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Uncovering the diversity of bats in the Mbam Minkom Massif, Cameroon: insights into the importance of tropical inselbergs

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We report the results of two expeditions (2019 and 2022) to the Mbam Minkom Massif (Centre Region, Cameroon), focused on an assessment of the montane area's bat fauna. We describe bat species' richness and highlight the incredible diversity and ecological importance of this highly threatened ecosystem. Across both years, we captured a total of 36 bat species representing 21 genera and six families on Mbam Minkom Massif and in the surrounding lowland forest. Our findings include two new species records for Cameroon, and two additional records of the recently described bat, *Pseudoromicia mbamminkom*. We provide accounts for all captured species, including new locality records, detailed capture locations, and notable taxonomic and distributional observations, as well as echolocation call data. Sampling curves suggest adequate sampling coverage, yet also the potential non-detection of several bat species, highlighting the need for further fieldwork to develop a comprehensive species checklist. Conservation strategies are urgently needed to protect this vital ecosystem and mitigate both the loss of forest cover and consequent species loss. Our findings illustrate the importance of the Mbam Minkom Massif and the need to better understand and conserve inselberg ecosystems within rainforests that are facing intense anthropogenic pressures.

Key words: Cameroon, diversity, taxonomy, Chiroptera, echolocation, bat, inselberg

INTRODUCTION

Cameroon is a nation of remarkable biological diversity, hosting some of the richest faunas and floras in Africa (Lovett *et al.*, 2000; Brooks *et al.*, 2001; Ceballos and Ehrlich, 2006; Schipper *et al.*, 2008). Cameroon's diverse landscapes set the stage for its remarkable diversity, from the Cameroon Volcanic Line (CVL) in the southwest to the central Adamawa Plateau and the southern plains and rolling hills in tropical lowland forest (Neba, 1987). One component of Cameroon's biodiversity remains woefully understudied: the fauna of inselbergs.

Inselbergs, rocky outcrops forming discrete ecosystems, are defined by their stark orographic relief, offering ecological niches distinct from their surroundings (Bornhardt, 1900; Twidale, 1981; Porembski and Barthlott, 2000). Importantly, inselbergs offer unique foraging and roosting sites for bats. For cave-dependent bat species, a third of all African bat species, they serve as crucial rock habitats for roosts (Happold and Happold, 2013; Herkt *et al.*, 2016). Despite the ecological importance of inselbergs, zoologists have paid little attention to how tropical inselbergs affect species diversity (Porembski and Barthlott, 2000).

Scattered across the western part of Cameroon's Southern plateau are several inselbergs. Independent of the volcanic phenomena of the CVL, these inselbergs are shaped by erosion of ancient Precambrian rock formations (Neba, 1987). The Mbam Minkom Massif emerges as a prominent feature among these, located approximately 15 km northwest of Yaoundé, the capital city, in the Centre Region (Neba, 1987). The massif runs in a SW-NE direction and has several peaks: Mt. Mbam Minkom (1295 m), Mt. Odou (1225 m), Mt. Nkolakie (1185 m), Mt. Nkoldjobe (1181 m), Mt. Nkoloman (1060 m), Mt. Ekondongo (1171 m), Mt. Miviami Zibin (1141 m), Mt. Zoabissima (1120 m) and Mt. Mbikal (1221 m) (Kuété, 1977). The area falls within the equatorial Guinean climate zone and is marked by four distinct seasons: a major rainy season from early March to mid-June, a minor dry season from mid-June to August, a minor rainy season from early September to mid-November, and a major dry season from mid-November to mid-March (Molua and Lambi, 2006). The forest of the massif hosts numerous endemic floral species restricted to a narrow elevation band (800 to 1200 m) and not present in the surrounding lowland rainforest (Noumi, 1998). The unique vegetative composition and geology of the massif result in a local climate of fog and fine rains, which affects regional water cycles. The massif is drained by several streams and river gorges that all originate from the massif (Fig. 1). Importantly, rivers such as the Mefou and Mfoundi are crucial to the city of Yaoundé; the Mfoundi river and its tributaries traverse the urban area, significantly contributing to the city's drainage and water supply (Djuikom *et al.*, 2006). The Mbam Minkom Massif is a major water catchment for the area, providing not only clean water to the city, but is a major source of income for the surrounding area. (Neba, 1987; Djuikom *et al.*, 2006; Simo *et al.*, 2009).

The fauna of the Mbam Minkom Massif has limited documentation in the scientific literature, and what exists is primarily focused on the Grey-necked rockfowl, *Picathartes oreas* (Awa *et al.*, 2009a, 2009b). Due to human pressure, large mammals are now extremely rare. However, the forest still harbors charismatic flagship species of global conservation concern, such as the giant ground pangolin (*Smutsia gigantea*) listed as Endangered by the IUCN red list (Nixon *et al.* 2019).

Cameroon's exceptional faunal diversity includes more than 120 bat species (ACR, 2024). However, the true extent of the bat fauna remains

unknown. A lack of baseline data, combined with unresolved taxonomy and systematics of many African bat groups, conceals the magnitude of the bat fauna with repercussions across biological disciplines. Importantly for threatened ecosystems, such as the Mbam Minkom Massif, conservation strategies are urgently needed to mitigate both the loss of forest cover and the consequent species loss. Bats play vital roles in forest ecosystems as highly productive seed dispersers and pollinators, as well as predators of insect pests, serving as important initiators of top-down trophic cascades (van Toor *et al.*, 2019; Frick *et al.*, 2020; Atagana *et al.*, 2021; Beilke and O'Keefe, 2023). Recent studies are uncovering the extraordinary diversity of bats in Cameroon, highlighting their ecological and economic importance in Afrotropical ecosystems, and identifying major threats to this diversity (Bakwo Fils *et al.*, 2014, 2021; Lebreton *et al.*, 2014; Atagana *et al.*, 2018, 2021; Waghiiwimbom *et al.*, 2019, 2020; Dongmo *et al.*, 2020; Mongombe *et al.*, 2020). In particular, Waghiiwimbom *et al.* (2020) and Atagana *et al.* (2018) have made significant contributions to our understanding of bat diversity in the Centre Region of Cameroon. Waghiiwimbom *et al.* (2020) provided detailed information on the species composition within forests, traditional farms and savannahs throughout the Centre Region. Research by Atagana *et al.* (2018) detailed bat species richness in the Mpem and Djim National Park, located approximately 140 km north of the Mbam Minkom Massif, further enriching our knowledge of the region's bat populations. However, to date, none of these studies have included the Mbam Minkom Massif. Our work included two surveys: a preliminary survey of four sites on the massif, completed in 2019; and a survey in 2022 of Mt. Mbam Minkom and the surrounding lowland rainforest.

MATERIALS AND METHODS

Survey Sampling 2019

We surveyed the northwestern and southwestern slopes of the Mbam Minkom Massif (Centre Region, Cameroon) in four camps across three elevational bands (Table 1 and Fig. 2). Surveys were carried out between 10 and 22 August 2019. Mist nets (four 6 × 3 m nets and two 12 × 3 m) were used to sample bat communities. The nets were opened before dusk (about 17:00) and closed at 01:00 hours, then reopened at 04:00 hours and closed at sunrise. The nets were scanned and the bats were removed every 15 minutes and placed individually in clean cotton bags for later processing.

The first two collecting sites were established on the northwest-facing slopes. Camp 1 was situated along a ridge at 1074 m. Three mist nets were set along the ridge that passed

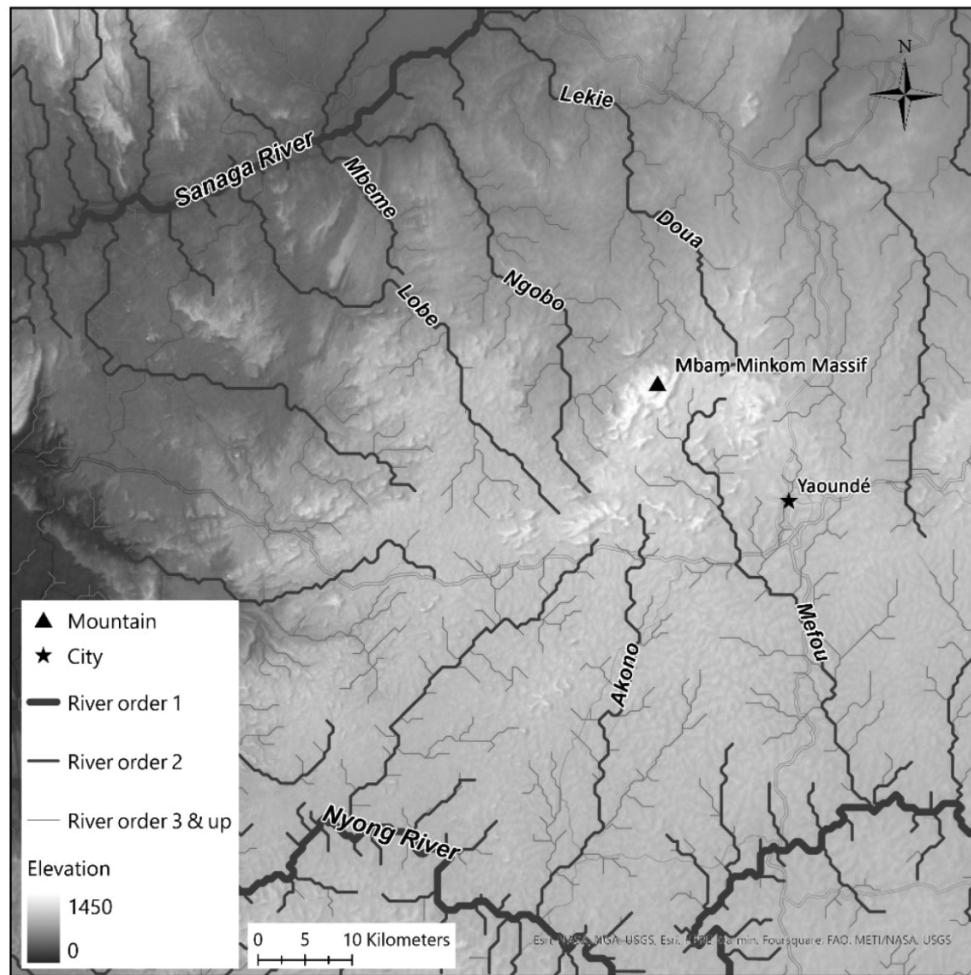


FIG. 1. Map of Mbam Minkom Massif and surrounding area overlaid with river data generated from HydroRIVERS (Lehner and Grill, 2013). Order number 1 represents the main stem river from mouth to source, order 2 represents all tributaries that flow into a 1st order river, and order 3 and up represents all tributaries that flow into a 2nd order river, etc

through a forest opening. Adjacent to the camp was a rock outcrop forming a catchment funnel, the source of the Bitemgu River; three nets were placed across the pooling water about 3 m apart at descending heights with the net nearest the rock outcropping at approximately 5 m, the next approximately 3 m and the final approximately 1 m above the water. Mist netting was carried out for four consecutive nights at Camp 1. Camp 2 was located at 785 m, adjacent to the Bitemgu River. Four nets

were placed across the river approximately 3 m apart. Two additional nets were set downstream, flanking an area where the river pooled. Both nets were set parallel to the river, running perpendicular to the forest openings on either side. Mist netting took place for three consecutive nights at Camp 2. Camps 3 and 4 were located on southeast-facing slopes of the massif. Camp 3 was located at the intersection of two small-scale trails used for timber extraction resulting in a small forest clearing at an

TABLE 1. Summary of survey locality information including survey year, and camp-specific dates, as well as the location, elevation (m a.s.l.), and coordinates (WGS84) of each camp

Camp	Year	Date	Location	Elevation	Coordinates
1	2019	10–13 Aug.	Mt. Mbam Minkom	1074	3.958000, 11.383317
	2022	24–26 July			
2	2019	14–16 Aug.	Mt. Mbam Minkom	785	3.969267, 11.380667
	2022	27–29 July			
3	2019	19–20 Aug.	Mbam Minkom Massif	884	3.916767, 11.373333
4	2019	21–22 Aug.	Mbam Minkom Massif	829	3.917867, 11.377317
5	2022	30 July–1 Aug.	Nkolakié	643	3.979483, 11.383350
6	2022	2–4 Aug.	Nkoleson	635	4.002017, 11.385733
7	2022	5–7 Aug.	Ntchama	578	4.042967, 11.389583
8	2022	8–10 Aug.	Ngong	571	4.084283, 11.385017

elevation of 884 m. The mist nets were placed perpendicularly along both trails, about 6 m apart. Mist netting took place for three consecutive nights at Camp 3. Camp 4 was located at 829 m just north of the village of Ozom II. Mist nets were placed along a river adjacent to a large clearcut. This site was ca. 400 m north of a large cocoa plantation. Mist netting was performed for a single night at Camp 4. A mixture of 6 and 12 m nets were set opportunistically depending on the nature of the environment. The total sampling effort across all sites was 5,335.2 m² of mist net hours.

Survey Sampling 2022

We survey two sites along the northwestern slopes of Mt. Mbam Minkom as well as four sites in a transect that extends 15 km from the base of the mountain north into the surrounding lowland forest (Table 1; Fig. 2) The surveys took place from 24 July–10 August. Three mist nets (two 6 × 3 m and one 9 × 3 m), one three-bank harp trap (Austbat), and one triple-high net system (Titley Scientific) with three 12 × 3 m nets were used to sample bat communities at each site. The nets and the trap

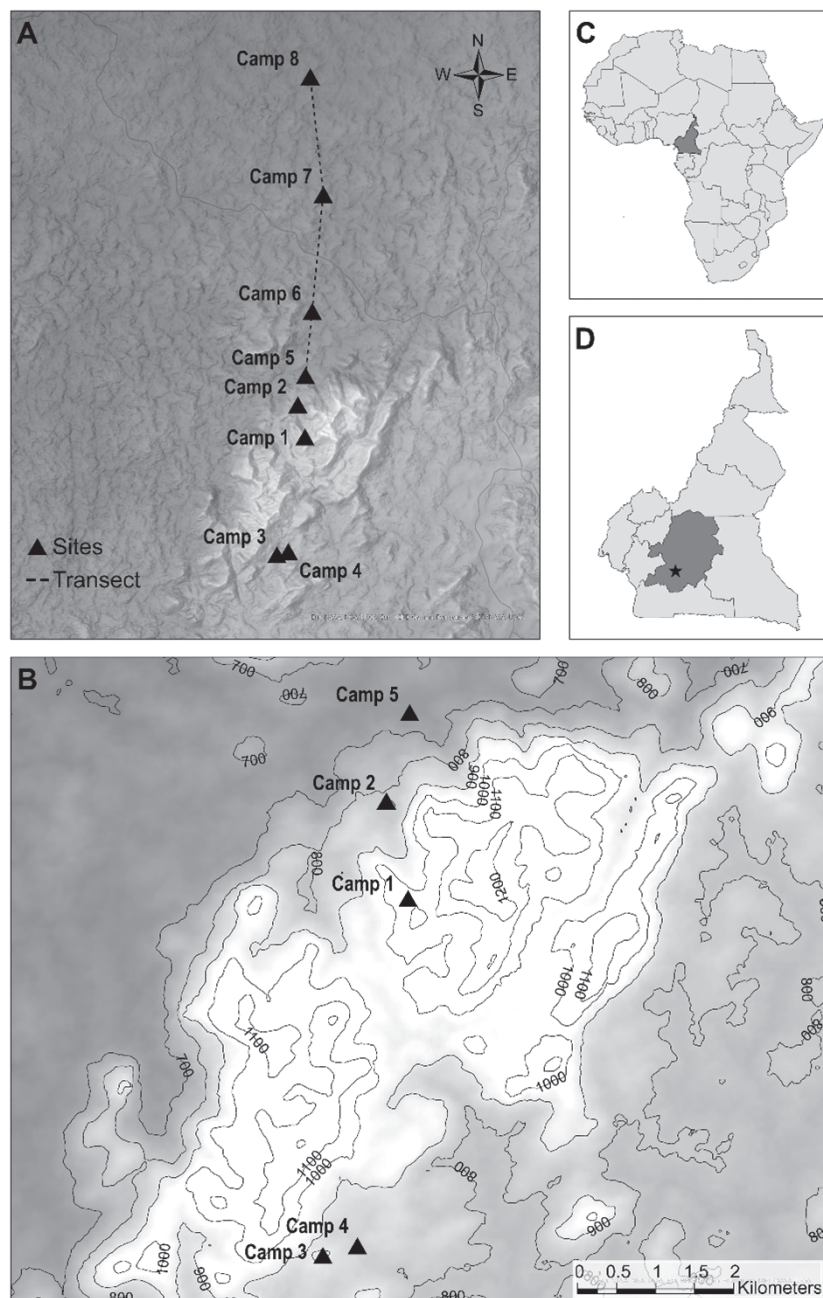


FIG. 2. Overview of Mbam Minkom Massif study area and collection sites: A — Digital elevation model (DEM) map with camp locations (black triangles) on Mbam Minkom Massif and transect (dotted line) extending into surrounding forest; B — Topographic map (in meters) of the massif illustrating the locations of Camps 1–5; C — Mainland Africa with Cameroon's geographical position highlighted in dark grey; D — Regions of Cameroon with the Centre Region highlighted in dark grey and Mbam Minkom Massif's location indicated by a star

were opened at 17:00 and closed at 01:00 hours. The nets and the harp trap were checked every 15 minutes and the bats were removed. The sampling was carried out over three nights at each site. The total sampling effort per site across the three nights was 2,743.7 m² mist net hours, totaling 2,743.7 m² mist net hours across the six sites. The total sampling effort across both survey years was 16,462.4 m² mist net hours.

The first two collecting sites were the same camps established on the northwest-facing slopes in 2019 (Camp 1 and 2). At Camp 1, the triple-high canopy net (three 12 m nets) was set over the river flowing from the catchment area. The harp trap was situated parallel to the river a meter from the canopy net in between a rock wall and a large tree. One mist net (6 × 3 m) was placed parallel to a small pooled area resulting from runoff from the catchment funnel. Two mist nets (9 × 3 m and 6 × 3 m) were set along the ridges that pass through forest openings. At Camp 2, all nets (including the canopy net) were set across the river approximately 3–6 m apart. The harp trap was set adjacent to a bend in the river between a large boulder and a tree. On the second night, two nets (6 × 3 m and 9 × 3 m) were repositioned based on observed bat movement to flank a ridge running parallel to the river. Camp 5 was located in Nkolakié, at the base of the mountain (643 m). The canopy net was installed across a pooled area of an adjacent river, near a forest opening leading to the mountain, and the 9 m net was placed perpendicular to the canopy net through an additional forest opening. Both 6 m nets were set across the river in a V-shaped 10 m down the river. The harp trap was placed across a pool area near a river extending south from the river. Camp 6 was located in Nkoleson, Okola Village, ca. 3 km north of Mt. Mbam Minkom. The canopy net was placed along a river in a riparian forest adjacent to a cocoa farm. A 6 m and a 9 m net were placed parallel to the river. The harp trap was placed across a forest gap 5 m upstream from the nets. The 6 m and 9 m nets were shifted to close a gap near the canopy net on the second night. Camp 7 was located in Ntchama, Okola Village ca. 9 km north of Mt. Mbam Minkom. The canopy net was placed on a sandbar parallel to a river because the river was too deep to cross safely. A 9 m net was placed in an adjacent opening 3 m behind the canopy net. Two 6 m nets were placed in a 10 m V-shaped field near a small bridge. The harp trap was placed in a small first clearing about 4 m off the main trail to the river. Camp 8 was located in Ngong. The canopy net was set across a river over a large log that created a pool area in the river. The harp trap was set nearby in a forest opening. A 6 m net was placed parallel to the river about 5 m downstream. The 6 and 9 m were set in a V-shaped shape across the river about 10 m downstream, past a small farming area.

