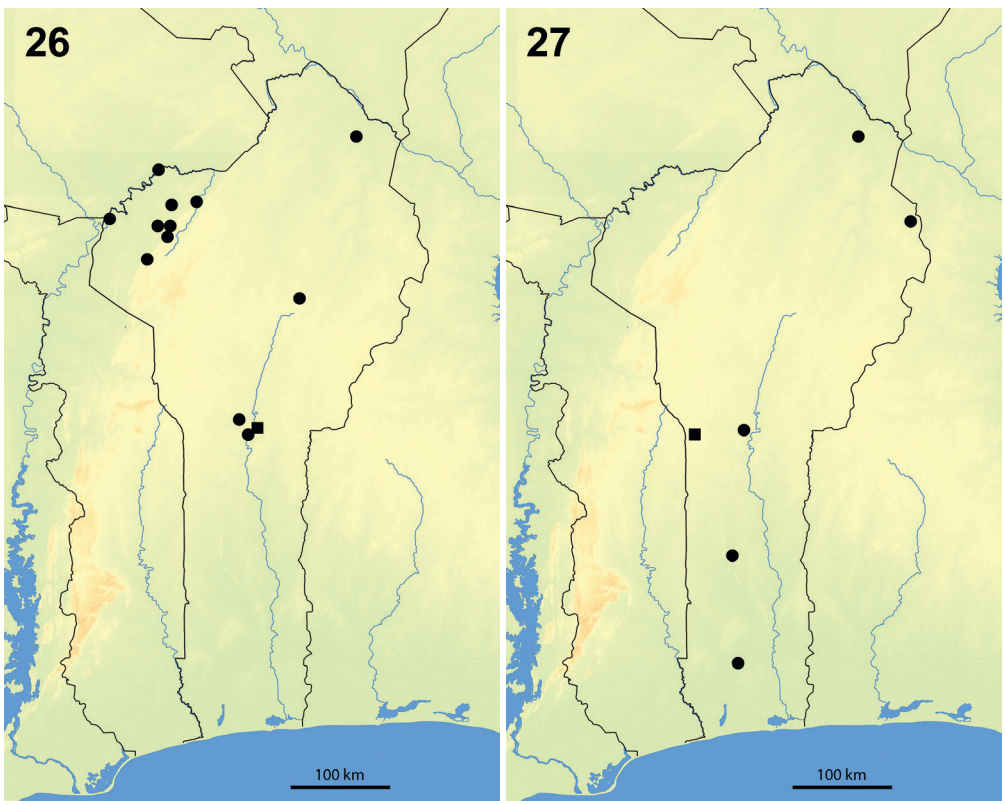
Scotophilus nigritellus is a common bat in West Africa, its range stretches across the savanna belt from Senegal to Cameroon (Van Cakenberghe & Seamark 2022). It was reported from all countries of the Dahomey Gap, although mostly under alternative names (Happold 1987, Grubb et al. 1998, Kangoyé et al. 2015, Amori et al. 2016). In Burkina Faso, *S. nigritellus* is the second most frequently recorded member of the genus and a similar frequency of records is available also from Benin (see Appendix 1). Twelve sites of this bat are known from the relatively dry northern part of the country, similarly as in the previous species (Fig. 26; Robbins 1980, Haquart & Rombaut 1995, Djossa 2007). The locality of the NMP specimen of *S. nigritellus* reported here does not represent an important occurrence spot, since from two sites in the same

area this bat was already mentioned by Djossa (2007), see Fig. 26. The dimensions of the NMP specimen of *S. nigritellus* from Benin are shown in Table 5.

Scotophilus livingstonii Brooks et Bickham, 2014

Material (1). 1 ♂ (NMP 91890 [S+A]), Manigri, 6 km SE of Bassila, 2 September 2007, leg. P. Benda.

Scotophilus livingstonii is a recently discovered species, Brooks & Bickham (2014) described it based on the results of a molecular genetic analysis published by Trujillo et al. (2009). The species is defined as the *dinganii* morphotype of the genus *Scotophilus* (i.e. medium-sized to large bat with a bright pelage colouration) possessing its own phylogenetic lineage (Vallo & Van Cakenberghe 2017, Demos et al. 2018). Until now, this lineage was found only in the samples collected from Kenya and Ghana (Trujillo et al. 2009, Demos et al. 2018). From West Africa, it is the only lineage confirmed in bats of the *dinganii* morphotype, while at least three



Figs. 26, 27. Distribution of bats in Benin; circles – published records (see Appendix 1), squares – new records. 26 – *Scotophilus nigritellus*. 27 – *Scotophilus livingstonii*.

Figs. 28, 29. Portraits of *Scotophilus nigritellus* from Koko near Alafiarou, Benin.

such lineages and possibly separate species were detected in East Africa (Vallo et al. 2011b, Brooks & Bickham 2014, Demos et al. 2018). Some authors thus co-identified the West African populations of this morphotype with *S. livingstonii* (see e.g., Decher et al. 2021), while others formally consider the latter species to occur in sympatry with *S. dinganii* (Smith, 1833) s.l., i.e. with those populations of the morphotype unallocated to a lineage, pending an additional research (Burgin et al. 2020, Van Cakenberghe & Seamark 2022).

However, the here presented NMP specimen from Benin was identified as belonging to the *livingstonii* lineage with the help of molecular genetic methods, it represents the only individual of the *dinganii* morphotype from the country examined by this approach. The analysis of the mitochondrial gene for cytochrome *b* showed the Beninese NMP specimen to be in agreement by 99.1–99.6% with the haplotypes referred to this lineage from Ghana by Trujillo et al. (2009). This finding enlarges the range of the lineage by one country and simultaneously, supports the view that *S. livingstonii* is the exclusive lineage of the *dinganii* morphotype present in West Africa. Therefore, we consider this morphotype findings from Benin as belonging to *S. livingstonii*.

In West Africa, the *Scotophilus* bats of the *dinganii* morphotype are distributed broadly in the savanna belt from Senegal to Cameroon (Rosevear 1965, Hayman & Hill 1971, Robbins et al. 1985, Happold 2013d). It occurs in the whole region of the Dahomey Gap, although in some of its parts, its records are not very frequent (Happold 1987, Kangoyé et al. 2015, Amori et al. 2016). In Benin, this bat was found only at five localities, but dispersed over the whole country, it is the only member of the genus documented in the southern part of the country (Fig. 27; Robbins 1980, Voglozin & Sinsin 2007, Van Cakenberghe & Seamark 2022). The newly collected NMP specimen completes the picture of distribution of this bat in Benin (Fig. 27). The dimensions of this specimen are shown in Table 5.

CONCLUSIONS

The NMP collection contains a rather small series of 58 specimens of bats from Benin belonging to 16 species of six families. These bats originate from seven localities covering mainly the central part of the country (Fig. 1), with a frequency of 2–6 species per locality, on average 3.4 species and 8.3 specimens per locality. Particular species originate from 1–3 localities, together representing 24 new records (species vs. locality), on average 1.5 records per species, and the species are represented by 1–11 specimens, on average 3.6 specimens per species.

If the review by Van Cakenberghe & Seamark (2022) of collections possessing the bats from Benin is correct concerning the numbers of specimens, the NMP collection of Beninese bats is the second largest (representing ca. 6% of the known specimens), after the most representative USNM collection (1,002 specimens, 36 species) and similarly numerous and diverse as the third ZMA collection (55 specimens, 16 species) and the MNHN collection (32 specimens, 15 species). Most of the NMP specimens (ca. two thirds) belong to common species, which could be frequently found in other collections containing material from Benin and the broader region of West Africa as well. However, some of the specimens have an undoubted value for zoological research, belonging to rare or even extremely rare species. Generally, the collection as a whole substantially complements the knowledge of distribution of the bat fauna of Benin, in some species contributes also to their morphological or phylogenetical aspects.

Seven bat species in the NMP collection could be classified as common faunal elements in Benin (*Eidolon helvum*, *Epomophorus gambianus*, *E. pusillus*, *Nycteris macrotis*, *Chaerephon pumilus*, *Mops condylurus*, *Scotophilus leucogaster*), one as medium frequent in the country (*Scotophilus nigritellus*), four species as rather rare (*Rhinolophus fumigatus*, *Hipposideros* cf. *ruber*, *Pseudoromicia rendalli*, *Scotophilus livingstonii*), and four species as very rare Beninese bats (*Hipposideros jonesi*, *H. abae*, *H.* cf. *lamottei*, *Scotophilus nigrita*).