Data Collection and Analysis

For bats identifiable in the field, a 3 mm wing punch was taken for later molecular analysis before their release near the capture site. Individuals not easily identified from external characters were collected as voucher specimens. Furthermore, 49 bats were released after identification without tissue sampling. External measurements were taken in millimeters with a ruler in the field and included: forearm length (FA), total length (TL — head and body plus tail), tail length, hindfoot length (including claw), ear pinna length (from notch) and tibia length; body mass was recorded to the nearest 0.1 g using a Pesola spring scale. The voucher specimens were remeasured in the laboratory using Mitutoyo digital calipers (± 0.01 mm) (Table 2). The collection

methods followed established methods (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016) that were approved by the Portland State University Institutional Animal Care and Use Committee under Protocols #74 and #1079. The euthanized bats were fixed with formaldehyde and stored in 95% ethanol in the field. Skulls were removed upon return to the laboratory. Following Monadjem *et al.* (2013a), cranial and dental measurements of voucher specimens were taken with calipers to the closest 0.01 mm (Table 3). All collected specimens have been deposited at the Field Museum of Natural History (Chicago, IL, USA) and stored in 70% ethanol.

Echolocation calls were recorded using a Titley Anabat Walkabout detector (Titley Scientific) and Echo Meter Touch 2 Pro Android (App 2.8.14, Wildlife Acoustics) at sampling rates of 500 and 384 kHz, respectively. For high-duty cycle bats in the families Rhinolophidae and Hipposideridae, we recorded resting-phase calls in hand. Bats in the families Nycteridae and Vespertilionidae were recorded in flight in a 2 × 4 m flight tent made from mosquito netting. The calls were analyzed using the Kaleidoscope Pro software (Wildlife Acoustics v. 5.6.0.c).

To evaluate species richness, diversity, and sample completeness, we applied an integrative framework including rarefaction and extrapolation using Hill numbers following Chao *et al.* (2014). We generate sample size-based rarefaction and extrapolation (R/E) curves that include 95% confidence intervals for species richness ($q = 0$) and Shannon's entropy index ($q = 1$), using abundance data from both survey years (Chao and Chiu, 2016; Chao *et al.*, 2020, 2021). The R/E curves and sample completeness values were produced in R using the iNEXT.3D and iNEXT.4steps packages (Hsieh *et al.*, 2016; Chao *et al.*, 2020, 2021; R Core Team, 2021).

Identification of Specimens

Identification of specimens follows standard morphological approaches, based on Rosevear (1965) and Aellen (1952), with updates from Grunwald *et al.* (2023), Hapold and Hapold (2013), Hutterer *et al.* (2019), Monadjem *et al.* (2020, 2021b), and Wilson and Mittermeier (2019). Morphological determinations were confirmed using sequences of the mitochondrial cytochrome *b* (*cyt-b*) gene sequences using standard techniques (Demos *et al.*, 2018, 2019b, 2020; Patterson *et al.*, 2019, 2020) and compared with existing sequences from GenBank. The species names follow Simmons and Cirranello (2024).

Genetics

Genomic DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen). The mitochondrial cytochrome *b* (*cyt-b*) gene was selected for amplification using the primer pair LGL 765 F and LGL 766R (Bickham *et al.*, 1995, 2004). PCR amplification, thermocycler settings, and sequencing were identical to those of Grunwald *et al.* (2023). Sequencing was carried out on an ABI 3100 thermocycler (Applied Biosystems, Bedford, MA, USA) at the Pritzker Laboratory for Molecular Systematics and Evolution (FMNH). Sequences were assembled and edited using GENEIOUS PRIME v.2024.0.5 (Biomatters Ltd.). Sequence alignments were made using MUSCLE (Edgar, 2004) with default settings in GENEIOUS. The protein-coding data from *cyt-b* were translated into amino acids to determine the codon positions and confirm the absence of premature stop codons, deletions, and insertions.

TABLE 2. External measurements of captured bats, detailing: forearm (FA), total length (TL), tail length, hindfoot length including claws (HF), ear length, tibia length, and body mass (all in mm except body mass in g). Measurements include mean ($\bar{x}$), standard deviation (SD), and range. Total capture numbers and sex distribution are also provided. Variability in capture totals and measurement counts across species is due to the release of some bats before measurements could be taken. Additionally, the accuracy of measurements is higher for voucher specimens, as external measurements were retaken in the laboratory using Mitutoyo digital calipers (± 0.01) by CV and AG

Family/Species	Capture totals	FA		TL		Tail	
		$\bar{x} \pm \text{SD}$	Range (<i>n</i>)	$\bar{x} \pm \text{SD}$	Range (<i>n</i>)	$\bar{x} \pm \text{SD}$	Range (<i>n</i>)
Pteropodidae							
<i>Casinycleris argynnis</i>	3 ♀♀	62.5 ± 0.5	62–63 (2)	103.5 ± 1.5	102–105 (2)	—	—
<i>Epomophorus pusillus</i>	15 (7 ♂♂, 8 ♀♀)	51.9 ± 2.0	49–55 (9)	93.5 ± 1.5	92–95 (2)	—	—
<i>Epomops franqueti</i>	2 ♀♀	84.5 ± 2.8	82–88 (2)	145	—	—	—
<i>Hypsignathus monstrosus</i>	3 (1 ♂, 2 ♀♀)	128.07 ± 4.33	123.7–132.4 (2)	242.5 ± 27.5	215–270 (2)	—	—
<i>Megaloglossus woermanni</i>	11 (1 ♂, 10 ♀♀)	40.6 ± 1.6	39–42 (2)	80.0 ± 0.0	80–80 (2)	—	—
<i>Myonycteris angolensis</i>	71 (7 ♂♂, 21 ♀♀)	78.0 ± 2.4	72–82 (20)	138.4 ± 5.9	128–148 (16)	11.2 ± 1.5	9–15 (16)
<i>M. torquata</i>	1 ♀	60.53	—	114	—	9.12	—
<i>Rousettus aegyptiacus</i>	10 (3 ♂♂, 7 ♀♀)	86.0 ± 2.2	83–90 (5)	145.3 ± 2.1	143–148 (3)	16.5 ± 2.4	14–18 (3)
<i>Scotonycteris zenkeri</i>	2 ♀♀	49.16 ± 0.64	48.5–49.8 (2)	80.0 ± 5.0	75–85 (2)	—	—
Rhinolophidae (3)							
<i>Rhinolophus alcyone</i>	8 (4 ♂♂, 4 ♀♀)	52.35 ± 0.82	50.7–53.5 (6)	95.6 ± 3.0	88–100 (8)	27.39 ± 1.08	26.0–29.5 (6)
<i>R. landeri</i>	13 (7 ♂♂, 6 ♀♀)	43.83 ± 1.06	43.0–45.9 (5)	78.5 ± 3.2	73–85 (13)	23.71 ± 0.64	23.0–24.9 (5)
<i>R. cf. simulator</i>	1 ♀	49.68	—	84	—	26.00	—
Hipposideridae							
<i>Doryrhina cyclops</i>	2 (1 ♂, 1 ♀)	67.5 ± 1.5	66–69 (2)	111.0 ± 3.0	108–114 (2)	27.0 ± 2.0	25–29 (2)
<i>Hipposideros beatus</i>	6 (5 ♂♂, 1 ♀)	43.3 ± 0.8	42–44 (5)	77.6 ± 3.7	73–83 (5)	25.2 ± 2.0	22–29 (5)
<i>H. curtus</i>	3 (1 ♂, 2 ♀♀)	45.4 ± 1.7	43–47 (3)	73.0 ± 2.8	69–75 (3)	22.6 ± 1.4	21–24 (3)
<i>H. fuliginosus</i>	4 (3 ♂♂, 1 ♀)	56.9 ± 0.7	56–58 (4)	94.4 ± 2.6	90–98 (4)	27.8 ± 2.4	24–30 (4)
<i>H. cf. ruber</i>	46 (29 ♂♂, 17 ♀♀)	52.0 ± 1.5	49–55 (42)	92.6 ± 3.3	87–101 (42)	33.7 ± 3.4	24–38 (41)
<i>Macronycteris gigas</i>	8 (2 ♂♂, 6 ♀♀)	105.6 ± 2.4	104–110 (7)	143.6 ± 12.6	116–156 (7)	30.9 ± 3.3	26–37 (7)
Nycteridae (3)							
<i>Nycteris arge</i>	2 ♂♂	44.50 ± 0.01	44.5–44.6 (2)	114.0 ± 1.0	113–115 (2)	57.17 ± 0.17	57.0–57.3 (2)
<i>N. grandis</i>	1 ♂	64.00	—	160	—	77.00	—
<i>N. major</i>	1 ♀	48.93	—	126	—	65.81	—
Molossidae							
<i>Mops brachypterus leonis</i>	1 ♀	38.72	—	103	—	29.80	—
<i>M. spurrelli</i>	1 ♀	29.04	—	86	—	25.29	—
<i>M. thersites</i>	1 ♂	39.66	—	100	—	34.15	—
Vespertilionidae							
<i>Afronycteris nanus</i>	1 ♀	31.33	—	77	—	31.87	—
<i>Glauconycteris argentata</i>	5 (4 ♂♂, 1 ♀)	41.0 ± 0.0	41–41 (5)	101.2 ± 2.4	99–105 (5)	45.2 ± 1.2	44–47 (5)
<i>G. egeria</i>	2 (1 ♂, 1 ♀)	39.86 ± 0.39	39.5–40.3 (2)	101.5 ± 0.5	101–102 (2)	44.12 ± 1.06	43.1–45.2 (2)
<i>Myotis bocagii</i>	2 (1 ♂, 1 ♀)	38.11 ± 0.40	37.7–38.5 (2)	92.0 ± 3.0	89–95 (2)	38.95 ± 0.05	38.9–39.0 (2)
<i>Nycticeinops crassulus</i>	1 ♂	29	—	80	—	32.00c	—
<i>N. happoldorum</i>	5 (3 ♂♂, 2 ♀♀)	34.97 ± 0.20	34.8–35.2 (4)	92.5 ± 2.9	89–97 (5)	34.46 ± 0.72	33.3–35.2 (4)
<i>Pipistrellus nanulus</i>	2 (2 ♂♂)	26.64 ± 0.44	26.2–27.1 (2)	66.0 ± 4.0	62–70 (2)	24.91 ± 0.85	24.1–25.8 (2)
<i>Pseudoromicia mbamminkom</i>	3 (2 ♂♂, 1 ♀)	35.42 ± 0.56	34.7–35.6 (3)	88.3 ± 4.9	82–94 (3)	33.02 ± 1.48	31.5–34.5 (2)
<i>P. roseveari</i>	2 ♂♂	36.51 ± 0.05	36.5–36.5 (2)	90.0 ± 1.4	89–91 (2)	36.29 ± 1.80	35.0–37.6 (2)
<i>P. sp. indet.</i>	2 ♀♀	30.18 ± 1.03	29.5–30.9 (2)	80.0 ± 2.8	78–82 (2)	29.79 ± 2.04	28.4–31.2 (2)
<i>P. tenuipinnis</i>	1 ♂	28.54	—	79	—	28.84	—
<i>Scotophilus nux</i>	1 ♀	56.21	—	140	—	55.41	—

Maximum likelihood (ML) analysis was performed with the software IQ-TREE v.2.2.2.7 (Nguyen *et al.*, 2015; Chernomor *et al.*, 2016) and tested for the best supported substitution model using ModelFinder Plus on the CIPRES Science Gateway v.3.1 (Miller *et al.*, 2010). The maximum likelihood tree generated in IQ-TREE is shown in Supplementary Information S1. The newly generated sequence data have been deposited in GenBank under accession numbers (PP942855–PP942895).

RESULTS

During the 2019 survey period, we captured 94 bats, 51 were collected as voucher specimens and 43 *Myonycteris angolensis* were released. This survey identified 17 species in 12 genera and five families and included the bat on which the description of

TABLE 2. Extended

Family/Species	HF		Ear		Tibia		Body mass	
	$\bar{x} \pm SD$	Range (n)	$\bar{x} \pm SD$	Range (n)	$\bar{x} \pm SD$	Range (n)	$\bar{x} \pm SD$	Range (n)
Pteropodidae								
<i>Casinonycteris argynnis</i>	14.0 $\pm$ 1.0	13–15 (2)	20.0 $\pm$ 0.0	20–20 (2)	–	–	34.50 $\pm$ 0.50	34.0–35.0 (2)
<i>Epomophorus pusillus</i>	14.4 $\pm$ 1.4	13–16 (2)	17.5 $\pm$ 0.5	17–18 (2)	21.63	–	26.00 $\pm$ 3.00	23.0–29.0 (2)
<i>Epomops franqueti</i>	22.30	–	28	–	35.40	–	80.0	–
<i>Hypsignathus monstrosus</i>	34.76 $\pm$ 0.06	34.7–34.8 (2)	36.0 $\pm$ 0.0	36–36 (2)	55.50 $\pm$ 3.10	52.4–58.6 (2)	–	–
<i>Megaloglossus woermanni</i>	10.5 $\pm$ 0.5	10–11 (2)	14.5 $\pm$ 2.5	12–17 (2)	18.73	–	17.00 $\pm$ 2.00	15.0–19.0 (2)
<i>Myonycteris angolensis</i>	21.4 $\pm$ 1.6	18–25 (16)	22.9 $\pm$ 1.2	20–25 (16)	31.79 $\pm$ 1.70	29.5–34.4 (5)	73.33 $\pm$ 9.21	56.0–92.5 (15)
<i>M. torquata</i>	16.43	–	20	–	24.52	–	35.0	–
<i>Rousettus aegyptiacus</i>	23.4 $\pm$ 0.4	23–24 (3)	23.0 $\pm$ 0.8	22–24 (3)	37.1 $\pm$ 3.2	37–41 (3)	85.33 $\pm$ 10.40	77.0–100.0 (3)
<i>Scotonycteris zenkeri</i>	11.94 $\pm$ 0.22	11.7–12.2 (2)	12.5 $\pm$ 1.5	11–14 (2)	21.05 $\pm$ 1.05	20.0–22.1 (2)	20.00 $\pm$ 5.00	15.0–25.0 (2)
Rhinolophidae (3)								
<i>Rhinolophus alcyone</i>	12.96 $\pm$ 0.72	11.9–14.3 (5)	23.0 $\pm$ 1.3	21–25 (8)	23.85 $\pm$ 0.60	24.2–25.9 (6)	14.57 $\pm$ 1.76	13.0–17.0 (8)
<i>R. landeri</i>	9.09 $\pm$ 0.80	7.7–10.0 (5)	17.7 $\pm$ 1.1	16–20 (13)	18.62 $\pm$ 0.68	17.9–19.7 (5)	7.30 $\pm$ 0.64	6.5–8.9 (13)
<i>R. cf. simulator</i>	9.0	–	25	–	–	–	8.5	–
Hipposideridae (6)								
<i>Doryrhina cyclops</i>	18.5 $\pm$ 0.5	18–19 (2)	32.5 $\pm$ 0.5	32–33 (2)	35.12	–	28.00 $\pm$ 4.00	24.1–32.1 (2)
<i>Hipposideros beatus</i>	7.4 $\pm$ 0.6	6–8 (5)	15.2 $\pm$ 1.7	12–17 (5)	16.48 $\pm$ 0.60	15.8–17.0 (3)	5.30 $\pm$ 0.73	4.9–6.8 (5)
<i>H. curtus</i>	8.1 $\pm$ 0.2	8–8 (3)	20.3 $\pm$ 1.0	19–21 (3)	19.30 $\pm$ 0.80	18.5–20.1 (2)	5.70 $\pm$ 0.36	5.4–6.2 (3)
<i>H. fuliginosus</i>	11.1 $\pm$ 0.5	10–12 (4)	19.0 $\pm$ 0.7	18–20 (4)	22.69 $\pm$ 0.60	22.1–23.3 (4)	12.13 $\pm$ 0.89	11.0–13.0 (4)
<i>H. cf. ruber</i>	9.2 $\pm$ 0.8	8–11 (42)	16.3 $\pm$ 1.8	10–19 (42)	21.5 $\pm$ 0.6	20–24 (42)	8.90 $\pm$ 1.01	7.5–12.0 (42)
<i>Macronycteris gigas</i>	24.7 $\pm$ 0.5	24–26 (7)	35.3 $\pm$ 1.0	33–36 (7)	44.44 $\pm$ 0.52	43.9–44.9 (3)	73.67 $\pm$ 5.12	66.0–82.5 (6)
Nycteridae (3)								
<i>Nycteris arge</i>	10.31 $\pm$ 0.23	10.1–10.5 (2)	30.0 $\pm$ 0.0	30–30 (2)	25.80 $\pm$ 0.60	25.2–26.4 (2)	9.40 $\pm$ 0.20	9.2–9.6 (2)
<i>N. grandis</i>	14	–	33	–	–	–	26.0	–
<i>N. major</i>	10.55	–	31	–	27.32	–	12.5	–
Molossidae (3)								
<i>Mops brachypterus leonis</i>	9.61	–	22	–	14.07	–	15.0	–
<i>M. spurrelli</i>	7.52	–	15	–	11.32	–	9.6	–
<i>M. thersites</i>	11.68	–	20	–	15.29	–	14.0	–
Vespertilionidae (12)								
<i>Afronycteris nanus</i>	5.71	–	10	–	13.00	–	3.5	–
<i>Glauconycteris argentata</i>	8.60 $\pm$ 0.49	8.0–9.0 (5)	12.0 $\pm$ 0.0	12–12 (5)	–	–	6.90 $\pm$ 0.20	6.5–7.0 (5)
<i>G. egeria</i>	6.56 $\pm$ 0.42	6.1–7.0 (2)	14.5 $\pm$ 0.5	14–15 (2)	18.50 $\pm$ 0.20	18.3–18.7 (2)	6.4	–
<i>Myotis bocagii</i>	9.78 $\pm$ 0.16	9.6–9.9 (2)	14.5 $\pm$ 0.5	14–15 (2)	18.15 $\pm$ 0.05	18.1–18.2 (2)	5.60 $\pm$ 0.40	5.2–6.0 (2)
<i>Nycticeinops crassulus</i>	8.00	–	11	–	–	–	4.0	–
<i>N. happoldorum</i>	8.63 $\pm$ 0.29	8.2–9.0 (4)	12.0 $\pm$ 0.0	11–12 (4)	14.57 $\pm$ 0.48	14.0–15.1 (4)	7.35 $\pm$ 0.27	6.5–7.6 (4)
<i>Pipistrellus nanulus</i>	4.63 $\pm$ 0.30	4.3–4.9 (2)	9.5 $\pm$ 0.5	9–10 (2)	9.95 $\pm$ 0.25	9.7–10.2 (2)	3.75 $\pm$ 0.15	3.6–3.9 (2)
<i>Pseudoromicia mbamminkom</i>	8.66 $\pm$ 0.34	8.2–9.0 (3)	12.7 $\pm$ 1.0	12–14 (3)	13.65 $\pm$ 0.25	13.4–13.9 (2)	5.70 $\pm$ 0.30	5.4–6.0 (2)
<i>P. roseveari</i>	9.70 $\pm$ 0.28	9.5–9.9 (2)	12.0	–	15.10 $\pm$ 0.20	14.9–15.3 (2)	6.00 $\pm$ 0.28	5.8–6.2 (2)
<i>P. sp. indet.</i>	6.80 $\pm$ 0.00	6.8–6.8 (2)	12.0 $\pm$ 1.4	11–13 (2)	10.65 $\pm$ 0.45	10.2–11.1 (2)	4.70 $\pm$ 0.14	4.6–4.8 (2)
<i>P. tenuipinnis</i>	6.39	–	11	–	10.65	–	3.8	–
<i>Scotophilus nux</i>	12.08	–	16	–	24.63	–	22.5	–

Pseudoromicia mbamminkom was based (Grunwald *et al.*, 2023). In the 2022 survey, we captured 159 bats, 62 collected as voucher specimens, contributing 19 additional species to the Mbam Minkom Massif checklist. In general, the two surveys resulted in the capture of 253 bats, including 36 species from 21 genera in six families. The R/E curves based on abundance data showed an estimated

species richness of 42 bat species and an estimated sample completeness of 84%, while the Shannon entropy index was lower, indicating a species diversity of 15 species and an estimated sample completeness of 96% (Fig. 3).