According to the published evidence (Appendix 1), the bat fauna of Benin has ben composed of 52 species belonging to eight families. Thirteen of them are housed in the NMP collection, making up 25% of the known fauna of the country. The evaluation of the NMP collection brought confirmation of three more species for the Beninese fauna, *Hipposideros jonesi*, *H. abae*, and *H.* cf. *lamottei*, plus confirmation of the occurrence of *Scotophilus livingstonii* and the D lineage of *Hipposideros* cf. *ruber* in the country based on molecular genetic evidence. The bat fauna of Benin now comprises 55 species in total, 29% of them are housed in the NMP collection.

Scotophilus nigrita, a rarely found bat species throughout its extensive range, was known from Benin only from an unspecified locality, the NMP collection possesses a specimen from a defined site, Manigri. In *Rhinolopus fumigatus*, the NMP series represents a new marginal record, making the known southern limits of its distribution range shifted markedly southwards.

The collection site of Awaya, near Dassa, in south-central Benin, brought records of six bat species – the largest number among the sampled sites – of them three new for the country's fauna. The bats were collected using a mistnet spread over a small stream in a mosaic landscape of woodland patches and agricultural areas. However, the species composition suggests a presence of a common underground roost of these bats, as indicated by a collective catch of *Rhinolophus fumigatus*, *Hipposideros jonesi*, *H. abae*, *H.* cf. *lamottei*, and *Nycteris macrotis*. Similar records, cave catches with a similar species composition (namely of the hipposiderids), were reported from caves in Burkina Faso – by Koch-Weser (1984) from Diébougou and Kangoyé et al. (2015) from Niangoloko.

In summary, the small collection of bats from Benin, created during a single research trip, represents a valuable series of specimens, providing an important addition to the knowledge of composition, distribution and morphometry of the bat fauna of the country.

A c k n o w l e d g e m e n t s

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APPENDIX 1

Check-list of the bat fauna of Benin

Systematic review of 55 species of bats recorded from the territory of Benin supplemented by a complete list of localities [in brackets, the known number of localities] representing a minimum of 409 records (species vs. locality); only the first report of a locality and its reference is mentioned per particular species, localities are arranged in chronological order (according to the publication date) and then in alphabetical order. The bat nomenclature used follows the current taxonomy (cf. Burgin et al. 2020; except those of the genera *Afronycteris* and *Pseudoromicia*).

Pteropodidae

***Eidolon helvum* (Kerr, 1792)** [19–20]

Whydah [= Ouidah] (Dobson 1878); Kpodave, Soubroukou, Tourou (Robbins 1980); Birni (Verschuren 1988); Borgou, [Dahomey] (Bergmans 1990); Tanguiéta (Haquart & Rombaut 1995); Abomey, Cotonou, Paouignan, Porto-Novo (Bergmans 2002); Lama Forest: Layon; Matéri, Tihoun, Sépounga-Lapouboussi, Pouri (Djossa 2007); Niaouli Forest (Djossa et al. 2008b); Lokoli Forest (Djossa et al. 2010); Manigri (this review).

***Rousettus aegyptiacus* (Geoffroy, 1810)** [2]

Pendjari river (N of Pendjari Park) (Haquart & Rombaut 1995); Pendjari Park (hunting zone) (Djossa 2007).

***Myonycteris leptodon* Andersen, 1908** [4]

Pendjari Park (hunting zone), Tanguiéta, Tihoun (Djossa 2007); Niaouli Forest (Djossa et al. 2010).

***Lissonycteris angolensis* (du Bocage, 1898)** [1]

Pendjari Park (hunting zone) (Djossa 2007).

***Megaloglossus woermanni* Pagenstecher, 1885** [3]

Lama Forest (Voglozin & Sinsin (2007); Niaouli Forest (Djossa et al. 2008b); Lokoli Forest (Djossa et al. 2010).

***Epomophorus gambianus* (Ogilby, 1835)** [39–40]

Bimbereke, Diho, Guene, Kouande, Nikki, Parakou, Segbana, Zizonkame (Robbins 1980); Pendjari Park: Pendjari river, Podiéga river (Green 1983); Batia, Tanguiéta, Tanougou Waterfall (Haquart & Rombaut 1995); Cotonou, Savé, Porto-Novo (Bergmans 2002); Agramarou, Betérou, Kandi, Koda, Koto, Lama Forest, Materi, Natitingou, Nodi, Pendjari Park (hunting zone), Pendjari Park (national park), Porga, Pouri, Sépounga-Lapouboussi, Tihoun (Djossa 2007); Niaouli Forest (Djossa et al. 2008b); Lokoli Forest (Djossa et al. 2010); [unknown site] (Van Cakenberghe & Seamark 2022); Chute de Kota, Djougou, Koko, Manigri, Tagayé, Tourou (this review).