Our findings include two new records for Cameroon: *Pseudoromicia roseveari* and *Nycticeinops happoldorum*, representing significant range

TABLE 3. Craniodental measurements (in mm) of voucher specimens, including: greatest length of skull (GLS), greatest skull height (GSH), condylo-incisive length (CIL), condylo-canine length (CCL), braincase breadth (BB), zygomatic breadth (ZB), postorbital width (POB), mastoid breadth (MAST), palatal length (PL), width across upper canines (C–C), maxillary toothrow length (C–M³), width across third molars (M³–M³), mandibular length (MAND), mandibular tooth row length (C–M₃). Measurements (all in mm) include mean ($\bar{x}$), standard deviation (SD), and range of values; they were taken by KA and AG

Family/Species	GLS		BB		ZB	
	$\bar{x} \pm \text{SD}$	Range (n)	$\bar{x} \pm \text{SD}$	Range (n)	$\bar{x} \pm \text{SD}$	Range (n)
Pteropodidae						
<i>Casinycotis argynnis</i>	27.52 $\pm$ 0.30	27.31–27.73 (2)	13.42 $\pm$ 0.01	13.40–13.43 (2)	20.76 $\pm$ 0.07	20.68–20.83 (2)
<i>Epomophorus pusillus</i>	28.89 $\pm$ 0.11	28.81–28.96 (2)	12.79 $\pm$ 0.18	12.66–12.91 (2)	17.62 $\pm$ 0.55	17.23–18.01 (2)
<i>Epomops franqueti</i>	43.17	–	17.09	–	25.02	–
<i>Hypsignathus monstrosus</i>	67.33 $\pm$ 5.20	62.13–72.53 (2)	21.74 $\pm$ 1.51	20.67–22.81 (2)	35.85 $\pm$ 1.90	33.95–37.75 (2)
<i>Megaloglossus woermanni</i>	27.18 $\pm$ 0.05	27.13–27.23 (2)	10.99 $\pm$ 0.15	10.84–11.14 (2)	14.06	–
<i>Myonycteris angolensis</i>	40.29 $\pm$ 1.37	37.42–42.70 (15)	15.60 $\pm$ 0.37	15.03–16.16 (14)	23.26 $\pm$ 1.02	21.11–25.05 (14)
<i>M. torquata</i>	32.46	–	13.36	–	19.76	–
<i>Rousettus aegyptiacus</i>	39.58 $\pm$ 0.35	39.23–39.93 (2)	16.76 $\pm$ 0.14	16.62–16.90 (2)	23.25 $\pm$ 0.30	22.95–23.54 (2)
<i>Scotonycteris zenkeri</i>	25.78 $\pm$ 0.86	24.92–26.64 (2)	11.58 $\pm$ 0.18	11.39–11.76 (2)	16.63 $\pm$ 0.61	16.01–17.24 (2)
Rhinolophidae						
<i>Rhinolophus alcyone</i>	23.38 $\pm$ 0.56	21.97–24.26 (8)	9.53 $\pm$ 0.27	9.22–9.97 (8)	11.99 $\pm$ 0.40	11.61–12.93 (8)
<i>R. landeri</i>	18.77 $\pm$ 0.28	18.22–19.21 (11)	8.05 $\pm$ 0.22	7.63–8.31 (13)	9.53 $\pm$ 0.18	9.14–9.79 (13)
<i>R. cf. simulator</i>	20.28	–	8.65	–	9.21	–
Hipposideridae						
<i>Doryrhina cyclops</i>	28.32 $\pm$ 0.17	28.14–28.49 (2)	11.13 $\pm$ 0.15	10.98–11.27 (2)	15.31 $\pm$ 0.09	15.22–15.39 (2)
<i>Hipposideros beatus</i>	16.84 $\pm$ 0.28	16.48–17.18 (4)	7.49 $\pm$ 0.12	7.37–7.70 (4)	9.37 $\pm$ 0.11	9.19–9.46 (4)
<i>H. curtus</i>	16.16 $\pm$ 1.19	14.56–17.42 (3)	7.75 $\pm$ 0.36	7.25–8.10 (3)	8.79 $\pm$ 0.04	8.75–8.83 (2)
<i>H. fuliginosus</i>	21.36 $\pm$ 0.08	21.26–21.46 (3)	9.38 $\pm$ 0.07	9.32–9.48 (3)	11.98 $\pm$ 0.34	11.54–12.37 (3)
<i>H. cf. ruber</i>	18.86 $\pm$ 0.33	18.37–19.53 (18)	8.68 $\pm$ 0.38	8.21–9.74 (18)	10.23 $\pm$ 0.33	9.57–10.80 (18)
<i>Macronycteris gigas</i>	37.61 $\pm$ 1.27	36.62–40.59 (7)	12.84 $\pm$ 0.38	12.28–13.25 (7)	20.36 $\pm$ 1.02	18.89–22.41 (7)
Nycteridae						
<i>Nycteris arge</i>	20.41 $\pm$ 0.23	20.18–20.64 (2)	8.47 $\pm$ 0.19	8.28–8.65 (2)	11.85 $\pm$ 0.01	11.83–11.86 (2)
<i>N. grandis</i>	26.96 $\pm$ 0	–	11.28	–	17.02	–
<i>N. major</i>	21.97 $\pm$ 0	–	9.76	–	12.13	–
Molossidae						
<i>Mops brachypterus leonis</i>	19.28	–	9.43	–	12.47	–
<i>M. spurrelli</i>	16.78	–	7.68	–	10.49	–
<i>M. thersites</i>	18.52	–	9.56	–	11.85	–
Vespertilionidae						
<i>Afronycteris nanus</i>	11.90	–	5.92	–	7.41	–
<i>Glauconycteris argentata</i>	12.07 $\pm$ 0.06	11.99–12.17 (5)	7.57 $\pm$ 0.14	7.47–7.84 (5)	8.96 $\pm$ 0.03	8.92–8.99 (3)
<i>G. egeria</i>	13.57 $\pm$ 0.00	13.57–13.57 (2)	7.23 $\pm$ 0.12	7.10–7.36 (2)	8.97 $\pm$ 0.12	8.85–9.08 (2)
<i>Myotis bocagii</i>	14.83 $\pm$ 0.07	14.76–14.89 (2)	7.30 $\pm$ 0.17	7.13–7.47 (2)	9.12 $\pm$ 0.13	9.03–9.21 (2)
<i>Nycticeinops crassulus</i>	12.81	–	6.95	–	–	–
<i>N. happoldorum</i>	14.54 $\pm$ 0.41	13.87–14.98 (4)	7.40 $\pm$ 0.22	7.25–7.78 (4)	9.71 $\pm$ 0.25	9.45–10.04 (4)
<i>Pipistrellus nanulus</i>	11.73 $\pm$ 0.12	11.64–11.81 (2)	6.20 $\pm$ 0.02	6.18–6.22 (2)	7.63 $\pm$ 0.10	7.53–7.73 (2)
<i>Pseudoromicia mbamminkom</i>	13.96 $\pm$ 0.47	13.45–14.38 (3)	7.01 $\pm$ 0.12	6.85–7.12 (3)	9.22 $\pm$ 0.10	9.11–9.35 (3)
<i>P. roseveari</i>	14.63 $\pm$ 0.24	14.46–14.80 (2)	7.36 $\pm$ 0.12	7.24–7.47 (2)	9.23 $\pm$ 0.20	9.03–9.42 (2)
<i>P. sp. indet.</i>	12.94 $\pm$ 0.35	12.69–13.19 (2)	6.37 $\pm$ 0.04	6.33–6.41 (2)	8.13 $\pm$ 0.01	8.12–8.14 (2)
<i>P. tenuipinnis</i>	12.24	–	6.16	–	–	–
<i>Scotophilus nux</i>	21.13	–	9.51	–	14.21	–

extensions for these species (~ 2,240 km). We also document the presence of two species of bats classified as Endangered by the IUCN: *Hipposideros curtus* and *Pseudoromicia roseveari* (assessed as *Neoromicia roseveari*); together with *Scotonycteris zenkeri* (Near Threatened); *Nycteris major* and *Glauconycteris egeria* listed as Data Deficient; and two species not yet evaluated, *Nycticeinops happoldorum* and *Pseudoromicia mbamminkom* (Monadjem, 2017; Jacobs *et al.*, 2019; Mickleburgh

et al., 2019; Tanishi, 2020; Obitte, 2021). We report additional captures of *P. mbamminkom*, detailing new capture localities, and present the first documentation of its echolocation call data. In addition, we provide external and craniodental measurements for 36 species of bat (Tables 2 and 3). Echolocation data is presented for 19 species recorded during our fieldwork, including acoustic measurements (Table 4) and sonograms (Figs. 5 and 6). For each captured species, we provide a species

TABLE 3. Extended

Family/Species	POB		MAST		GSH	
	$\bar{x} \pm SD$	Range (n)	$\bar{x} \pm SD$	Range (n)	$\bar{x} \pm SD$	Range (n)
Pteropodidae						
<i>Casinycteris argynnis</i>	5.21 $\pm$ 0.05	5.16–5.26 (2)	12.39 $\pm$ 0.11	12.28–12.50 (2)	–	–
<i>Epomophorus pusillus</i>	5.47 $\pm$ 0.11	5.39–5.54 (2)	12.66 $\pm$ 0.04	12.63–12.69 (2)	10.76	–
<i>Epomops franqueti</i>	7.16	–	17.47	–	14.52 $\pm$ 0.0	–
<i>Hypsingnathus monstrosus</i>	11.62 $\pm$ 0.73	10.89–12.35 (2)	22.43 $\pm$ 1.51	21.36–23.49 (2)	21.04 $\pm$ 1.51	19.53–22.54 (2)
<i>Megaloglossus woermanni</i>	4.27 $\pm$ 0.16	4.11–4.43 (2)	9.66 $\pm$ 0.14	9.52–9.79 (2)	8.12	–
<i>Myonycteris angolensis</i>	7.27 $\pm$ 0.61	6.08–8.28 (14)	14.76 $\pm$ 0.46	14.02–15.68 (14)	13.24 $\pm$ 0.47	12.68–13.79 (5)
<i>M. torquata</i>	5.34	–	12.03	–	10.68	–
<i>Rousettus aegyptiacus</i>	7.73 $\pm$ 0.16	7.57–7.88 (2)	15.95 $\pm$ 0.25	15.70–16.19 (2)	14.40 $\pm$ 0.26	14.14–14.66 (2)
<i>Scotonycteris zenkeri</i>	4.91 $\pm$ 0.07	4.84–4.98 (2)	10.97 $\pm$ 0.15	10.82–11.12 (2)	9.85 $\pm$ 0.06	9.79–9.91 (2)
Rhinolophidae						
<i>Rhinolophus alcyone</i>	3.00 $\pm$ 0.20	2.64–3.29 (8)	10.90 $\pm$ 0.30	10.62–11.54 (8)	8.58 $\pm$ 0.60	7.74–9.54 (6)
<i>R. landeri</i>	1.95 $\pm$ 0.44	1.57–2.52 (13)	9.03 $\pm$ 0.13	8.86–9.25 (13)	6.80 $\pm$ 0.30	6.48–7.33 (5)
<i>R. cf. simulator</i>	2.43	–	9.53	–	–	–
Hipposideridae						
<i>Doryrhina cyclops</i>	2.96 $\pm$ 0.08	2.88–3.04 (2)	11.58 $\pm$ 0.40	11.18–11.97 (2)	10.36	–
<i>Hipposideros beatus</i>	2.81 $\pm$ 0.22	2.61–3.15 (4)	8.77 $\pm$ 0.17	8.54–8.95 (4)	6.57 $\pm$ 0.49	6.08–7.06 (2)
<i>H. curtus</i>	2.91 $\pm$ 0.29	2.55–3.26 (3)	9.02 $\pm$ 0.51	8.35–9.58 (3)	5.98 $\pm$ 0.05	5.92–6.03 (2)
<i>H. fuliginosus</i>	3.42 $\pm$ 0.04	3.38–3.48 (3)	10.69 $\pm$ 0.07	10.61–10.77 (3)	8.52 $\pm$ 0.06	8.48–8.61 (3)
<i>H. cf. ruber</i>	2.95 $\pm$ 0.12	2.75–3.15 (18)	9.83 $\pm$ 0.21	9.41–10.26 (18)	7.05 $\pm$ 0.25	6.61–7.51 (9)
<i>Macronycteris gigas</i>	3.69 $\pm$ 0.17	3.41–3.95 (7)	16.40 $\pm$ 0.90	14.51–17.72 (7)	16.25 $\pm$ 0.84	15.17–17.21 (3)
Nycteridae						
<i>Nycteris arge</i>	5.05 $\pm$ 0.21	4.84–5.25 (2)	9.18 $\pm$ 0.01	9.17–9.19 (2)	8.86 $\pm$ 0.28	8.59–9.13 (2)
<i>N. grandis</i>	7.89	–	11.83	–	–	–
<i>N. major</i>	5.72	–	9.12	–	9.62	–
Molossidae						
<i>Mops brachypterus leonis</i>	3.96	–	11.11	–	7.61	–
<i>M. spurrelli</i>	3.57	–	9.74	–	6.08	–
<i>M. thersites</i>	4.22	–	10.71	–	6.94	–
Vespertilionidae						
<i>Afronycteris nanus</i>	3.46	–	6.74	–	4.29	–
<i>Glauconycteris argentata</i>	4.83 $\pm$ 0.06	4.76–4.94 (5)	7.71 $\pm$ 0.17	7.53–7.94 (5)	–	–
<i>G. egeria</i>	4.03 $\pm$ 0.06	3.97–4.08 (2)	8.37 $\pm$ 0.09	8.28–8.45 (2)	5.62 $\pm$ 0.08	5.54–5.69 (2)
<i>Myotis bocagii</i>	3.54 $\pm$ 0.05	3.48–3.59 (2)	7.65 $\pm$ 0.03	7.62–7.68 (2)	5.29	–
<i>Nycticeinops crassulus</i>	3.68	–	7.48	–	–	–
<i>N. happoldorum</i>	4.17 $\pm$ 0.14	3.92–4.29 (4)	8.36 $\pm$ 0.21	8.08–8.67 (4)	10.90 $\pm$ 0.08	10.76–10.96 (4)
<i>Pipistrellus nanulus</i>	3.56 $\pm$ 0.07	3.49–3.62 (2)	6.70 $\pm$ 0.12	6.58–6.81 (2)	4.32 $\pm$ 0.03	4.28–4.35 (2)
<i>Pseudoromicia mbaminkom</i>	3.69 $\pm$ 0.14	3.52–3.86 (3)	7.80 $\pm$ 0.11	7.68–7.94 (3)	5.08 $\pm$ 0.03	5.05–5.11 (2)
<i>P. roseveari</i>	4.06 $\pm$ 0.22	3.84–4.27 (2)	7.93 $\pm$ 0.14	7.79–8.07 (2)	5.73 $\pm$ 0.16	5.57–5.89 (2)
<i>P. sp. indet.</i>	3.60 $\pm$ 0.07	3.53–3.67 (2)	6.96 $\pm$ 0.14	6.82–7.09 (2)	4.64 $\pm$ 0.02	4.62–4.66 (2)
<i>P. tenuipinnis</i>	3.60	–	7.01	–	4.48	–
<i>Scotophilus nux</i>	5.09	–	12.70	–	8.37	–

account with relevant taxonomic and ecological notes.

SPECIES ACCOUNTS

Family Pteropodidae Gray, 1821
 Subfamily Rousettinae K. Andersen, 1912
 Tribe Scotonycterini Bergmans, 1997
Casinycteris argynnis Thomas, 1910
 Golden Short-palated Fruit Bat
 IUCN Red List status: Least concern
 (Fig. 4A)

Type locality

“Bitye, Ja River, SE Kameruns. Alt. 2000’.”
 Bitye (ca. 3.0056°N, 12.3492°E, 656 m) is located at its closest point ca. 12 km SW of the Dja River (also known as the Ngoko River).

New locality records

Three *C. argynnis* were caught in 2019 on the southwestern slope of the Mbam Minkom Massif, at Camp 3. An adult female was captured on August 19 followed by a female carrying a single neonate on August 20. No *C. argynnis* was captured in 2022.