***Epomophorus pusillus* Peters, 1868** [33–34]

Bimbereke, Diho, Guene, Kouande, Parakou, Segbana (Robbins 1980); Pendjari Park: Pendjari river, Mare Diwouni (Green 1983); Agouagou, [Dahomey] (Bergmans 1989); Batia, Porga, Tanougou Waterfall (Haquart & Rombaut 1995); Cotonou (Bergmans 2002); Banigri, Betérou, Bondjagou, Lama Forest: Koto, Materi, Natitingou, Nodi, Pendjari Park (hunting zone), Pendjari Park (national park), Pouri, Sépounga-Lapouboussi, Tanguiéta, Tanougou Camp, Tihoun (Djossa 2007); Lokoli Forest (Djossa et al. 2010); Agouagon, Porto-Novo or Abomey (Van Cakenberghe & Seamark 2022); Awaya, Chute de Kota, Manigri (this review).

***Epomops franqueti* (Tomes, 1860)** [5]

Kpodave (Robbins 1980); Lama Forest (Voglozin & Sinsin 2007); Niaouli Forest (Djossa et al. 2008b); Lokoli Forest (Djossa et al. 2010); Groß-Popo [= Grand-Popo] (Van Cakenberghe & Seamark 2022).

***Hypsignathus monstrosus* Allen, 1861** [3]

Niaouli Forest, Pendjari Park (national park) (Djossa 2007); Lama Forest (Voglozin & Sinsin 2007).

***Nanonycteris veldkampi* (Jentink, 1888)** [16–17]

Godomey, Niaouli Forest (Bekker & Ekué 2004); Lama Forest: Massi, Lokoli, Materi, Nodi, Pendjari Park (hunting zone), Pendjari Park (national park), Porga, Pouri, Sépounga-Lapouboussi, Tanguiéta, Tihoun, Wari-Maro Forest: Bangiri, Betérou (Djossa 2007); Kouffe Mts. (Djossa & Sinsin 2010); [unknown site] (Van Cakenberghe & Seamark 2022).

Rhinolophidae

***Rhinolophus landeri* Martin, 1838** [6]

Diho (Robbins 1980); Tanougou Waterfall (Haquart & Rombaut 1995); Pendjari Park (hunting zone), Pendjari Park (national park), Sépounga-Lapouboussi, Wari-Maro Forest: Mont Soubakpérou Cave (Djossa 2007).

***Rhinolophus fumigatus* Rüppell, 1842** [5]

Nikki (Robbins 1980); [Bimbereke (Robbins 1980), misidentified, see above and Djossa (2007)]; Pendjari Park, Tanougou, Wari-Maro Forest: Mont Agougou Omonso Cave (Djossa & Sinsin 2010); Awaya (this review).

***Rhinolophus* cf. *darlingi* Andersen, 1905** [3]

Bimbereke (Djossa 2007, cf. Robbins 1980); Sépounga-Lapouboussi, Wari-Maro Forest: Mont Agougou Omonso Cave (Djossa 2007).

Hipposideridae

***Hipposideros jonesi* Hayman, 1947** [1]

Awaya (this review).

***Hipposiderus abae* Allen, 1917** [1]

Awaya (this review).

***Hipposideros beatus* Andersen, 1906** [2]

Lama Forest (Voglozin & Sinsin 2007); Agouagon (Van Cakenberghe & Seamark 2022).

***Hipposideros* cf. *tephrus* Cabrera, 1906** [9–10]

Guene, Nikki, Soubroukou, Zizonkame (Robbins 1980); Pendjari Hotel (Verschuren 1988); Niaouli Forest (Bekker & Ekué 2004); Agouagon, Guéné–Nikki road, Kandi–Malanville road, [unknown site] (Van Cakenberghe & Seamark 2022).