TABLE 3. Extended

Family/Species	MAND		C–C		C–M ³	
	$\bar{x} \pm \text{SD}$	Range (<i>n</i>)	$\bar{x} \pm \text{SD}$	Range (<i>n</i>)	$\bar{x} \pm \text{SD}$	Range (<i>n</i>)
Pteropodidae						
<i>Casinycteris argynnis</i>	21.95 $\pm$ 0.11	21.84–22.05 (2)	6.45 $\pm$ 0.36	6.09–6.80 (2)	9.28 $\pm$ 0.04	9.23–9.32 (2)
<i>Epomophorus pusillus</i>	22.08 $\pm$ 0.51	21.72–22.44 (2)	5.92 $\pm$ 0.08	5.86–5.98 (2)	9.08 $\pm$ 0.14	8.98–9.18 (2)
<i>Epomops franqueti</i>	34.34	–	8.36 $\pm$ 0.0	–	14.08	–
<i>Hypsignathus monstrosus</i>	54.58 $\pm$ 4.48	50.10–59.06 (2)	14.35 $\pm$ 1.51	12.84–15.86 (2)	22.35 $\pm$ 1.35	21.00–23.69 (2)
<i>Megaloglossus woermanni</i>	20.95 $\pm$ 0.13	20.82–21.08 (2)	5.20 $\pm$ 0.34	4.86–5.53 (2)	8.86 $\pm$ 0.04	8.81–8.90 (2)
<i>Myonycteris angolensis</i>	31.79 $\pm$ 1.27	28.64–33.84 (14)	7.87 $\pm$ 0.29	7.42–8.52 (13)	15.89 $\pm$ 0.60	14.85–17.00 (14)
<i>M. torquata</i>	25.15	–	6.63 $\pm$ 0	–	11.31	–
<i>Rousettus aegyptiacus</i>	31.42 $\pm$ 0.19	31.23–31.61 (2)	7.67 $\pm$ 0.41	7.26–8.08 (2)	15.35 $\pm$ 0.15	15.20–15.49 (2)
<i>Scotoonycteris zenkeri</i>	19.61 $\pm$ 0.09	19.52–19.69 (2)	5.88 $\pm$ 0.04	5.84–5.92 (2)	8.26 $\pm$ 0.09	8.17–8.35 (2)
Rhinolophidae						
<i>Rhinolophus alcyone</i>	16.19 $\pm$ 0.38	15.74–16.96 (8)	6.21 $\pm$ 0.15	6.01–6.43 (7)	8.76 $\pm$ 0.29	8.32–9.21 (8)
<i>R. landeri</i>	12.34 $\pm$ 0.20	12.02–12.63 (12)	4.74 $\pm$ 0.13	4.55–4.98 (12)	6.59 $\pm$ 0.25	6.26–7.16 (13)
<i>R. cf. simulator</i>	12.5	–	4.62	–	6.82	–
Hipposideridae						
<i>Doryrhina cyclops</i>	19.35 $\pm$ 0.05	19.29–19.40 (2)	7.27 $\pm$ 0.19	7.08–7.46 (2)	10.37 $\pm$ 0.05	10.32–10.42 (2)
<i>Hipposideros beatus</i>	10.67 $\pm$ 0.15	10.50–10.90 (4)	4.08 $\pm$ 0.18	3.77–4.23 (4)	5.86 $\pm$ 0.22	5.66–6.24 (4)
<i>H. curtus</i>	10.73 $\pm$ 0.28	10.48–11.13 (3)	4.20 $\pm$ 0.50	3.79–4.90 (3)	5.42 $\pm$ 0.28	5.04–5.72 (4)
<i>H. fuliginosus</i>	14.54 $\pm$ 0.07	14.44–14.59 (3)	5.30 $\pm$ 0.09	5.18–5.41 (3)	7.76 $\pm$ 0.15	7.57–7.94 (3)
<i>H. cf. ruber</i>	11.99 $\pm$ 0.28	11.48–12.62 (18)	4.57 $\pm$ 0.31	3.95–5.56 (17)	6.53 $\pm$ 0.12	6.32–6.76 (19)
<i>Macronycteris gigas</i>	26.27 $\pm$ 0.66	25.23–27.58 (7)	10.57 $\pm$ 0.30	10.04–10.83 (7)	13.51 $\pm$ 0.34	13.16–14.15 (7)
Nycteridae						
<i>Nycteris arge</i>	13.54 $\pm$ 0.15	13.39–13.69 (2)	4.77 $\pm$ 0.02	4.75–4.79 (2)	6.75 $\pm$ 0.09	6.66–6.83 (2)
<i>N. grandis</i>	18.97	–	7.30	–	9.13	–
<i>N. major</i>	14.96	–	5.32	–	7.61	–
Molossidae						
<i>Mops brachypterus leonis</i>	14.01	–	5.21	–	6.91	–
<i>M. spurrelli</i>	12.20	–	4.93	–	6.48	–
<i>M. thersites</i>	14.05	–	5.65	–	6.85	–
Vespertilionidae						
<i>Afronycteris nanus</i>	28.27	–	3.27	–	3.99	–
<i>Glauconycteris argentata</i>	8.68 $\pm$ 0.07	8.55–8.75 (5)	4.26 $\pm$ 0.17	4.07–4.53 (4)	4.08 $\pm$ 0.03	4.04–4.12 (5)
<i>G. egeria</i>	9.22 $\pm$ 0.16	9.06–9.38 (2)	4.42 $\pm$ 0.11	4.31–4.52 (2)	4.22 $\pm$ 0.06	4.16–4.28 (2)
<i>Myotis bocagii</i>	10.81 $\pm$ 0.18	10.63–10.99 (2)	3.79 $\pm$ 0.13	3.66–3.92 (2)	5.38 $\pm$ 0.05	5.33–5.43 (2)
<i>Nycticeinops crassulus</i>	9.19	–	4.22	–	4.45	–
<i>N. happoldorum</i>	10.90 $\pm$ 0.08	10.76–10.96 (4)	4.88 $\pm$ 0.03	4.86–4.94 (3)	5.16 $\pm$ 0.13	4.98–5.30 (4)
<i>Pipistrellus nanulus</i>	8.42 $\pm$ 0.01	8.41–8.43 (2)	3.75 $\pm$ 0.07	3.68–3.81 (2)	4.11 $\pm$ 0.01	4.10–4.12 (2)
<i>Pseudoromicia mbaminkom</i>	10.27 $\pm$ 0.22	10.07–10.58 (3)	4.29 $\pm$ 0.17	4.07–4.47 (3)	4.75 $\pm$ 0.12	4.60–4.89 (3)
<i>P. roseveari</i>	10.40 $\pm$ 0.04	10.35–10.44 (2)	4.44 $\pm$ 0.09	4.35–4.53 (2)	5.03 $\pm$ 0.07	4.96–5.10 (2)
<i>P. sp. indet.</i>	9.47 $\pm$ 0.02	9.45–9.49 (2)	4.23 $\pm$ 0.03	4.19–4.26 (2)	4.32 $\pm$ 0.05	4.27–4.36 (2)
<i>P. tenuipinnis</i>	8.88	–	3.92	–	3.94	–
<i>Scotophilus nux</i>	15.32	–	6.92	–	7.16	–

New vouchers

FMNH 240664♀, 240665♀, 240666 (neonate; sex undet.).

Remarks

This species is found in southeastern Cameroon and eastern Gabon, in the southwestern Central African Republic (hereafter referred to as CAR), the Republic of the Congo, and throughout the Democratic Republic of the Congo (hereafter DRC — Hassanin, 2014). Our findings include additional documentation of *C. argynnis* in the

Centre Region similar to those found in Waghiiwimbom *et al.* (2019) and Atagana *et al.* (2018).

The estimated habitat of this species includes Northwestern Congolian lowland forest, Eastern Congolian swamp forest, and Southern Congolian forest-savanna mosaic (Jetz *et al.*, 2012; Happold, 2013a; Waghiiwimbom *et al.*, 2020). Our capture location was within an ecotone of submontane and lowland tropical forest at the intersection of two trails, resulting in a small forest clearing at an elevation of 884 m.

TABLE 3. Extended

Family/Species	M ³ -M ³		C-M ₃	
	$\bar{x} \pm \text{SD}$	Range (n)	$\bar{x} \pm \text{SD}$	Range (n)
Pteropodidae				
<i>Casinonycteris argynnis</i>	11.01 $\pm$ 0.08	10.92–11.09	11.62 $\pm$ 0.05	11.56–11.67 (2)
<i>Epomophorus pusillus</i>	9.44 $\pm$ 0.30	9.23–9.65 (2)	10.17 $\pm$ 0.21	10.02–10.32 (2)
<i>Epomops franqueti</i>	12.32	–	15.93	–
<i>Hypsignathus monstrosus</i>	20.51 $\pm$ 1.30	19.21–21.81 (2)	28.34 $\pm$ 1.71	26.63–30.04 (2)
<i>Megaloglossus woermanni</i>	6.68 $\pm$ 0.39	6.29–7.06 (2)	10.35 $\pm$ 0.09	10.26–10.43 (2)
<i>Myonycteris angolensis</i>	12.01 $\pm$ 0.46	11.24–12.68 (14)	17.92 $\pm$ 0.85	16.72–19.18 (14)
<i>M. torquata</i>	8.83	–	13.13	–
<i>Rousettus aegyptiacus</i>	11.77 $\pm$ 0.25	11.51–12.02 (2)	17.25 $\pm$ 0.27	16.98–17.52 (2)
<i>Scotonycteris zenkeri</i>	7.91 $\pm$ 0.18	7.73–8.08 (2)	9.10 $\pm$ 0.26	8.83–9.36 (2)
Rhinolophidae				
<i>Rhinolophus alcyone</i>	8.36 $\pm$ 0.17	8.16–8.73 (8)	9.61 $\pm$ 0.31	9.09–10.05 (8)
<i>R. landeri</i>	6.75 $\pm$ 0.15	6.56–7.00 (13)	7.58 $\pm$ 0.35	6.99–8.03 (11)
<i>R. cf. simulator</i>	6.67	–	8.25	–
Hipposideridae				
<i>Doryrhina cyclops</i>	10.83 $\pm$ 0.20	10.63–11.02 (2)	11.73 $\pm$ 0.24	11.49–11.97 (2)
<i>Hipposideros beatus</i>	6.47 $\pm$ 0.18	6.33–6.78 (4)	6.63 $\pm$ 0.16	6.42–6.80 (4)
<i>H. curtus</i>	6.01 $\pm$ 0.20	5.79–6.27 (3)	5.57 $\pm$ 0.13	5.39–5.71 (3)
<i>H. fuliginosus</i>	8.01 $\pm$ 0.24	7.67–8.21 (3)	8.37 $\pm$ 0.04	8.32–8.41 (3)
<i>H. cf. ruber</i>	6.85 $\pm$ 0.18	6.53–7.20 (18)	7.31 $\pm$ 0.36	6.67–7.83 (18)
<i>Macronycteris gigas</i>	13.64 $\pm$ 0.26	13.29–14.11 (7)	15.87 $\pm$ 0.56	14.81–16.27 (7)
Nycteridae				
<i>Nycteris arge</i>	7.28 $\pm$ 0.11	7.17–7.39 (2)	7.36 $\pm$ 0.13	7.23–7.48 (2)
<i>N. grandis</i>	10.56	–	11.08	–
<i>N. major</i>	7.21	–	8.18	–
Molossidae				
<i>Mops brachypterus leonis</i>	8.06	–	7.19	–
<i>M. spurrelli</i>	7.32	–	7.06	–
<i>M. thersites</i>	7.94	–	7.54	–
Vespertilionidae				
<i>Afronycteris nanus</i>	5.03	–	4.02	–
<i>Glauconycteris argentata</i>	6.00 $\pm$ 0.04	5.95–6.05 (5)	5.35 $\pm$ 0.06	5.26–5.47 (4)
<i>G. egeria</i>	5.84 $\pm$ 0.03	5.81–5.87 (2)	4.63 $\pm$ 0.14	4.49–4.77 (2)
<i>Myotis bocagii</i>	5.35 $\pm$ 0.09	5.26–5.44 (2)	5.71 $\pm$ 0.10	5.61–5.81 (2)
<i>Nycticeinops crassulus</i>	5.53	–	5.38	–
<i>N. happoldorum</i>	4.88 $\pm$ 0.04	4.86–4.94 (4)	6.64 $\pm$ 0.24	6.11–6.81 (4)
<i>Pipistrellus nanulus</i>	4.68 $\pm$ 0.03	4.65–4.71 (2)	4.38 $\pm$ 0.01	4.36–4.39 (2)
<i>Pseudoromicia mbaminkom</i>	5.52 $\pm$ 0.20	5.28–5.78 (3)	5.44 $\pm$ 0.48	5.05–6.02 (3)
<i>P. roseveari</i>	5.92 $\pm$ 0.24	5.68–6.16 (2)	5.47 $\pm$ 0.04	5.42–5.51 (2)
<i>P. sp. indet.</i>	5.29 $\pm$ 0.12	5.17–5.41 (2)	4.72 $\pm$ 0.06	4.65–4.78 (2)
<i>P. tenuipinnis</i>	5.11	–	4.29	–
<i>Scotophilus nux</i>	9.04	–	8.04	–

Scotonycteris zenkeri Matschie, 1894

Zenker's Fruit Bat

IUCN Red List status: Near threatened

(Fig. 4B)

Type locality

“Yaunde [= Yaoundé] Station,” Centre Region, Cameroon.

New locality records

In 2022, we captured two *S. zenkeri*. One female was caught at Camp 1, another at Camp 2.

New vouchers

FMNH 241852♀, 241853♀.

Remarks

Recent taxonomic revisions within the Scotonycterini tribe have elucidated the distribution and classification of *Scotonycteris zenkeri* (Hassanin, 2014; Hassanin *et al.*, 2015). As originally described, the tribe included three species, *S. zenkeri*, *S. ophiodon*, and *C. argynnis* (reviewed by Bergmans, 1994). Subsequent analyses reassigned *S. ophiodon* to *Casinonycteris*, and added *C. campomaanensis*

from southwestern Cameroon (Hassanin, 2014). Using mitochondrial data, Hassanin *et al.* (2015) identified the phylogeographic structure in *S. zenkeri*, delineating four distinct clades: Upper Guinea, Cameroon, western Equatorial Africa, and eastern DRC. Although nuclear data corroborated the structure of three clades, it highlighted potential male-mediated gene flow between western Equatorial Africa and eastern DRC clades. This discordance between mitochondrial and nuclear data led to the reclassification of *S. zenkeri* into three distinct species, assigning the nominal *S. zenkeri* population to the Cameroon region and suggesting new species designations for the Upper Guinea and Equatorial Africa populations (Hassanin *et al.*, 2015). Consequently, it is thought that the current distribution of *S. zenkeri* is restricted to the forests of southwestern Cameroon and southeastern Nigeria. However, the occurrence of this species in southeastern Nigeria remains to be confirmed.

Scotonycteris zenkeri is found in both undisturbed and moderately disturbed lowland forests and

has been recorded up to 1100 m in Cameroon's Mt Kupe and Rumpi Hills (Eisentraut, 1973). During our study, we captured one female in undisturbed forest at 1074 m and a male in moderately disturbed forest at 774 m on Mt. Mbam Minkom. Both bats were caught in a canopy net set over the Bitemgu river.

Tribe Rousettini K. Andersen, 1912

Rousettus aegyptiacus

(É. Geoffroy Saint-Hilaire, 1810)

Egyptian Rousette

IUCN Red List status: Least concern

Type locality

Giza (Great Pyramid), Egypt.

New locality records

In 2022, we captured 10 *R. aegyptiacus*; seven at Camp 2 (5 ♀♀, 2 ♂♂), one female each at Camp 5 and Camp 6, and one male at Camp 7.

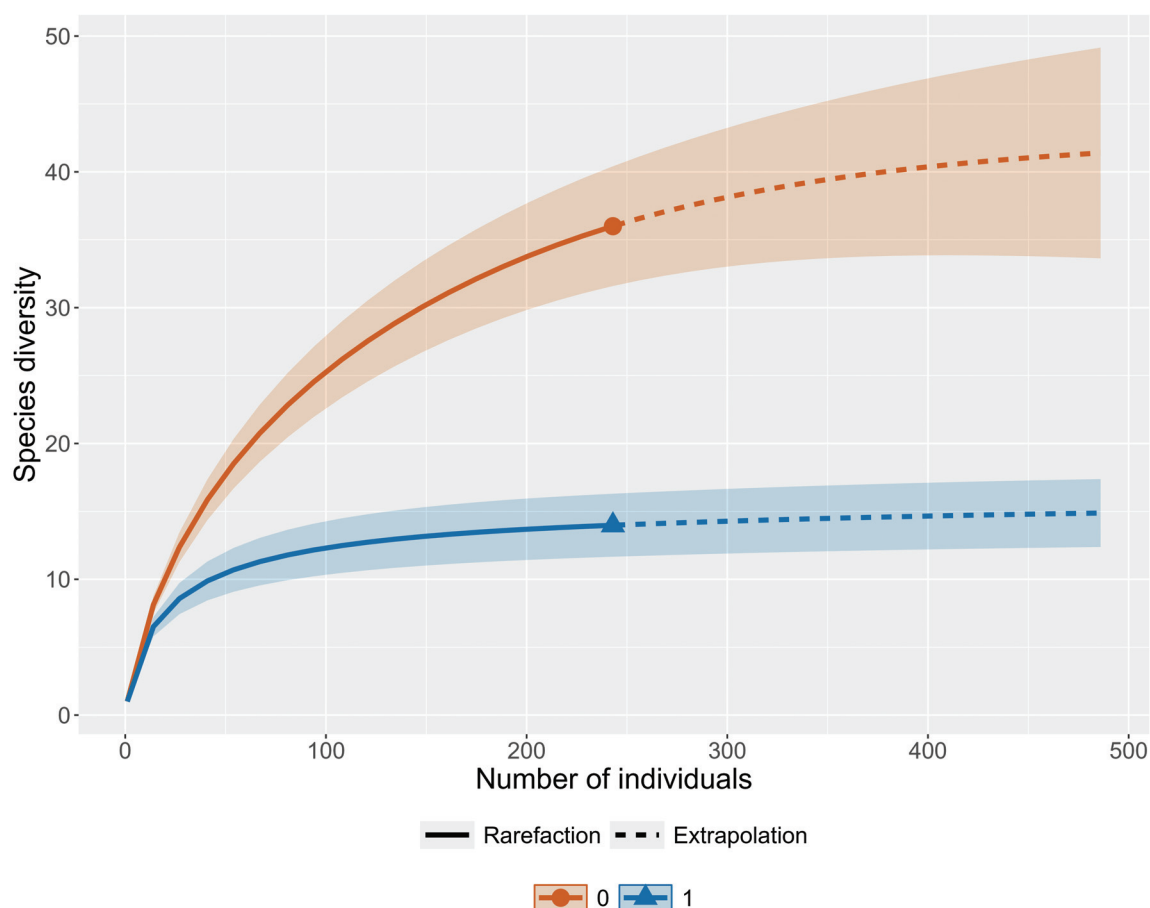


FIG. 3. Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves for species richness ($q = 0$; orange line) and Shannon diversity ($q = 1$; blue line) with 95% confidence intervals (shaded areas). These curves aggregate survey data from all sites across two years, 2019 and 2022

TABLE 4. Echolocation call parameters of bats recorded during surveys. Number of individuals recorded (Indiv) and number of pulses (N) are given for each species. Parameters include: Fmin — estimate of minimum signal frequency, Fmax — estimate of maximum signal frequency, Fpeak — frequency which has the highest energy, Dur — signal duration. Values represent mean ($\bar{x}$), standard deviation (SD), and range for each measurement

Family/Species	Indiv.	N	Fppeak (kHz)		Fmin (kHz)		Fmax (kHz)		Dur (ms)	
			$\bar{x} \pm \text{SD}$	Range	$\bar{x} \pm \text{SD}$	Range	$\bar{x} \pm \text{SD}$	Range	$\bar{x} \pm \text{SD}$	Range
Rhinolophidae										
<i>Rhinolophus alcyone</i>	2	52	63.6 $\pm$ 0.4	63.3–64.1	57.7 $\pm$ 2.1	55.4–60.9	64.2 $\pm$ 0.3	64.0–64.7	68.0 $\pm$ 11.7	23.0–83.3
<i>R. landeri</i>	2	12	103.2 $\pm$ 0.5	102.8–103.8	85.0 $\pm$ 1.4	83.2–86.6	104.6 $\pm$ 0.8	103.9–105.3	75.0 $\pm$ 16.5	53.7–88.7
<i>R. cf. simulator</i>	1	32	70.7 $\pm$ 0.2	70.1–71.1	58.7 $\pm$ 2.3	55.2–61.5	71.4 $\pm$ 0.5	70.8–72.1	32.4 $\pm$ 4.6	27.7–39.7
Hipposideridae										
<i>Doryrhina cyclops</i>	2	48	58.9 $\pm$ 0.5	58.7–59.7	50.5 $\pm$ 6.1	46.5–59.7	59.5 $\pm$ 0.8	58.9–60.7	20.0 $\pm$ 2.1	16.6–23.2
<i>Hipposideros beatus</i>	4	162	129.4 $\pm$ 4.0	127.8–138.6	114.3 $\pm$ 8.4	107.4–129.3	132.1 $\pm$ 4.5	129.0–140.6	5.4 $\pm$ 1.5	3.6–8.5
<i>H. curtus</i>	2	79	97.0 $\pm$ 4.5	91.7–100.9	90.0 $\pm$ 4.6	84.6–95.1	98.2 $\pm$ 5.0	93.1–102.6	11.0 $\pm$ 0.4	9.3–11.4
<i>H. fuliginosus</i>	2	61	109.9 $\pm$ 0.2	109.7–110.1	92.6 $\pm$ 6.0	86.7–98.8	111.1 $\pm$ 0.1	111.0–111.2	6.0 $\pm$ 1.6	2.8–9.2
<i>H. cf. ruber</i>	6	95	142.6 $\pm$ 3.4	133.3–146.7	123.2 $\pm$ 2.7	120.3–128.5	143.3 $\pm$ 4.2	133.3–145.5	5.5 $\pm$ 1.1	4.2–7.0
<i>Macronycteris gigas</i>	4	115	51.9 $\pm$ 1.0	50.7–53.6	46.2 $\pm$ 1.1	44.5–47.9	52.7 $\pm$ 0.7	52.2–53.9	11.9 $\pm$ 2.0	9.1–14.6
Vespertilionidae										
<i>Afronycteris nanus</i>	1	12	77.2 $\pm$ 3.3	72.7–80.6	63.4 $\pm$ 1.2	59.9–64.6	115.2 $\pm$ 7.6	112.8–117.8	2.7 $\pm$ 0.7	2.1–3.5
<i>Glauconycteris argentata</i>	2	41	42.5 $\pm$ 0.5	42.2–42.9	40.6 $\pm$ 0.1	40.5–40.6	75.1 $\pm$ 4.3	64.8–78.2	1.7 $\pm$ 0.1	1.6–1.8
<i>G. egeria</i>	2	24	26.3 $\pm$ 2.5	21.5–37.0	22.0 $\pm$ 2.1	19.9–26.1	53.8 $\pm$ 2.6	47.3–56.2	2.6 $\pm$ 0.6	1.6–3.3
<i>Myotis bocagii</i>	2	133	40.1 $\pm$ 1.0	39.0–42.0	31.4 $\pm$ 4.2	28.8–42.0	67.9 $\pm$ 5.6	61.9–76.5	3.2 $\pm$ 0.7	2.2–4.3
<i>Nycticeinops happoldorum</i>	3	27	46.8 $\pm$ 1.6	43.7–49.4	41.2 $\pm$ 1.6	39.0–43.7	87.4 $\pm$ 10.4	61.5–100.1	2.2 $\pm$ 0.2	2.1–2.6
<i>Pipistrellus nanulus</i>	2	27	57.3 $\pm$ 0.6	57.0–58.0	54.0 $\pm$ 1.6	51.3–55.2	106.0 $\pm$ 6.0	100.6–113.5	2.4 $\pm$ 0.3	2.2–2.9
<i>Pseudoromicia mbamminkom</i>	1	22	41.6 $\pm$ 2.4	36.0–42.9	34.2 $\pm$ 0.8	33.5–36.8	58.4 $\pm$ 1.5	55.6–68.4	2.5 $\pm$ 0.3	2.0–2.9
<i>Ps. roseveari</i>	2	20	39.9 $\pm$ 2.6	35.7–55.3	37.9 $\pm$ 1.2	34.8–38.8	53.1 $\pm$ 6.1	41.2–72.8	2.0 $\pm$ 0.3	1.6–2.4
<i>Ps. sp. indet.</i>	1	7	44.3 $\pm$ 0.4	44.0–44.8	39.8 $\pm$ 0.8	39.2–41.2	72.1 $\pm$ 0.0	72.1–72.1	2.3 $\pm$ 0.2	2.1–2.6
<i>Scotophilus nux</i>	1	23	43.7 $\pm$ 1.0	42.7–44.9	41.2 $\pm$ 2.8	38.1–44.1	75.1 $\pm$ 5.8	71.5–83.8	2.0 $\pm$ 0.2	1.7–2.2



FIG. 4. Portraits of 33 species collected from Mbam Minkom Massif and surrounding forest in 2019 and 2022. (A) *Casinycteris argynnis*, (B) *Scotonycteris zenkeri*, (C) *Megaloglossus woermanni*, (D) *Myonycteris angolensis*, (E) *Myonycteris torquata*, (F) *Epomophorus pusillus*, (G) *Epomops franqueti*, (H) *Hypsignathus monstrosus* (male), (I) *H. monstrosus* (female), (J) *Rhinolophus alcyone*, (K) *R. landeri*, (L) *R. cf. simulator*, (M) *Doryrhina cyclops*, (N) *Hipposideros beatus*, (O) *H. curtus*, (P) *H. fuliginosus*, (Q) *H. ruber*, (R) *Macronycteris gigas*, (S) *Nycteris arge*, (T) *N. grandis*, (U) *N. major*, (V) *Mops brachypterus leonis*, (W) *M. spurrelli*, (X) *M. thersites*, (Y) *Glauconycteris argentata*, (Z) *G. egeria*, (aa) *Myotis bocagii*, (bb) *Nycticeinops happoldorum*, (cc) *Pipistrellus nanulus*, (dd) *Pseudoromicia mbamminkom*, (ee) *P. roseveari*, (ff) *P. sp. indet.* (medium brown color morph), (gg) *P. sp. indet.* (grey-brown color morph), (hh) *P. tenuipinnis*, (ii) *Scotophilus nux*

New vouchers

FMNH 241850♀, 241851♀.

Remarks

Individuals were distinguished from morphologically similar *Myonycteris angolensis* and *M. torquata* by the point of attachment of the wing membrane and different patterns of the palatal ridge (Happold, 2013e, 2013n). Specifically, in *R. aegyptiacus*, the wing membrane attaches at the first toe, in contrast to the second toe attachment in *Myonycteris* (Happold, 2013i, 2013n). *Rousettus aegyptiacus* is characterized by four undivided palatal ridges and three divided ridges, with the first ridge extending to the toothrow and the seventh partially located in the dental region. On the contrary, *M. angolensis* has three undivided and four divided palatal ridges, with the first ridge not extending labially to the toothrow, and the seventh and eighth ridges located postdentally.

Rousettus aegyptiacus has been recorded in all biotic zones in Africa, with the exception of the Mediterranean Coastal, Saharan Arid, and Sahel Savanna zones. Our captures on Mt. Mbam Minkom occurred predominantly in mildly disturbed forests. A female bat was captured at the base of the mountain near residential clearings. We captured one individual in a disturbed forest near an agricultural clearing and a male in a secondary forest near subsistence farms. Most of our bat captures, eight in total, occurred in a canopy net, with an additional two bats captured using mist nets.

Tribe Myonycterini Lawrence and Novick, 1963

Megaloglossus woermanni Pagenstecher, 1885
Woermann's Bat

IUCN Red List status: Least concern
(Fig. 4C)

Type locality

"Sibange-Farm" [Gabon]. "exact locality untraced" (Rosevear, 1965: 123). This location is likely on the shores of Mondah Bay, northeast of Libreville, based on the type localities of other organisms: including *Sibangea arborescens* D. Oliver, 1883 (Malpighiales: Putranjivaceae), which is listed as "Munda, Sibange Farm" and named after the locality. Tanshi *et al.* (2022) noted the type locality as "Sigange near Libreville".

New locality records

Across both years, we captured 11 *M. woermanni*. A single lactating female was captured at

Camp 3 in 2019. Ten *M. woermanni* were captured in 2022; eight (7 ♀♀, 1 ♂) at Camp 5, one female at Camp 7, and one female with a neonate was caught and immediately released at Camp 8.

New vouchers

FMNH 240667♀, 241842♀.

Remarks

This species is widely distributed throughout much of Central Africa extending west into Nigeria and Benin. It is found in primary and secondary tropical lowland forests, as well as clearings, banana plantations, and other cultivated tropical forest areas (Happold, 2013h). Characterized by a long and slender rostrum, this genus is easily recognizable as the only nectar specialist in Africa (Happold, 2013h; Tanshi *et al.*, 2021). Most of our *M. woermanni* captures occurred at the base of the mountain, in minimally disturbed forest, adjacent to residences and areas of subsistence agriculture plots. We also captured a female in minimally disturbed secondary forests and another female carrying a neonate in a similar habitat adjacent to a cocoa farm. Of our total captures, nine *M. woermanni* occurred in a canopy net, with two individuals caught in a mist net.

Myonycteris angolensis (Bocage, 1898)

Angolan Fruit Bat

IUCN Red List status: Least concern
(Fig. 4D)

Type locality

Pungo Andongo, north of the Cuanza River, Cahata, Quibula, Angola.

New locality records

Across both surveys, we captured 71 *M. angolensis*. During the 2019 survey, 43 *M. angolensis* were captured: 26 at Camp 1, 12 at Camp 2, and five at Camp 3. In 2022, we captured 28 *M. angolensis*. Of these, three (1 ♀, 2 ♂♂) were captured at Camp 1, 16 (12 ♀♀, 4 ♂♂) at Camp 2, and three females at Camp 5. Only six bats were caught in the surrounding lowlands: four were captured at Camp 6 (3 ♀♀, 1 ♂); and two females were captured at Camp 8.

New vouchers

FMNH 240669♀, 240670♀, 240671♀, 240672♂, 240673♂, 240674♂, 240675♀, 240676♂, 240677♂, 241844♀, 241845♂, 241846♂, 241847♀, 241848♀.

Remarks

Comprehensive assessments of phylogenetic relationships among pteropodids based on complete mitochondrial sequences (Hassanin *et al.*, 2020) and on nuclear and mitochondrial genes (Almeida *et al.*, 2016, 2020; Nesi *et al.*, 2021) appear to resolve *angolensis* as nested within *Myonycteris*. Individuals of *M. angolensis* were distinguished from *M. torquata* based on size and pattern of the palatal ridge. *M. angolensis* is larger (FA of 68–90 mm) compared to *M. torquata* (FA of 56–67 mm — Happold, 2013*i*). Additionally, *M. angolensis* is characterized by a distinctive pattern of palatal ridges, consisting of three undivided and four divided ridges, two of which are located posterior to the upper dentition (Happold, 2013*i*).

This species is widely distributed across West and Central Africa, extending from Senegal east to Ethiopia and south to Mozambique and Angola (Happold, 2013*i*). Most of our captures were on Mt. Mbam Minkom, with *M. angolensis* being the bat most frequently caught at Camps 1–3. Two roosting caves were identified during the 2022 survey. At Camp 1, a guide led us to a cave approximately 600 m southeast of the camp, which served as a roost for both *Hipposideros* cf. *ruber* and *M. angolensis*. Similarly, a guide identified a roosting cave approximately 300 meters southwest of Camp 6. We set up two 6-meter nets around the cave entrances/exits, capturing several individuals of *M. angolensis* and *Hipposideros* cf. *ruber*. The captured bats were released near the cave.

Myonycteris torquata (Dobson, 1878)
Little Collared Fruit Bat
IUCN Red List status: Least concern
(Fig. 4E)

Type locality

“Africa (Angola).” Restricted by Bergmans (1976) to “Lower Cuanza Region” and further restricted by Crawford-Cabral and Mesquitela (1989) to “Golungo Alto,” Cuanza Norte Province, northern Angola.

New locality records

A single female *M. torquata* was captured at Camp 7 in 2022.

New vouchers

FMNH 241849♀.

Remarks

The distribution of this species extends throughout Central Africa, from Cameroon to southwestern

South Sudan, southward to southern DRC and northern Angola. It is also found on Bioko Island. It is differentiated in the field from the morphologically similar *M. angolensis* by size and pattern of the palatal ridge (see the *M. angolensis* account). This individual was caught in a canopy net set parallel to a river in a secondary lowland forest.

Tribe Epomophorini Gray, 1866

Epomophorus pusillus Peters, 1868

Peters’s Dwarf Epauletted Fruit Bat

IUCN Red List status: Least concern

(Fig. 4F)

Type locality

“Westafrika [= West Africa], Gambia, Gabon, Yoruba.” Restricted by Bergmans (1989) to Yoruba [= Yorubaland], SE Nigeria.

New locality records

Across both surveys, 15 *E. pusillus* were captured. In 2019, a female was captured at Camp 3. In 2022, we captured 14 individuals; three (1 ♀, 2 ♂♂) at Camp 2, 10 at Camp 5 (4 ♀♀, 5 ♂♂, and one released before its sex was determined), and one female at Camp 6.

New vouchers

FMNH 240668♀, 241838♀.

Remarks

Formerly classified as *Micropteropus pusillus*, this species has been reclassified as *Epomophorus pusillus*. Recent revisions of the genus *Epomophorus* have expanded it to include species historically classified within the genus, species subsequently transferred to *Epomops*, species considered as a subgenus of *Epomophorus* (i.e., *Micropteropus pusillus*), and species originally described within *Micropteropus*. This comprehensive reclassification is supported by findings from several recent phylogenetic studies (Nesi *et al.*, 2013; Almeida *et al.*, 2016, 2020; Amador *et al.*, 2018; Hassanin *et al.*, 2020), and is further supported by Almeida *et al.* (2020) through their reinterpretation of palatal ridge patterns.

Epomophorus pusillus has a recorded range extending from Senegal to western Ethiopia and southward to Angola. It generally avoids the interior Congolian forest, favoring a low-elevation forest-savanna mosaic, and is uncommon in closed tropical forest habitats (Thomas and Henry, 2013). Our

observations support the notion that *E. pusillus* may penetrate into tropical forests along roadways, cutovers, plantations, and agricultural clearings (Thomas and Henry, 2013). The majority of *E. pusillus* were captured in minimally disturbed forest near the base of Mt. Mbam Minkom, adjacent to residential clearings.

Recent studies further support its preference for open and edge habitats, although it may occasionally and opportunistically inhabit more dense forests. Waghiiwimbom *et al.* (2020) reported observations of *E. pusillus* in forested areas of the Centre Region, however, the majority of their captures were in more open habitats including traditional farms (63%) and savannahs (30%). Similarly, Atagana *et al.* (2018) recorded *E. pusillus* in a variety of habitats, including forests, swampy savannahs, and forest-savannah transition zones within Mpem and Djim National Park. Tanshi *et al.* (2021) captured a single individual in southeastern Nigeria, within a forest approximately 1 km from the forest edge.

Bakwo Fils *et al.* (2021) suggested that disturbed areas might offer additional resources beneficial to *E. pusillus*, noting its absence in undisturbed habitats of Cameroon's Afromontane Forest biome. With the forest around Mt. Mbam Minkom becoming more open, it could offer a more suitable habitat for this species.

Epomops franqueti (Tomes, 1860)
Franquet's Epauletted Fruit Bat
IUCN Red List status: Least concern
(Fig. 4G)

Type locality
"Gabon".

New locality records

In 2022, we captured two female *E. franqueti* at Camp 6.

New vouchers

FMNH 241839♀.

Remarks

Epomops franqueti is found mainly in lowland tropical forests, but has also been recorded in montane areas, forest-woodland-grassland mosaic, and dry and wet woodland (Bergmans, 1994; Happold, 2013b). Observations in Gabon and Cameroon may indicate a preference for secondary forest, as well as edge and open habitats, including disturbed

habitats (Bradbury, 1981; Happold, 2013b; Atagana *et al.*, 2018; Waghiiwimbom *et al.*, 2020; Bakwo Fils *et al.*, 2021). Our findings are consistent with these patterns; both *E. franqueti* captures occurred in a secondary forest adjacent to a cocoa farm and dispersed subsistence crop patches. Both individuals were caught in a canopy net set across a river.

Hypsignathus monstrosus H. Allen, 1861
Hammer-headed Fruit Bat
IUCN Red List status: Least concern
(Fig. 4H–I)

Type locality
"Western Africa."

New locality records

In 2022, we captured three *H. monstrosus*. Two females were captured at Camp 6, and a single male at Camp 7.

New vouchers

FMNH 241840♀, 241841♂

Remarks

Continental Africa's largest bat species, *H. monstrosus* inhabits tropical moist forest and forest-savanna mosaic across West and Central Africa, extending from Sierra Leone to western Uganda, and southwestward to NW Angola, with isolated occurrences in W Kenya and Ethiopia. Our records align with the established distribution: the two females were captured in riparian forest adjacent to a cocoa farm and dispersed subsistence agriculture plots, and the male was captured in minimally disturbed secondary lowland forest ca. 500 m from a large property clearing. We also observed this species roosting in trees toward the northwest edge of Yaoundé, indicating its adaptability to certain urban environments. All *H. monstrosus* were caught in a canopy net.

Family Rhinolophidae Gray, 1825

Rhinolophus alcyone Temminck, 1853
Halcyon Horseshoe Bat
IUCN Red List status: Least concern
(Fig. 4J)

Type locality
"Boutry River, Guinea [= Ghana]."

New locality records

Across both years, we captured eight *R. alcyone*. In 2019, a female *R. alcyone* was captured at Camp 2, and another at Camp 4. Six individuals were captured in 2022; one female at Camp 1, a single male at Camp 5, 6, and 7, and one female and one male at Camp 8.

New vouchers

FMNH 240678♀, 240679♀, 241854♀, 241855♂, 241856♂, 241857♂, 241858♀, 241859♂.

Remarks

This species is predominantly found in tropical moist lowland forests, but also in forest-savanna mosaic. It is distributed throughout much of western and central Africa; scattered records in the Congo may reflect inadequate sampling in the region (Happold, 2013; Monadjem *et al.*, 2017e). We captured *R. alcyone* both on Mt. Mbam Minkom and in the surrounding forest, including all sites extending out from the mountain, although the capture numbers at each site were very low.

Bats recorded during our surveys had a peak frequency of 63.6 ± 0.4 (63.3–64.1) kHz aligning with calls recorded at 67.6 kHz in Nigeria (Tanshi *et al.*, 2021), however, much lower than calls reported at 87 kHz from Uganda (Burgin, 2019a; Monadjem *et al.*, 2020).

Rhinolophus landeri Martin, 1838

Lander's Horseshoe Bat

IUCN Red List status: Least concern

(Fig. 4K)

Type locality

Bioko Island, Equatorial Guinea.

New locality records

Across both years, 13 *R. landeri* were captured. In 2019, we captured eight individuals: six at Camp 2 (2 ♀♀, 4 ♂♂), and one female and one male at Camp 3. In 2022, we captured five individuals: one male at Camp 2, and four individuals (3 ♀♀, 1 ♂) at Camp 7.

New vouchers

FMNH 240681♀, 240682♀, 240683♂, 240684♂, 240685♂, 240686♂, 240687♂, 240688♀, 241860♂, 241861♀, 241862♂, 241863♀, 241864♀.