***Hipposideros fuliginosus* (Temminck, 1853)** [1]
Lokoli Forest (Djossa et al. 2010).

***Hipposideros* cf. *lamottei* Brosset, 1985** [1]
Awaya (this review).

***Hipposideros* cf. *ruber* (Noack, 1893)** [8]
Hotel Pendjari (Green 1983); Pendjari Park (hunting zone), Pendjari Park (national park), Sépounga-Lapouboussi, Tanguiéta, Tanougou Cave (Djossa 2007); Parakou–Malanville road (Van Cakenberghe & Seamark 2022); Tagayé (this review).

***Macronycteris gigas* (Wagner, 1845)** [9]
Kpodave (Robbins 1980); Batia, Tanougou Waterfall (Haquart & Rombaut 1995); Lama Forest, Pendjari Park (national park), Tanguiéta, Tanougou Cave (Djossa 2007); Lokoli Forest, Niaouli Forest (Djossa et al. 2010).

***Doryrhina cyclops* (Temminck, 1853)** [4]
Kpodave (Robbins 1980); Lama Forest (Voglozin & Sinsin 2007); Niaouli Forest (Djossa et al. 2008b); Pendjari Park (Djossa & Sinsin 2010).

M e g a d e r m a t i d a e

***Lavia frons* (Geoffroy, 1810)** [10–11]
Pendjari Park [E of Mare Diwouni] (Green 1983); Pendjari Camp (Verschuren 1988); Batia, Porga (Haquart & Rombaut 1995); Bondjagou, Pendjari Park (hunting zone), Pendjari Park (national park), Porto-Novo, Sépounga-Lapuboussi, Tanguiéta, [unknown site] (Djossa 2007).

E m b a l l o n u r i d a e

***Coleura afra* (Peters, 1852)** [3]
Batia, Tanougou Waterfall (Haquart & Rombaut 1995); Tanougou Cave (Djossa 2007).

***Taphozous perforatus* Geoffroy, 1818** [1]
Pendjari Park (Haquart & Rombaut 1995).

***Taphozous mauritianus* Geoffroy 1818** [4]
Kpodave (Robbins 1980); Aguago [= Agouagon], Sépounga-Lapuboussi, Tanguiéta (Djossa 2007).

N y c t e r i d a e

***Nycteris hispida* (Schreber, 1774)** [15]
Guene, Nikki, Segbana, Zizonkame (Robbins 1980); Pendjari Park (Green 1983); Arli (Hotel Pendjari), Batia, Porga, Pendjari river (N Pendjari Park) (Haquart & Rombaut 1995); Porto-Novo (Bekker & Ekué 2004); Augaugon, Bondjagou, Pendjari Park (hunting zone), Tanguiéta (Djossa 2007); Lama Forest (Voglozin & Sinsin 2007).

***Nycteris thebaica* Geoffroy, 1818** [5–6]
Guene, Zizonkame (Robbins 1980); Pendjari Park: Pendjari river (Green 1983); Wari-Maro Forest: Mont Adjaboutou (Djossa & Sinsin 2010); Park W, [unknown site] (Van Cakenberghe & Seamark 2022).

***Nycteris gambiensis* (Andersen, 1912)** [5]
Bimbereke, Guene, Nikki, Soubroukou, Zizonkame (Robbins 1980).

***Nycteris macrotis* Dobson, 1876** [20–21]

Bimbereke, Zizonkame (Robbins 1980); Porga (Van Cakenberghe & De Vree 1985); Buèm Hills (Haquart & Rombaut 1995); Angaradebou (Bergmans 2002); Biguina, Dassari, Idadjo, Materi, Pendjari Park (hunting zone), Pendjari Park (national park), Pouri, Tanguiéta, Tanougou Cave, Wari-Maro Forest: Mont Soubakperou Cave (Djossa 2007); Bodjecali, Mékrou river, Tanougou Waterfall, [unknown site] (Van Cakenberghe & Seamark 2022); Awaya, Tagayé (this review).

M o l o s s i d a e

***Chaerephon pumilus* (Cretzschmar, 1830)** [25–26]

Whedda [= Ouidah] (De Vree 1971); Guene, Ketou, Kpodave, Parakou, Porga, Segbana, Soubroukou, Zizonkame (Robbins 1980); Pendjari Park (Green 1983); Bodjécali-Malanville (Bergmans 2002); Lokossa (Bekker & Ekué 2004); Betérou, Hotel Pendjari, Lama Forest, Nodi, Pendjari Park (hunting zone), Porto-Novo, Sépounga-Lapouboussi, Tanguiéta, Wari-Maro, [Dahomey] (Djossa 2007); Lokoli Forest (Djossa et al. 2010); Nikki (Van Cakenberghe & Seamark 2022); Chute de Kota, Djougou (this review).