Remarks

Recent molecular work suggests that *R. landeri* represents a complex constituted by multiple

species-level taxa, including *R. lobatus* (Peters, 1852), formerly treated as a subspecies (Taylor *et al.*, 2018; Demos *et al.*, 2019b). The validity and limits of *R. landeri* and *R. lobatus*, along with their synonyms, have been uncertain since their first generic revision (Patterson *et al.*, 2024). Demos *et al.* (2019b) distinguished four well-defined lineages within the *landeri* group. This included support for *R. lobatus* as distinct from *R. landeri* and an additional unnamed clade (referred to as *R. cf. landeri*) in East Africa. However, the geographic ranges of these forms remain uncertain, because Happold (2013g) included virtually all of sub-Saharan Africa in the range of *R. landeri*. The relationships and geographical distribution within the *landeri* complex, including a reevaluation of distribution based on recent genetic findings, are detailed in Patterson *et al.* (2024).

During our study, all captures of *R. landeri* occurred on the Mbam Minkom Massif in the primary and secondary forest. In particular, some bats displayed a unique coloration that appeared to blend characteristics of both the grey and orange morphs. These individuals had greyish-brown dorsal fur and light grey ventral fur, with a distinctive broad orange band throughout the ventral midsection fading to grey near the flanks.

We recorded the echolocation calls of two individuals with a peak frequency of 103.2 ± 0.5 (102.8–103.8) kHz and an average duration of 75.0 ± 16.5 (53.7–88.7) ms. Our recordings are consistent with those from *R. landeri* individuals across West Africa, including Guinea (103.3 kHz — Burgin, 2019c), Burkina Faso (105.6–108.5 kHz — Burgin, 2019c), Liberia (104.3 kHz — Taylor *et al.*, 2018), and Nigeria (102 kHz — Tanshi *et al.*, 2021).

Rhinolophus cf. simulator K. Andersen, 1904

Bushveld Horseshoe Bat

IUCN Red List status: Least concern

(Fig. 4L)

Type locality

“Mazoe [Valley], Mashonaland,” Zimbabwe.

New locality records

In 2019, a single female *R. cf. simulator* was captured at Camp 3.

New vouchers

FMNH 240680♀.

Remarks

This individual was initially identified as *Rhinolophus* sp. in the field because its external morphology did not match any species with a known distribution in Cameroon. The measurements somewhat align with those of the nominal *R. simulator* as reported by Cotterill (2013), Cotterill and Happold (2013), and Monadjem *et al.* (2020). However, nose-leaf and forearm measurements are slightly larger than the known ranges for *R. simulator* (FA = 49.68 — Cotterill and Happold, 2013; Monadjem *et al.*, 2020). Furthermore, the ears are relatively large (25 mm; 51.0% of the FA).

Additionally, the peak call frequency was observed at 70.7 ± 0.2 (70.1–71.1) kHz with an average call duration of 32.4 ± 4.6 (27.7–39.7) ms. This contrasts with CF components recorded at 84–86 kHz in Malawi, 83.2–84.4 kHz in Eswatini and 80.6–83 kHz in South Africa (Cotterill and Happold, 2013; Burgin, 2019d; Monadjem *et al.*, 2020). For further comparison, *R. denti* has been recorded at 110.9 kHz in South Africa (Burgin, 2019b). Given the morphological, distributional, and acoustic discordance, combined with the unresolved phylogenetic relationships within the simulator clade, we are unable at this time to confidently identify this specimen as *R. simulator*. We captured this individual in a mist net set along a timber extraction trail in the ecotone of moderately disturbed submontane and lowland forests.

Family Hipposideridae Lydekker, 1891

Doryrhina cyclops (Temminck, 1853)

Cyclops Leaf-nosed Bat

IUCN Red List status: Least concern

(Fig. 4M)

Type locality

“Boutry River, coast of Guinea” [= Ghana].

New locality records

Across both years, we captured two *D. cyclops*. One male was captured at Camp 1 in 2019, and one female at the same location in 2022.

New vouchers

FMNH 240689♂, 241866♀.

Remarks

Based on morphological and molecular evidence, Foley *et al.* (2017) elevated *Doryrhina* from a subgenus within *Hipposideros* to the genus level, placing it sister to the genus *Macronycteris*,

and thus reclassifying *D. cyclops* from its previous designation as *Hipposideros cyclops*. *Doryrhina cyclops* is not easily distinguished from *D. camerunensis* in the field but can be distinguished morphologically by size: *D. cyclops* is smaller with a forearm length less than 74.0 mm, while *D. camerunensis* is larger with a forearm length exceeding 74.0 mm (Hill, 1963; Happold, 2013f). Our specimens had an average FA length consistent with *D. cyclops* (FA = 67.5 ± 2.1 mm).

Doryrhina cyclops is found across West and Central Africa, including scattered locations in East Africa (Fahr, 2013a; Happold, 2013f). We captured *D. cyclops* on Mt. Mbam Minkom, near the origin of the Bitemgu River, in a transitional undisturbed primary forest at an elevation of 1,074 meters. One individual was caught using a mist net set a meter above the pooled river and another in the same location in a canopy net.

This species is known to emit calls at 51.4 ± 0.5 kHz in Uganda (Monadjem *et al.*, 2011), 59.7 (58.4–60.8) kHz in West Africa (Decher and Fahr, 2005), including 55.5 kHz from Mount Nimba (Monadjem *et al.*, 2013b), and 59.8 (58.5–61.1) kHz in Nigeria (Tanshi *et al.*, 2021). We recorded calls exhibiting a peak frequency of 58.9 ± 0.5 (58.7–59.7) kHz, consistent with those documented in West Africa.

Hipposideros beatus Andersen, 1906

Benito Roundleaf Bat

IUCN Red List status: Least concern

(Fig. 4N)

Type locality

“15 miles from Benito River” [Equatorial Guinea]. The Benito River spans the country from E to W, rising in Gabon. It is possible that Andersen was referring to the mouth of the Benito River, at Mbini (ca. 1.593°N, 9.623°E). However, absent an explicit statement from Andersen, or field notes from the collector (G. L. Bates), the type locality should be considered as the vicinity of the Benito River (locally known as the Mbini or Uoro River) in Equatorial Guinea. A second specimen listed in the description is noted as having been collected, also by G. L. Bates, in “Efulen, Cameroons” [= Efulan] in the South Region. A final paratype is listed from the US National Museum with a locality of “Mt. Coffee, Liberia”.

New locality records

Six *H. beatus* were captured over both years. Two were captured in 2019: a male at Camp 1, and

another male at Camp 2. Four *H. beatus* were captured in 2022: a male at Camp 6 and three individuals (1 ♀, 2 ♂♂) at Camp 8.

New vouchers

FMNH 240690♂, 240691♂, 241868♂, 241869♂, 241870♀.

Remarks

Hipposideros beatus has a discontinuous distribution across West and Central Africa, ranging from Sierra Leone to South Sudan and Kenya (Happold, 2013e; Webala *et al.*, 2019b). Patterson *et al.* (2020) identified reciprocal monophyly and a 4.4% divergence of the mtDNA sequence divergence between West African populations of *H. beatus* and those of Central and East Africa, suggesting genetic differentiation. This indicates the need for more research to elucidate the relationships among these populations. Our fieldwork resulted in the capture of *H. beatus* in four locations: two within intact primary forest on Mt. Mbam Minkom and two in adjacent areas, including moderately disturbed forest and secondary forest near a cocoa farm.

Webala *et al.* (2019b) provided the first report of *H. beatus* in Kenya, documenting echolocation call data with CF components ranging from 114.8–123.7 kHz, highlighting that the CF-component frequency was highly consistent across individual calls (variation 0.0–0.2 kHz) but varied up to 10 kHz among individuals. The authors also noted that calls from Côte d'Ivoire exhibited CF components at 139–147 kHz, approximately 20 kHz higher than those from Kenya; however, this population is recognized as a different subspecies (Happold, 2013e). *Hipposideros beatus* calls are documented at 129 kHz on Mount Nimba (Monadjem *et al.*, 2013a) and at 125.9 ± 2.3 (113.6–142.9) kHz in Nigeria (Tanshi *et al.*, 2021). The echolocation calls recorded during this study exhibited a peak frequency of 129.4 ± 4.0 (127.8–138.6) kHz, and a call duration of 5.4 ± 1.5 (3.6–8.5) ms.

Hipposideros curtus G. M. Allen, 1921
Short-tailed Roundleaf Bat
IUCN Red List status: Endangered
(Fig. 4O)

Type locality

“Sakbayeme, Cameroons.” Sakbayémé, on the N shore of the Sanaga River, in the Sanaga-Maritime Department of the Littoral Region of Cameroon, at ca. 4.052°N, 10.570°E, 244 m.

New locality records

Across both years, we captured three *H. curtus*: one male at Camp 3 in 2019, and two females in 2022, one at Camp 2 and another at Camp 7.

New vouchers

FMNH 240692♂, 241871♀, 241872♀.

Remarks

Hipposideros curtus is restricted to Cameroon, Nigeria, and Equatorial Guinea, including both the mainland and Bioko Isl. (Tanshi, 2020). This tropical moist lowland forest species relies on undisturbed caves. It is classified as Endangered on the IUCN Red List, primarily due to its restricted range and suspected population decline. The decline is driven by ongoing forest habitat degradation, including clear-cutting and wildfires, as well as disturbances and destruction of its cave roosts and heavy hunting of its syntopic cave rooster, *R. aegyptiacus* (Tanshi, 2020; Tanshi *et al.*, 2021). Additionally, hunting of *Myonycteris angolensis* in the region, may negatively influence sensitive cave populations of *H. curtus*. Our observations here suggest that the Mbam Minkom Massif may serve as a roosting habitat for *H. curtus*, underscoring the need to protect this mountain and its adjacent forest for the species' preservation.

Hipposideros curtus captures occurred in minimally disturbed forest both on and near the Mbam Minkom Massif. In 2019, *H. curtus* was captured in a mist net set over a river on the southwest slopes of the mountain; the two captures in 2022 occurred in a canopy net set over a river on the mountain and a harp trap set in a forest gap in the surrounding lowlands.

We recorded two individuals with a peak frequency of 97.0 ± 4.5 (91.7–100.9) kHz, and an average call duration of 11.0 ± 0.4 (9.3–11.4) ms. This is consistent with the findings of Tanshi *et al.* (2021), who recorded a peak frequency of 86.4 ± 0.2 (43.4–96.2) kHz from three individuals in Nigeria. In particular, there was a variation of nearly 8 kHz in peak frequency between our two recorded individuals; one female produced calls at 92.3 kHz and the other at 100.7 kHz slightly exceeding the maximum recorded by Tanshi *et al.* (2021) in Nigeria.

Hipposideros fuliginosus (Temminck, 1853)
Sooty Roundleaf Bat
IUCN Red List status: Least concern
(Fig. 4P)

Type locality

“La côte de Guinée” [= coast of Guinea].

New locality records

Four *H. fuliginosus* were captured in 2022: one female at Camp 2, one male at Camp 6, and two males at Camp 7.

New vouchers

FMNH 241873♀, 241874♂, 241875♂, 241876♂.

Remarks

Hipposideros fuliginosus is mainly found in tropical moist forests, exhibiting a disjointed distribution throughout West Africa and the central Congo basin, with isolated records in the DRC and Uganda Fahr (2013b) identified two morphologically distinct populations that may constitute distinct lineages: a smaller western group extending from Guinea through Cameroon to Gabon (FA = 55.0; 51–60 mm), and a larger eastern group (FA = 62.6; 60–64 mm) found in scattered locations throughout the DRC, CAR, and Uganda. Our captures are consistent with the smaller, western population's measurements (FA = 56.92 ± 0.82 mm; GLS = 21.36 ± 0.10 mm).

Hipposideros ruber and *H. fuliginosus* can be difficult to distinguish morphologically. We observed a size disparity between captured individuals: *H. fuliginosus* individuals were slightly larger (FA = 56.92 ± 0.82 mm; GLS = 21.36 ± 0.10 mm, $n = 4$), compared to *H. cf. ruber* (FA = 52.0 ± 1.5 mm; GLS = 18.86 ± 0.34 mm, $n = 42$). However, the small sample size prevented a statistical evaluation of the size difference. Molecular analyses using *cyt-b* data, in conjunction with phylogenetic findings from Patterson *et al.* (2020), placed our specimens close to *H. fuliginosus* individuals from Guinea-Bissau (Vallo *et al.*, 2008; Patterson *et al.*, 2020).

Echolocation calls of captured bats demonstrated a peak frequency of 109.9 ± 0.2 (109.7–110.1) kHz, and an average duration of 6.0 ± 1.6 (2.8–9.2) ms. These calls exhibited a lower frequency compared to those documented in Côte d'Ivoire (113–121 kHz — Fahr, 2013b) and Guinea (120–123 kHz — Monadjem *et al.*, 2020), yet they more closely resemble calls observed in Nigeria (107.0 kHz — Tanshi *et al.*, 2021). Echolocation calls can be used to distinguish *H. fuliginosus* from *H. cf. ruber*; the calls recorded in our study for *H. cf. ruber* exhibited a considerably higher peak frequency of 142.6 ± 3.4 (133.3–146.7) kHz.

Hipposideros cf. ruber (Noack, 1893)

Noack's Leaf-nosed Bat

IUCN Red List status: Least concern

(Fig. 4Q)

Type locality

“Lugerrunjere-Fluss” [Ngerengere River, Eastern Province, Tanzania]. Swynnerton, (1945) specified that “The type of *Phyllorhina ruber* [sic] Noack was collected on the Ngerengere River, probably near Ngerengere village, 32 miles east of Morogoro, on the old Bagamoyo-Tabora caravan-route, at an altitude of about 600 ft. [183 m].”

New locality records

Across both years, we captured 46 *Hipposideros cf. ruber*. Nine *H. cf. ruber* were collected in 2019: four males at Camp 1; one male and one female at Camp 2 and three males at Camp 3. We captured 37 *H. cf. ruber* in 2022: 21 individuals (4 ♀♀, 17 ♂♂) at Camp 1, eight bats (7 ♀♀, 1 ♂) at Camp 2, one male at Camp 6, three bats (1 ♀, 2 ♂♂) at Camp 7, and four females at Camp 8.

New vouchers

FMNH 240693♂, 240694♂, 240695♂, 240696♂, 240697♀, 240698♂, 240699♂, 240700♂, 240701♂, 241877♂, 241878♂, 241879♂, 241880♀, 241881♀, 241882♀, 241883♀, 241884♂, 241885♂, 241886♀

Remarks

Phylogenetic analyses have shown that *H. ruber* represents a complex comprising several morphologically cryptic species, with multiple lineages identified within this complex (Vallo *et al.*, 2008; Monadjem *et al.*, 2013b; Patterson *et al.*, 2020; Baldwin *et al.*, 2021). Vallo *et al.* (2008) suggested that two allopatric lineages may recently have become sympatric in Cameroon. Currently, clades within the *H. ruber* complex remain unnamed due to insufficient sequence data for typical *H. ruber*. These authors highlight that the reliance of mitochondrial DNA on maternal inheritance might cause oversplitting of taxa. Instead, a combination of morphometric, echolocation, and comprehensive genetic data are needed to resolve divergence within the *ruber* complex and accurately define their geographical ranges (Vallo *et al.*, 2008; Patterson *et al.*, 2020; Baldwin *et al.*, 2021).

The majority of our captures identified as *H. cf. ruber* occurred on the mountain, possibly due to our proximity to a roost site. During the 2022 survey, we located two roosting caves housing both *H. cf. ruber* and *M. angolensis*; one approximately 600 m southwest of Camp 1, and another 300 m southwest of Camp 6.

The echolocation calls of captured bats displayed a peak frequency of 142.6 ± 3.4 (133.3–

146.7) kHz and an average call duration of 5.5 ± 1.1 (4.2–7.0) ms. Webala *et al.* (2019b) suggested that *H. cf. ruber* may emit calls at varying frequencies ranging from 132 to 144 kHz across Africa, with substantial intraspecific variation observed at a single locality in Kenya. This variation may be attributable to sexual dimorphism resulting in a bimodal frequency distribution, with males calling at 132–135 kHz and females at 140–145 kHz. However, they noted that their sample size was insufficient for a definitive statistical test (Webala *et al.*, 2019b). Furthermore, the phylogenetic analyses by Monadjem *et al.* (2013a), using *cyt-b* data, showed that *H. cf. ruber* specimens from Liberia and Guinea grouped closely with a lineage from Cameroon, with less than a 2.5% difference. This group displayed a call frequency of 147.7 ± 1.45 (145–150) kHz.

Our observations fall within this broad frequency range noted in Webala *et al.* (2019b), although we did not detect a distinct frequency distribution pattern based on sex. Our findings are consistent with those of Monadjem *et al.* (2013a) and documented calls from Nigeria (143.6 ± 0.3 ; 138.1–148.1 kHz —Tanshi *et al.*, 2021).

Macronycteris gigas (Wagner, 1845)
Giant Leaf-nosed Bat
IUCN Red List status: Least concern
(Fig. 4R)

Type locality
Benguela, Angola.

New locality records

Across both years, we captured a total of eight *M. gigas*. Four females were captured at Camp 2 in 2019. In 2022, we captured three bats (2 ♀♀, 1 ♂) at Camp 2 and one male at Camp 8.

New vouchers

FMNH 240702♀, 240703♀, 240704♀, 240705♀, 241888♀, 241889♂, 241890♀.

Remarks

Recent molecular and morphological analyses by Foley *et al.* (2017) have led to the reestablishment of the genus *Macronycteris* (Gray, 1866) for this species and other members of the *commersonii* group of *Hipposideros*. This was confirmed by broader taxonomic sampling by Patterson *et al.* (2020). However, more work is needed to better distinguish between *M. gigas* and *M. vittata*, as well as between *M. commersonii* and *M. cryptovalorona*. The four species

are reciprocally monophyletic in *cyt-b* sequences but conflated using nuclear intron sequences (Fig. 5 of Patterson *et al.*, 2020); a morphological analysis of these forms is underway (D. Rossoni, P. W. Webala, L. Torrent, M. Bartonjo, S. M. Goodman, C. Montauban, A. Tian, A. Weber, C. Ibáñez, A. Guillén *et al.*, unpublished data). *Macronycteris gigas* predominantly inhabits rainforests and echolocates at a lower frequency (approximately 55 kHz) compared to the smaller, morphologically similar savanna species *M. vittata* (approximately 66 kHz —Happold, 2013g; Tanshi *et al.*, 2021).

Macronycteris gigas occurs from Senegal to the CAR, with additional records further east and south from Namibia, Gabon, the DRC, Tanzania, and Kenya. Records from Tanzania and coastal Kenya require further investigation to determine their relationship to populations in the primary forest belt west of the Albertine Rift (Monadjem *et al.*, 2020).

Seven of our eight captures of *M. gigas* occurred on Mt. Mbam Minkom, in minimally disturbed forest, at an elevation of 785 m, with a single male captured approximately 15 km from the mountain's base, in a secondary forest near cocoa and subsistence farms. The echolocation calls of captured individuals of *M. gigas* exhibited a peak frequency of 51.9 ± 1.0 (50.7–53.6) kHz, and an average call duration of 11.9 ± 2.0 (9.1–14.6) ms, aligning with observations from West Africa including 54–56 kHz in Kenya (Happold, 2013g; Webala *et al.*, 2019b), 52 kHz in Liberia (Monadjem *et al.*, 2020), and 51.8 ± 0.3 (51.2–52.6) kHz in Nigeria (Tanshi *et al.*, 2021).

Family Nycteridae Van Der Hoeven, 1855

Nycteris arge Thomas, 1903
Bates's Slit-faced Bat

IUCN Red List status: Least concern
(Fig. 4S)

Type locality
“Efulen, Cameroons” [= Cameroon].

New locality records

We captured two male *N. arge* in 2022: one at Camp 5, and another at Camp 8.

New vouchers

FMNH 241892♂, 241893♂.

Remarks

In the field, we initially identified these individuals as *N. arge* based on their morphological charac-

teristics. Phylogenetic analysis using *cyt-b* data placed these specimens in Clade 1B (see the account for *Nycteris major*) but positioned basal to all other clades within this group (Demos *et al.*, 2019a). Due to ongoing uncertainties within Nycteridae, we were unable to definitively assign a species name to these specimens based solely on molecular data. However, their external and cranial measurements fall within the known range of *N. arge*. Further investigation is required to clarify molecular relationships and accurately define species boundaries within Nycteridae.

This species is recorded primarily in tropical moist lowland forest, coastal forest, forest-savanna mosaic, and also in montane and swamp forest, with occasional occurrences in relict and gallery forest, and woodland (Fahr, 2013c). While typically observed in undisturbed forest, its ability to persist in degraded forest remains uncertain (Juste and Ibáñez, 1994; Fahr, 2013c; Monadjem *et al.*, 2017c).

We captured both bats using canopy nets placed across a river. One individual was captured at the base of Mt. Mbam Minkom, in a minimally disturbed forest adjacent to residential clearings. The second individual was captured approximately 15 km north of the mountain, in a secondary forest close to scattered cocoa plantations and subsistence farms. Given that the species is classified as Data Deficient on the IUCN Red List, there is a growing need for focused ecological surveys (Mickleburgh *et al.*, 2019).

Nycteris grandis Peters, 1865
Large Slit-faced Bat
IUCN Red List status: Least concern
(Fig. 4T)

Type locality

Guinea. However, Grubb *et al.* (1998: 76) state: “Type locality: Usually given as “Guinea” but the type, in the Leiden Museum, was collected in 1863 by Nagtglas, and ascribed to Côte d’Or (Jentink, 1888: 170). The type locality may be further restricted to the vicinity of Elimina [Ghana] which is the only definite locality Jentink cited for any of the Nagtglas material.”

New locality records

One male *N. grandis* was caught at Camp 3 in 2019.

New vouchers

FMNH 240706♂.

Remarks

This species is broadly distributed across West and Central Africa showing a significant gap before it reappears in coastal Kenya and eastern Tanzania, with additional isolated records in Zambia, Zimbabwe, and Mozambique (Happold, 2013k; Monadjem *et al.*, 2017d). This species has scattered records across western, central, and southern Cameroon (Atagana *et al.*, 2018). *Nycteris grandis* is easily

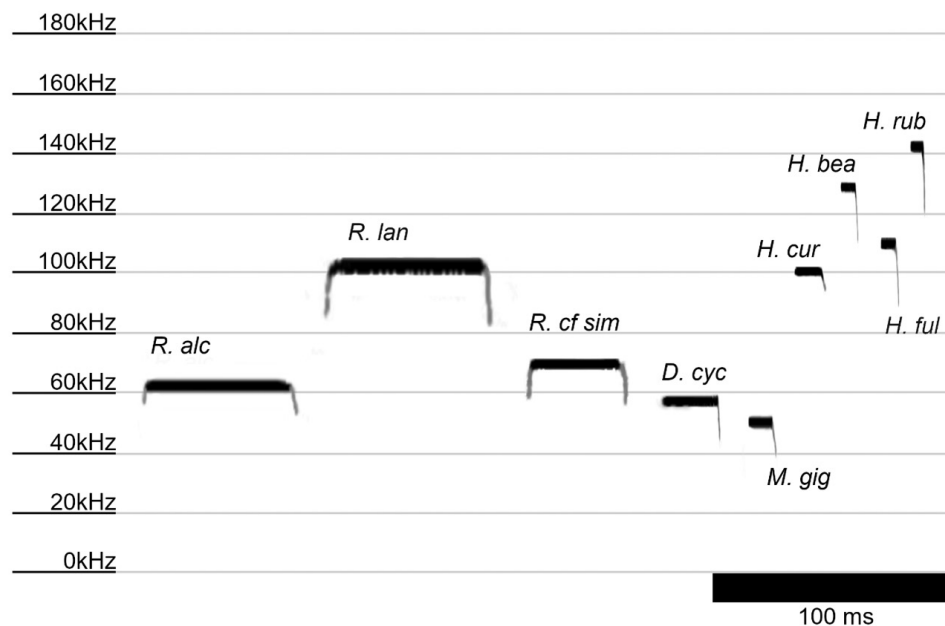


FIG. 5. Sonogram of narrowband acoustic pulses, primarily CM pulses, recorded during the study. Species are represented by a single pulse and include: *Rhinolophus alcyon* (*R. alc*), *R. landeri* (*R. lan*), *R. cf. simulator* (*R. cf. sim*), *Doryrhina cyclops* (*D. cyc*), *Macronycteris gigas* (*M. gig*), *Hipposideros beatus* (*H. bea*), *H. curtus* (*H. cur*), *H. fuliginosus* (*H. ful*), and *H. cf. ruber* (*H. rub*)

identified based on its large size (FA > 57 mm), as well as its trifold upper incisors, shared only with the much smaller *N. hispida* and *N. aurita* (Happold, 2013k). We captured an individual on the southwest slope of the massif at an elevation of 884 m in a mist net set across the intersection of two logging trails.

Nycteris major (K. Andersen, 1912)
Dja Slit-faced Bat
IUCN Red List status: Data Deficient
(Fig. 4U)

Type locality

“Ja R., Cameroons” [= Dja River, Cameroon].

New locality records

A female *N. major* was caught at Camp 8 in 2022.

New vouchers

FMNH 241896♀.

Remarks

The phylogenetic relationships and species diversity within Nycteridae remain undefined. Demos *et al.* (2019a) used nuclear and mitochondrial data to analyze phylogenetic relationships within the Nycteridae family, focusing on species-group relationships of *Nycteris*. Their analysis divided the family into four distinct subclades: 1A, 1B, 2A, and 2B. Within these subclades, two lineages initially identified as *N. arge* in the field were distinguished as separate entities, *N. arge* clades 1 and 2, suggesting that they belong to different species groups (Demos *et al.*, 2019a). Our specimen grouped within Clade 1B which includes *N. arge* clade 2, and two *N. nana* clades. Phylogenetic analysis using *cyt-b* data positioned our specimen as closely related to *N. arge* clade 2.

Nycteris arge and *N. major* are morphologically similar. Our specimen exhibits morphological traits typical of the *arge* group, including the tragus shape (characteristic shape with concave kink on the outer margin at half its length, according to Monadjem *et al.* (2020), and a well-developed posterior lower premolar situated in the tooth row. It aligns more closely with *N. major*, distinguished by its larger size (FA = 48.93 mm) and skull characteristics, including a more pronounced and extended sagittal crest, compared to the two specimens identified as *N. arge* (FA = 44.58 ± 0.09, 44.51–44.64). Notably, analyses by Demos *et al.* (2019a) did not include *N. intermedia* and *N. major*. Given the ongoing ambiguity in species-group relationships within Nycteridae, we classify our specimen as *N. major* based

on these morphological comparisons. We captured *N. major* using a canopy net set over a pooled river area in moderately secondary forest adjacent to cocoa and subsistence farms.

Family Molossidae Gervais, 1855

Mops brachypterus leonis (Thomas, 1908)
Short-winged Free-tailed Bat
IUCN: Least concern
(Fig. 4V)

Type locality

Sierra Leone.

New locality records

We captured a single female *M. b. leonis* at Camp 8 in 2022.

New vouchers

FMNH 241897♀.

Remarks

Monadjem *et al.* (2016) noted that the taxon *M. b. leonis*, spanning the Afrotropical forest zone from Sierra Leone to eastern DRC, may be distinct from the taxon *brachypterus*, confined to coastal East Africa and western Uganda (Thorn and Kerbis Peterhans, 2009; Monadjem *et al.*, 2016). The relationship between these two taxa warrants further investigation (Monadjem *et al.*, 2016). In addition, Stanley (2008), in his description of *Mops bakarii* — a species closely resembling *M. brachypterus* — noted morphological distinctions between the holotype and other specimens labeled as *M. brachypterus* from various regions. Distinct characters included the presence of basisphenoid pits on the ventral aspect of the cranium behind the palate, and the holotype's robust upper canines, akin to those of *M. bakarii*, but distinct from specimens labeled as *M. brachypterus* from eastern and central Africa. These findings highlight the need for a comprehensive taxonomic reassessment of these species (Stanley, 2008).

Our specimen exhibits an anterior upper premolar aligned within the tooth row that matches the cingulum height of the posterior premolar. In contrast to *Mops spurrelli* and *Mops thersites* captured during our surveys, the anterior palatal emargination is narrow but comparatively wider. The ears are relatively short, not extending the full length of the muzzle when laid forward. The dorsal fur is reddish-brown, and the ventral fur is pale

yellow that fades to orange towards the flanks. In particular, the ventral fur darkens to orange, extending onto the wing membrane with pelage, a characteristic not documented in existing descriptions of *M. brachypterus*. The wings and uropatagium are dark brown. This individual was captured in the lower net of a canopy net set across a pooled area in a river, ca. 15 km from the Mbam Minkom Massif, in moderately disturbed secondary forest, adjacent to cocoa and subsistence farms.

Mops spurrelli (Dollman, 1911)
Spurrell's Free-tailed Bat
IUCN Red List status: Least concern
(Fig. 4W)

Type locality

"Bibianaha, 60 miles [= 97 km] W. of Kumasi, Gold Coast [= Ghana]. Altitude 700 feet [= 213 m]."

New locality records

We captured a female *M. spurrelli* at Camp 8 in 2022.

New vouchers

FMNH 241898♀.

Remarks

Field measurements indicate that the captured specimen is consistent with *M. spurrelli*, which is a small free-tailed bat (GLS = 16.78 mm; FA = 29.04 mm). Its dorsal fur is dark reddish-brown, transitioning to cream on the venter, with dark brown wings and uropatagium. The ears are relatively short and extend halfway along the muzzle when laid flat. Morphologically, *M. spurrelli* closely resembles *M. nanulus*, but can be distinguished by the characteristics of the skull. Specifically, skull differentiation is apparent in the number of lower incisors — two pairs in *M. nanulus* compared to one pair in *M. spurrelli* (Monadjem *et al.*, 2020), with this specimen possessing a single pair of bifid lower incisors. Furthermore, the lower canine cingula is markedly enlarged and in contact, and the anterior palate is narrowly emarginated. The complexity of unresolved phylogenetic relationships within African Molossidae species requires a comprehensive revision to aid in the genetic identification of members of this group.

Mops spurrelli is found mainly in tropical moist lowland forests, although it has also been recorded in secondary forests and woodland savannas adjacent to tropical forests (Happold, 2013o; Taylor,

2019). This individual was captured approximately 15 km north of the Mbam Minkom Massif in the lower net of a canopy net, set across a pooled area of a river within moderately disturbed secondary forest, adjacent to cocoa and subsistence farms.

Mops thersites (Thomas, 1903)
Railer Free-tailed Bat
IUCN Red List status: Least concern
(Fig. 4X)

Type locality

"Efulen, Cameroons" [= Cameroon].

New locality records

A male *M. thersites* was captured at Camp 8 in 2022.

New vouchers

FMNH 241899♂.

Remarks

The external and cranial measurements of this specimen correspond to the recognized range of *M. thersites* (Happold, 2013p; Monadjem *et al.*, 2020). Distinct craniodental characters include: a moderately developed sagittal crest with weakly-developed lambdoidal crest; the anterior upper premolar is within the toothrow and taller than the cingulum of the posterior premolar, and the anterior palate is very narrowly emarginated. The dorsal fur is medium reddish-brown and the individual exhibits a naked rump. The ventral pelage is light brown fading to medium brown near the flanks and extending sparsely onto the wing membrane.

Molecular analysis was conducted, using *cyt-b* data, for identification, but the taxonomic placement of the specimen is still unclear, largely due to unresolved phylogenetic relationships and poor taxonomic sampling within African Molossidae.

Mops thersites exhibits a somewhat disjunct distribution, recorded from Sierra Leone to Cameroon (excluding Togo and Benin), and from Cameroon to northeastern and south-central DRC, Uganda, and Rwanda. The presence of the species in Zanzibar and Mozambique islands remains uncertain (Happold, 2013p). We captured *M. thersites* in the lower net of a canopy net set across a pooled area in a river, ca. 15 km from the Mbam Minkom Massif, in moderately disturbed secondary forest, adjacent to cocoa and subsistence farms.

Family Vespertilionidae Gray, 1821

Afronycteris nanus (Peters, 1852)

Banana Serotine

IUCN Red List status: Least concern

Type locality

Inhambane, Mozambique.

New locality records

We caught a single female *A. nanus* at Camp 6 in 2022.

New vouchers

FMNH 241916♀.

Remarks

Recent work by Monadjem *et al.* (2021b), based on *cyt-b* data, demonstrated that the existing classification of *Neoromicia* was paraphyletic. This resulted in the establishment of the monophyletic genus *Afronycteris*, exclusively comprising the species previously classified as *Neoromicia nana*, and renamed *Afronycteris nana* (Monadjem *et al.*, 2021b); although the latter used *A. nana*, the original spelling, *nanus*, of Peters (1852: 63) is in more widespread use because as a noun, it is not required to change with the gender of the genus.

Afronycteris nanus has a broad distribution across sub-Saharan Africa, from Senegal in the west to Eritrea, Ethiopia, and Somalia in the east, extending south to southeastern South Africa (Monadjem *et al.*, 2017b; Moratelli, 2019a). Its actual range might be more extensive than currently known, indicating the need for additional research to clarify its distribution (Monadjem *et al.*, 2017b). This individual was captured along a river in riparian forest adjacent to a cocoa farm.

Echolocation calls recorded from a single individual exhibited a peak frequency of 77.2 ± 3.3 (72.7–80.6) kHz. This frequency is higher than those documented in Eswatini and Durban (65.4–72.2 kHz) and in Kenya (63.0–69.9 kHz — Moratelli, 2019a; Monadjem, 2020). However, it aligns with the frequency range observed in Uganda, recorded at 79.8 ± 8.2 kHz (Moratelli, 2019a).

Glauconycteris argentata (Dobson, 1875)

Common Butterfly Bat

IUCN Red List status: Least concern

(Fig. 4Y)

Type locality

“Cameroon Mountains, western equatorial Africa,” Cameroon.

New locality records

We captured five *G. argentata* (1 ♀, 4 ♂♂) at Camp 2 in 2019. We did not capture any *G. argentata* in 2022.

New vouchers

FMNH 240709♂, 240710♂, 240711♂, 240712♂, 240713♀.

Remarks

The distribution of this species is not well known but is thought to extend across Central and East Africa, with disjunct records from Cameroon, Equatorial Guinea (Rio Muni), DRC, Rwanda, Burundi, Uganda, Kenya, Tanzania, and possibly northern Malawi, with the southernmost record from northwestern Angola (Happold, 2013c; Monadjem *et al.*, 2017a).

All *G. argentata* captures took place in 2019 in undisturbed forest at a single location on Mt. Mbam Minkom. All captures occurred in mist nets placed over rivers or streams. In 2022, despite expanded survey locations and intensified trapping efforts, we did not capture any *G. argentata*. Surveys in Cameroon and East Africa have found *G. argentata* in disturbed habitats, indicating that it is an edge-tolerant species (Webala *et al.*, 2019a; Bakwo Fils *et al.*, 2021).

We documented echolocation calls from two individuals with a peak frequency of 42.5 ± 0.5 (42.2–42.9) kHz. These frequencies correspond with calls previously recorded in Gabon (40.3–47.1 kHz) and Kenya (36.2–44.8 kHz — Moratelli, 2019b).

Glauconycteris egeria Thomas, 1913

Bibundi Butterfly Bat

IUCN Red List status: Data Deficient

(Fig. 4Z)

Type locality

“Bibundi,” Western Province, Cameroon.

New locality records

In 2022, we captured two *G. egeria*; one female at Camp 5, and one male at Camp 8.

New vouchers

FMNH 241912♀, 241913♂.

Remarks

Glauconycteris egeria has limited representation in museum collections (Happold, 2013d; Hassanin *et al.*, 2018; 24 specimens are listed in the Global Biodiversity Information Facility database (<https://www.gbif.org>) and 12 specimens are mentioned in the iDigBio website (<https://www.idigbio.org>), as of this writing. It is known from isolated records in Central Africa, including Cameroon, and the CAR, with four additional specimens recorded in Uganda (Happold, 2013d; Hassanin *et al.*, 2018). The records are predominantly from dense tropical and secondary forests, with some records in a forest-savanna mosaic. More recent surveys in Cameroon suggest that *G. egeria* is a forest species found principally in undisturbed habitats and may be absent from farmland and savannah regions (Atagana *et al.*, 2018; Waghihiwimbom *et al.*, 2020; Bakwo Fils *et al.*, 2021).

Both individuals were captured using a canopy net set over a river. The female was caught at the base of the mountain within minimally disturbed forest adjacent to residential clearings. The male was captured in a secondary forest near residential areas and cocoa and subsistence farms. Our captures of *G. egeria* occurred in forested areas, close to the forest edge. Given its Data Deficient status (Jacobs *et al.*, 2019), further research on this species is needed.

The echolocation calls recorded from two individuals exhibited a peak frequency of 26.3 ± 2.5 (21.5–37.0) kHz. No call data suitable for comparison was identified in the literature review. However, it should be noted that these calls are relatively low compared to other *Glauconycteris* species, which typically call around 40 kHz.

Myotis bocagii (Peters, 1870)

Rufous Mouse-eared Bat

IUCN Red List status: Least concern

(Fig. 4aa)

Type locality

“Duque de Bragança, Angola.” [= Kalandula, Malanje Province, Angola].

New locality records

We captured two *M. bocagii* in 2022, one male and one female at Camp 8.

New vouchers

FMNH 241923♂, 241924♀.

Remarks

Myotis bocagii is widely distributed across sub-Saharan Africa. Its range extends discontinuously from Sierra Leone in West Africa, through Central Africa, to East Africa and Ethiopia, and continues southward to northeastern South Africa (Jetz *et al.*, 2012; Happold, 2013j; Monadjem and Jacobs, 2017; Patterson *et al.*, 2019). Specimen-based locality data suggest a distribution gap from eastern Ghana (Togo Gap) to Cameroon between West African and the remaining African records. Patterson *et al.* (2019) found little genetic differentiation between specimens from Kenya, Tanzania, DRC, and Ghana, although modest differentiation distinguished this group from an individual from Senegal. The Senegalese specimen was reported and sequenced by Koubínová *et al.* (2013) and may correspond to a distinct taxon. The mean genetic distance (*p*-distance), based on the *cyt-b* gene, between this specimen (Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic IVB S508) and other African specimens (including West Africa) analyzed by Patterson *et al.* (2019) is 0.031 ± 0.003 , while *p*-distances among *M. bocagii* exclusive of IVB S508 are 0.014 ± 0.008 . A mitochondrial *p*-distance of this magnitude is suggestive of interspecific differentiation based on the summary data of Baker and Bradley (2006). The topology of the phylogenetic tree obtained by Patterson *et al.* (2019) is similarly suggestive.