***Chaerephon major* (Trouessart, 1897)** [2]

Mont Ratier (Bergmans 2002); Bori (Djossa 2007).

***Chaerephon nigeriae* Thomas, 1913** [3]

Segbana (Freeman 1981); Pendjari Park (Djossa & Sinsin 2010); Park W (Van Cakenberghe & Seamark 2022).

***Mops condylurus* (Smith, 1833)** [19–20]

Ayitedjou, Ketou, Kpodave, Porga, Soubroukou (Robbins 1980); Garou, Koko, 15 km S of Lokossa (Bergmans 2002); Damè-Wogon (Bekker & Ekué 2004); Batia Camp, Lama Forest: Massi, Matéri, Pendjari Park (hunting zone), Pouri, Tihoun (Djossa 2007); Lokoli Forest, Niaouli Forest (Djossa et al. 2010); Porto-Novo, [unknown site] (Van Cakenberghe & Seamark 2022); Djougou (this review).

***Mops brachypterus* (Peters, 1852)** [2]

Porga (Djossa & Sinsin 2010, cf. Robbins 1980); Kétou (Van Cakenberghe & Seamark 2022).

***Mops midas* (Sundevall, 1843)** [1]

Pendjari Park: Mare Diwouni (Haquart & Rombaut 1995).

***Mops nanulus* Allen, 1917** [1]

Nikki (Robbins 1980).

V e s p e r t i l i o n i d a e

***Myotis bocagii* (Peters, 1870)** [3]

Pendjari Park: Pendjari river [3 km N of Hotel Pendjari] (Green 1983); Bondjagou (Djossa 2007); Lokoli Forest (Djossa et al. 2010).

***Scotoecus hirundo* (de Winton, 1899)** [3]

Bimbereke (Robbins 1980); Pendjari Park (Haquart & Rombaut 1995); Wari-Maro (Djossa & Sinsin 2010).

***Scotoecus albofuscus* (Thomas, 1890)** [2]

Bimbereke (Robbins 1980); Pendjari Park (Haquart & Rombaut 1995).

***Pipistrellus nanulus* Thomas, 1904** [3–4]

Bimbereke (Robbins 1980); Lama Forest (Voglozin & Sinsin 2007); Pendjari Park (Djossa & Sinsin 2010); [Dahomey] (Van Cakenberghe & Seamark 2022).

***Pipistrellus inexpectatus* Aellen, 1959** [3]

Bimbereke, Segbana (Robbins 1980); Pendjari Park (Stechert et al. 2014).

***Nycticeinops schlieffennii* (Peters, 1859)** [7]

Bimbereke (Robbins 1980); Pendjari river (N of Pendjari Park) (Haquart & Rombaut 1995); Angaradebou (Bergmans 2002); Kouffé Mts. Forest: Aoro; Pendjari Park (hunting zone), Porga, Sépounga-Lapouboussi (Djossa 2007).

***Mimetillus moloneyi* (Thomas, 1891)** [1]

Lokoli Forest (Djossa et al. 2010).

***Afronycteris nana* (Peters, 1852)** [19]

Porto-Novo (Theodor 1956); Bimbereke (Poché 1975); Guene, Kpodave, Segbana, Soubroukou, Zizonkame (Robbins 1980); Deme (Bekker & Ekué 2004); Agonvè (Lake Azri), Bondjagou, Cotonou, Lama Forest: Koto, Pendjari Park (hunting zone), Pendjari Park (national park), Parakou, Sépounga-Lapouboussi, Tanguiéta (Djossa 2007); Lokoli Forest, Niaouli Forest (Djossa et al. 2010).

***Neoromicia capensis* (Smith, 1829)** [1]

Soubroukou (Robbins 1980); the USNM specimens from three other sites referred to this species by Robbins (1980) were re-identified as of *N. somalica* (see Djossa 2007).

***Neoromicia guineensis* (du Bocage, 1889)** [7]

Segbana (Robbins 1980); Garou (Bergmans 2002); Batia, Pendjari Park (hunting zone), Wari-Maro Forest: Térou, Wari-Maro (Djossa 2007); Mékrou river (Van Cakenberghe & Seamark 2022).

***Neoromicia somalica* (Thomas, 1901)** [11]

Batia, Bimbereke, Parakou, Pendjari Park (national park), Segbana, Tanguiéta, Wari-Maro Forest: Betérou, Térou, Wari-Maro (Djossa 2007); Lokoli Forest (Djossa et al. 2010); Mékrou river (Van Cakenberghe & Seamark 2022).

***Pseudoromicia rendalli* (Thomas, 1889)** [6]

Zizonkame (Robbins 1980); Pendjari Park (national park), Tanguiéta, Tihoun (Djossa 2007); Agouagon (Van Cakenberghe & Seamark 2022); Djougou (this review).

***Glauconycteris variegata* (Tomes, 1861)** [4–5]

Segbana (Robbins 1980); Pendjari river (N of Pendjari Park), Tanougou Waterfall (Haquart & Rombaut 1995); Pendjari Park (hunting zone), [unknown site] (Djossa 2007).

***Glauconycteris poensis* (Gray, 1842)** [2]

Kpodave (Robbins 1980); Niaouli Forest (Djossa et al. 2010).

***Scotophilus nigrita* (Schreber, 1774)** [1–2]

[Dahomey] (Robbins 1978); Manigri (this review).

***Scotophilus leucogaster* (Cretzschmar, 1830)** [26]

Bimbereke, Guene, Nikki, Parakou, Segbana (Robbins 1980); Batia, Pendjari river (N of Pendjari Park), Porga, Tanougou Waterfall (Haquart & Rombaut 1995); Batia Camp, Betérou, Bondjagou, Hotel Pendjari, Materi, Nodi, Pendjari Park (hunting zone), Pendjari Park (national park), Pouri, Sépounga-Lapouboussi, Tanguiéta, Tanougou Camp, Tihoun (Djossa 2007); Bodjecali (Van Cakenberghe & Seamark 2022); Djougou, Tagayé, Tourou (this review).

***Scotophilus nigritellus* de Winton, 1899** [13]

Bimbereke, Guene (Robbins 1980); Pendjari river (N of Pendjari Park), Porga, Tanougou Waterfall (Haquart & Rombaut 1995); Batia, Bondjagou, Pendjari Park (hunting zone), Pendjari Park (national

park), Tanguiéta, Wari-Maro, Wari-Maro Forest: Ouémé and Térou confluence (Djossa 2007); Koko (this review).

***Scotophilus livingstonii* Brooks et Bickham, 2014** [6]

Zizonkame (Robbins 1980); Lama Forest (Voglozin & Sinsin 2007); Guéné, Ségbana, Wari-Maro Forest (Van Cakenberghe & Seamark 2022); Manigri (this review).

Doubtful / revised reports

***Epomophorus labiatus* (Temminck, 1837)**

Lama Forest (Voglozin & Sinsin 2007, as *Epomophorus* cf. *labiatus*). This record, by its authors considered uncertain concerning the species identifiation, is here refused as a record of a new member of the Beninese fauna, since it represents the only specimen of the species in West Africa proper. Although Rosevear (1965), Happold & Happold (1978), and Happold (1987) reported *E. labiatus* from Nigeria (under *E. anurus* von Heuglin, 1864), Bergmans (1988) revised the species identification of the concerned specimens and referred them to *E. gambianus*. The westernmost confirmed records of *E. labiatus*, an East African bat species, come from the region of Lake Chad (Bergmans 1988, Claessen & de Vree 1991, Burgin et al. 2020), some 1,500 km east of the Lama Forest.

***Macronycteris vittata* (Peters, 1852)**

Djossa & Sinsin (2010) mentioned a pair of very similar (sibling) species, *Macronycteris gigas* and *M. vittata* as the bats occurring in Benin. Although we cannot absolutely exclude the presence of both species in Benin, here we pooled all available records under one species, *M. gigas* (see above), since we consider it more probable. While *M. gigas* is a bat species broadly distributed in West Africa, *M. vittata* is mostly a southern and central African species, its occurrence in West Africa remains questionable (see e.g. Foley et al. 2017, Tanshi et al. 2021). Djossa & Sinsin (2010) considered the records from savannas as of *M. vittata* and from forests as *M. gigas* (although the whole territory of Benin lies in the zone of savannas). Their view of two species being present in Benin was based on the following published identifications (all under the older conception referring these species to the genus *Hipposideros*): Robbins (1980): *H. commersonii gigas*; Haquart & Rombaut (1995), Voglozin (2003), and Voglozin & Sinsin (2007): *H. commersonii*; and Djossa (2007): *H. vittatus*.

***Nycteris major* (Andersen, 1912)**

Bimbereke (Robbins 1980). Accepted as a record of this species from Benin by Bergmans (2002) and Capo-Chichi et al. (2004). However, the respective USNM specimen was re-identified as *N. macrotis* (see Djossa 2007, Fahr 2013c).

***Mops spurrelli* (Dollman, 1911)**

Benin (Koopman 1993). Accepted as an evidence of this species from Benin by Bergmans (2002), Capo-Chichi et al. (2004), and Djossa & Sinsin (2010). However, the recent authors do not consider Benin to be a part of the confirmed range of this bat (Burgin et al. 2020, Van Cakenberghe & Seamark 2022).

APPENDIX 2

Gazetteer

Altitude in metres a. s. l.; NM = number in the map in Fig. 1

site	coordinates	altitude	NM
Awaya, 10 km E of Dassa (Collines Dept.)	07°47'N, 02°16'E	176	1
Chute de Kota, 5 km S of Kota Monogou (Atakora Dept.)	10°13'N, 01°27'E	505	2
Djougou, NW margin of the town (Donga Dept.)	09°43'N, 01°39'E	409	3
Koko, 11 km NW of Alafiarou (Borgou Dept.)	09°05'N, 02°20'E	273	4
Manigri, 6 km SE of Bassila (Donga Dept.)	08°59'N, 01°42'E	382	5
Tagayé, 15 km SW of Natitingou (Atakora Dept.)	10°15'N, 01°16'E	493	6
Tourou, 10 km W of Parakou (Borgou Dept.)	09°19'N, 02°32'E	337	7

APPENDIX 3

GenBank Accession Numbers of the NMP bats from Benin

species	NMP	haplotype (GenBank No.)			reference
		cyt-*b*	ND1	16S	
Rhinolophus fumigatus	91837	KC579372	–	–	Benda & Vallo (2012)
Rhinolophus fumigatus	91838	KC579373	–	–	Benda & Vallo (2012)
Hipposideros jonesi	91842	EU934471	–	–	Vallo et al. (2008)
Hipposideros abae	91850	EU934446	–	–	Vallo et al. (2008)
Hipposideros abae	91851	EU934447	–	–	Vallo et al. (2008)
Hipposideros cf. *lamottei*	91848	EU934474	–	–	Vallo et al. (2008)
Hipposideros cf. *lamottei*	91849	EU934475	–	–	Vallo et al. (2008)
Hipposideros cf. *ruber*	91879	EU934476	–	–	Vallo et al. (2008)
Nycteris macrotis	91835	PP294730	–	–	this review
Nycteris macrotis	91836	PP294729	–	–	this review
Nycteris macrotis	91878	PP294731	–	–	this review
Chaerephon pumilus	91867	–	PP054380	–	this review
Chaerephon pumilus	91868	–	PP054383	–	this review
Chaerephon pumilus	91869	–	PP054384	–	this review
Chaerephon pumilus	91870	–	PP054385	–	this review
Chaerephon pumilus	91871	–	PP054382	–	this review
Chaerephon pumilus	91872	–	PP054382	–	this review
Chaerephon pumilus	91884	–	PP054381	–	this review
Chaerephon pumilus	91885	–	PP054381	–	this review
Mops condylurus	91873	–	PP054386	–	this review
Mops condylurus	91874	–	PP054386	–	this review
Mops condylurus	91875	–	PP054386	–	this review
Mops condylurus	91876	–	PP054386	–	this review
Pseudoromicia rendalli	91866	–	–	PP058349	this review
Scotophilus nigrita	91889	KF305856	–	–	Vallo et al. (2015)
Scotophilus leucogaster	91853	JX281748	–	–	Vallo et al. (2013)
Scotophilus nigritellus	91857	JX281743	–	–	Vallo et al. (2013)
Scotophilus livingstonii	91890	PP294732	–	–	this review