Individuals were captured in the lower net of a canopy net set over a pooled area in a river, in moderately disturbed secondary forest, near cocoa and subsistence farms. We recorded echolocation calls from two individuals, displaying a peak frequency of 40.1 ± 1.0 (39.0–42.0) kHz. These frequencies represent an intermediate range compared to those recorded in Malawi and South Africa; 34–35 kHz in Malawi ($n = 1$), and 44.6 ± 2.4 kHz in South Africa (Schoeman and Jacobs, 2008; Happold, 2013j; Monadjem *et al.*, 2020).

Nycticeinops crassulus (Thomas, 1904)

Broad-headed Serotine

IUCN Red List status: Least concern

Type locality

“Efulen, Cameroons” [= Cameroon].

New locality records

In 2019, a male *N. crassulus* was captured at Camp 3. None were captured in 2022.

New vouchers

FMNH 240707♂.

Remarks

This species originally was described as *Pipistrellus crassulus* by Thomas (1904). The taxonomy has undergone several changes, including placement in a variety of genera and subgenera over the past years, including *Hypsugo* Kolenati, 1856, and *Parahypsugo* Hutterer *et al.*, 2019. However, recent molecular data support the recognition of *Nycticeinops* (Monadjem *et al.*, 2021b). *Nycticeinops crassulus* may have a widespread distribution in Central Africa, although specimen-based data and distribution maps show three discontinuous clusters of records from East to West Africa (Fahr, 2013d; Monadjem and Fahr, 2017).

We captured this individual in a mist net set across a timber extraction trail in moderately disturbed forest adjacent to intact submontane forest on the southern slopes of the Mbam Minkom Massif.

Nycticeinops happoldorum (Hutterer, Decher,
Monadjem, and Astrin, 2019)
Happolds' pipistrelle
IUCN Red List status: Not evaluated
(Fig. 4bb)

Type locality

Western Spur Valley, Simandou Mts
(08°33'26.44"N, 08°55'16.50"W), ca. 737 m,
Macenta, Guinea.

New locality records

Five *N. happoldorum* were captured across both years. One male was captured at Camp 2 in 2019. Two males and two females were captured at Camp 2 in 2022.

New material

FMNH 240708♂, 241900♂, 241901♀, 241902♀,
241903♂.

Remarks

Molecular analyses, based on *cyt-b* data, align these specimens closely with *N. happoldorum*, originally described from seven bats captured on the Simandou Mountains of Guinea (Hutterer *et al.*, 2019). Hutterer *et al.* (2019) further documented a solitary specimen of *N. happoldorum* from Mount Nimba, Liberia (Monadjem *et al.*, 2013a), suggesting a somewhat broader distribution.

The dental morphology of the individuals captured during this study exhibits variation compared to the typical *N. happoldorum* (originally described as *Parahypsugo happoldorum* by Hutterer *et al.*, 2019). Specifically, in the type series of *N. happoldorum*, I¹ features a second cusp shorter than the primary, with I² approximately half the length of I¹, and showing signs of a second cusp. In addition, P¹ is absent, though this observation is based on a relatively small sample size (Hutterer *et al.*, 2019). On the contrary, our specimens display a tri-cuspid I¹, where the second cusp is slightly shorter than the first and the third is marginally shorter than the second. The height of I² closely matches that of I¹'s third cusp or is approximately half the length of I¹, P¹ is present, but notably reduced in size and lingually positioned. Given the morphological inconsistencies and the limited number of comparative specimens, further analyses are needed, including additional molecular, morphological, and acoustic evaluations, to confirm this identification. Presently, the distribution records of *N. happoldorum* are limited to the aforementioned specimens.

Our findings represent a significant range extension (2,240 km) for *N. happoldorum* and the first record for Cameroon. Throughout both years, *N. happoldorum* was exclusively documented at Camp 2 on Mt. Mbam Minkom, in minimally disturbed forest at an elevation of 785 m. No captures were recorded in the lower-altitude forest surrounding the mountain. Acoustic data were collected from three individuals with a peak frequency of 46.8 ± 1.6 (43.7–49.4) kHz, and an average call duration of 2.2 ± 0.2 (2.1–2.6) ms.

Pipistrellus nanulus Thomas, 1904
Tiny Pipistrelle
IUCN Red List status: Least Concern
(Fig. 4cc)

New locality records

In 2022, we captured two male *P. nanulus* at Camp 8.

New vouchers

FMNH 241908♂, 241909♂.

Type locality

"Efulen, Cameroons [= Cameroon]."

Remarks

Pipistrellus nanulus is widely distributed across West and Central Africa, extending from Senegal to

Cameroon, Gabon, and Equatorial Guinea, including Bioko Isl. (Van Cakenberghe and Happold, 2013a). Additionally, there is a disjunct population in East Africa, found in eastern DRC, Uganda, and western Kenya (Van Cakenberghe and Happold, 2013a; López-Baucells, 2019). Genetic analysis using *cyt-b* data have identified some genetic divergence between the western and eastern populations (Monadjem *et al.*, 2021a); the *p*-distance between the two populations is 0.04, somewhat higher than the admittedly limited range of intraspecific distances recorded for *Myotis* (Baker and Bradley, 2006). These data suggest the need for a detailed evaluation of these populations.

Our molecular analyses, using *cyt-b* data, indicate that these specimens belong to a clade that is sister to the *P. nanulus* specimens identified in West Africa. Morphologically, our specimens exhibit characteristics consistent with *P. nanulus*, including a moderately concave forehead and I^1 being bicuspid, with I^2 extending to three-quarters the length of I^1 . However, unlike *P. nanulus*, where I^2 is also bicuspid, in our specimens, I^2 is unicuspid (Van Cakenberghe and Happold, 2013a; López-Baucells, 2019). Considering that the type locality for this species is in southwestern Cameroon, it is possible that our captures represent *P. nanulus*, raising the possibility that the specimens from West Africa and East Africa could represent distinct species. This finding further emphasizes the need for a comprehensive reevaluation of the taxonomic and geographic delineations of *P. nanulus*.

During this study, we captured *P. nanulus* in both minimally disturbed forest on Mt. Mbam Minkom, as well as 15 km north of the mountain in lower elevation secondary forest. We documented calls from two individuals with a peak frequency of 57.3 ± 0.6 (57.0–58.0) kHz. While echolocation data on this species are limited, these calls are lower than an individual recorded in northern Cameroon at 65.5 kHz (López-Baucells, 2019).

Pseudoromicia mbamminkom Grunwald,
Demos, Nguéagni, Tchamba, Monadjem,
Webala, Kerbis Peterhans, Patterson,
and Ruedas, 2023
Mbam Minkom Serotine
IUCN Red List status: Not evaluated
(Fig. 4dd)

Type locality

Mount Mbam Minkom, Centre Region, Cameroon.

New locality records

We captured one female *P. mbamminkom* at Camp 2 in 2019. We captured two males at Camp 5 in 2022.

New vouchers

FMNH 240714♀ (holotype), 241914♂, 241915♂.

Remarks

Pseudoromicia mbamminkom was initially described from a solitary specimen captured on Mt. Mbam Minkom during our 2019 survey. The specimen was diagnosed morphologically and molecularly using *cyt-b* data. In 2022, we captured two additional male specimens at the base of Mt. Mbam Minkom, using a canopy net set across the Bitemgu River. These findings provide additional distributional data. The absence of captures in the surrounding forest indicates a need for further research to determine whether this species is restricted to the mountain or has a more extensive range.

Echolocation call data were not obtained for *P. mbamminkom* in 2019 (Grunwald *et al.*, 2023), resulting in the omission of acoustic data from the initial description. Here, we provide acoustic data and parameters for this species (Table 4) accompanied by a sonogram (Fig. 7). We recorded calls from one individual at two different frequencies. The higher peak frequency, 41.6 ± 2.4 (36.0–42.9) kHz, aligns more closely with other *Pseudoromicia* species and has an average call duration of 2.5 ± 0.3 (2.0–2.9) ms. However, this individual was also recorded calling at a lower frequency of 23.8 ± 0.8 kHz ($n = 7$).

Pseudoromicia roseveari (Monadjem, Richards,
Taylor, and Stoffberg, 2013)
Rosevear's Serotine
IUCN Red List status: Endangered
(Fig. 4ee)

Type locality

East Nimba Nature Reserve, Nimba Province, Liberia.

New locality records

Two *P. roseveari* were captured in 2022: one male at Camp 2, and another at Camp 7.

New vouchers

FMNH 241917♂, 241918♂.

Remarks

Prior to our study, *P. roseveari* was known by six specimens from two locations: Mt. Nimba in Liberia and the Simandou Range in Guinea, with all captures occurring over small streams in primary forests. The species is listed as Endangered on the IUCN Red List (Monadjem, 2017), primarily due to its limited distribution and small area of occupancy, restricted to two populations increasingly threatened by deforestation through logging, mining, and slash-and-burn agriculture.

Our findings introduce an additional locality, thus extending the known range of *P. roseveari*, by 2,240 km, and establish the first record for Cameroon. Both of our captures occurred in minimally disturbed forest; a male was caught on Mt. Mbam Minkom, at 785 m, in a canopy net set across a river, and another male was captured ca. 9 km from the mountain, in intact forest, in a canopy net set parallel to a river. Similar to other known habitats of *P. roseveari*, the Mbam Minkom Massif and the surrounding forest, face deforestation from timber extraction and slash-and-burn agricultural practices.

Echolocation calls from this individual exhibited a peak frequency of 39.9 ± 2.6 (35.7–55.3) kHz and an average call duration of 2.0 ± 0.3 (1.6–2.4) ms.

Pseudoromicia sp. indet.
(Fig. 4ff–gg)

New locality records

In 2022, we caught two female *Pseudoromicia* sp., one at Camp 5, and another at Camp 8.

New vouchers

FMNH 241920♀, 241921♀.

Remarks

Specimens were initially identified as *P. rendalli* based on the basis of external morphological characteristics observed in the field. Most external measurements align with the known range for *P. rendalli*. However, the forearm lengths of the specimens, 30.91 mm (FMNH 241920) and 29.45 mm (FMNH 241921), respectively, are positioned within and marginally outside the typical range of 31–37 mm for female *P. rendalli* (Moratelli, 2019c; Monadjem *et al.*, 2020). The body masses of the specimens, 4.6 g and 4.8 g, also slightly deviate from the typical body mass range of 5–9 g for this species (Moratelli, 2019c). The individuals exhibited varying color morphs (Fig. 4). In one individual, the dorsal pelage is medium brown, and a cream-colored ventral pelage, with individual hairs showing a gradient

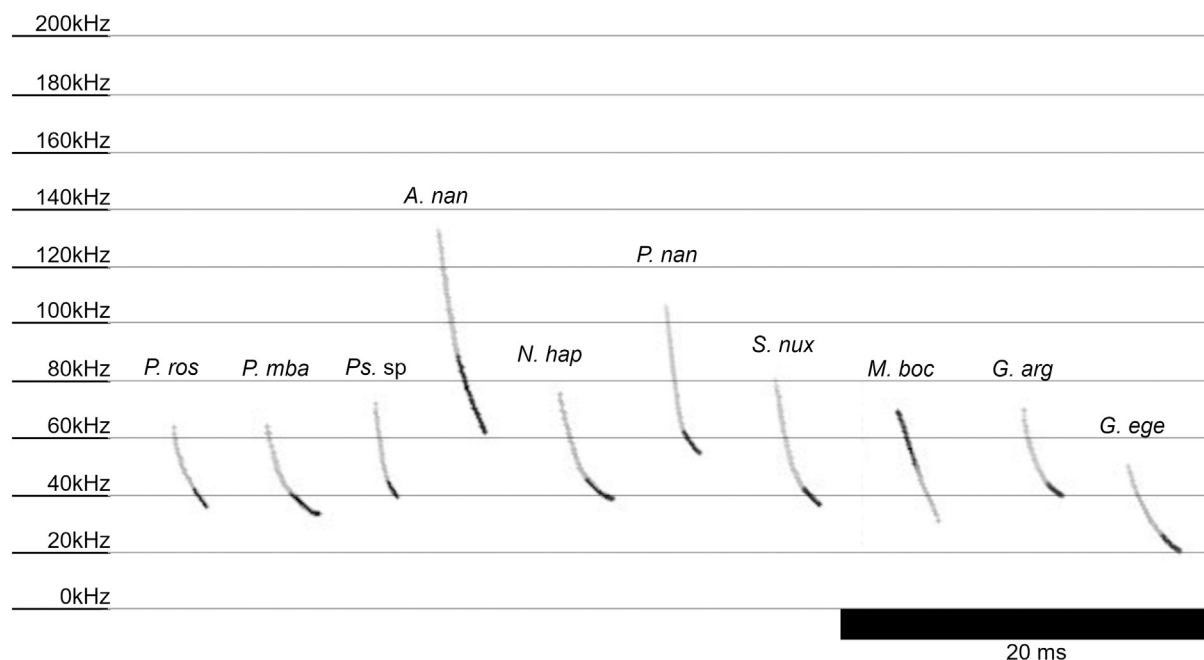


FIG. 6. Sonogram of broadband acoustic pulses, primarily FM pulses, recorded during the study. Species are represented by a single pulse and include: *Pseudoromicia roseveari* (*Ps. ros*), *P. mbamminkom* (*Ps. mba*), *P. sp. indet.* (*Ps. sp*), *Afronycteris nanus* (*A. nan*), *Nycticeinops* cf. *happoldorum* (*N. hap*), *Pipistrellus nanulus* (*P. nan*), *Scotophilus nux* (*S. nux*), *Myotis bocagii* (*M. boc*), *Glauconycteris argentata* (*G. arg*), and *G. egeria* (*G. ege*). Pulses from bats in the family Nycteridae as well as *Nycticeinops crassulus* and *Pseudoromicia tenuipinnis* are not included as we were unable to collect quality call data from these species

from dark brown at the base to cream at the tips. The other individual displayed a grayish-brown dorsal pelage with a lighter brown horizontal stripe mid-way down the back, and a white ventral pelage, with individual hairs transitioning from dark brown at the base to white at the tips. Wings and interfemoral membranes are white and translucent, and ears range from a translucent pink to a very light brownish hue. The greatest length of the skull measures 12.94 ± 0.35 mm. It is slightly concave in the forehead region, with present but underdeveloped sagittal and lambdoid crests. Dental characters include a bicuspid I^1 and a unicuspid I^2 , with I^2 slightly less than half the length of I^1 . P^1 is absent with the single upper premolar homologous with P^2 , resulting in a dental formula of $2113/3123 = 32$.

Genetic analysis, using *cyt-b* sequencing, placed these individuals as sister to *Pseudoromicia kityoi*, *P. mbamminkom*, and *P. roseveari*. In contrast, *P. rendalli* specimens from the CAR and Senegal were identified as sister to this specific group, as well as to additional species within *Pseudoromicia*, including *P. brunnea*, *P. isabella*, *P. nyanza*, and *P. tenuipinnis*.

Acoustic data collected from a single specimen (FMNH 241921) exhibited a peak frequency of 44.3 ± 0.4 (44.0–44.8) kHz, a minimum frequency of 39.8 ± 0.8 (39.2–41.2) kHz, a maximum frequency of 72.1 ± 0.0 (72.1–72.1) kHz, and a duration of 2.3 ± 0.2 ms. *P. rendalli* recorded in Malawi demonstrated a start frequency of 76 kHz and an end frequency of 42–44 kHz, although the peak frequency was not specifically noted (Moratelli, 2019c). These characteristics, though slightly higher, may suggest alignment with our recorded calls.

We captured a single female in a harp trap set across a river in a forest clearing at the base of Mt. Mbam Minkom. Another female was captured in a canopy net, approximately 15 km north of the mountain in secondary forest, adjacent to cocoa and subsistence farms.

Pseudoromicia tenuipinnis (Peters, 1872)
White-winged Serotine
IUCN Red List status: Least concern
(Fig. 4hh)

Type locality

The type locality for *P. tenuipinnis* is designated as “Bonlah village, near Yekepa at the base of Mount Nimba, Liberia,” according to the neotype designated by Decher *et al.* (2016). The holotype,

originally an adult female from “Guinea” (Peters, 1872: 264) housed in the Berlin Museum, was reported lost (Decher *et al.*, 2016).

New locality records

A single male *P. tenuipinnis* was caught in 2022 at Camp 5.

New vouchers

FMNH 241922♂.

Remarks

Recent work by Monadjem *et al.* (2021b) reasigned *tenuipinnis* to *Pseudoromicia*, based on *cyt-b* data. This species is distributed in West and Central Africa. However, individuals previously classified as *P. tenuipinnis* in Uganda and Kenya have now been identified as *P. nyanza* (Monadjem *et al.*, 2021b). The range limits for the two species have not yet been established. We captured a single *P. tenuipinnis* near the base of Mt. Mbam Mountain in a harp trap set across a river in a forest clearing.

Scotophilus nux Thomas, 1904

Nut-colored Yellow Bat

IUCN Red List status: Least Concern

(Fig. 4ii)

Type locality

“Efulen, Cameroons” [= Cameroon].

New locality records

In 2022, we captured one female *S. nux* at Camp 8.

New vouchers

FMNH 241905♀.

Remarks

Scotophilus nux has been recorded from Sierra Leone to western Kenya, including Côte d’Ivoire, Ghana, southeastern Nigeria, Cameroon, and northwest DRC; gaps in range between Cameroon and northwest DRC, and between Ghana and Nigeria, necessitate additional research to determine if these gaps are due to inadequate sampling or actual absences (Van Cakenberghe and Happold, 2013b).

The single *S. nux* was captured in a canopy net set over a pooled area in a river in a secondary forest, adjacent to residential clearings and cocoa and subsistence farms. We recorded the echolocation calls of one individual at a peak frequency of 43.7 ± 1.0 (42.7–44.9) kHz. These calls are consistent with

frequencies previously recorded in Uganda (43 kHz) and Gabon (44.5 kHz) (Van Cakenberghe and Happold, 2013b).

DISCUSSION

At both local and regional levels, inselbergs support increased diversity (Mares, 1997; Porembski and Barthlott, 2000; Bayliss *et al.*, 2024), a phenomenon further underscored by the richness of the bat assemblage observed on the Mbam Minkom Massif and its surrounding forest. These isolated specialized habitats provide critical habitat for endemic species, play an important role in regional hydrological cycles, and serve as potential microrefugia for plants and animals (Porembski *et al.*, 2016). Notably, while tropical inselbergs are ecologically significant formations, the proximity of the Mbam Minkom Massif to the CVL (245.1 km), considered over broad spatial and temporal scales, along with its position on the edge of several ecoregions—the Atlantic Equatorial Coastal Forest, the Cross-Sanaga-Bioko Coastal Forest, the Northern Congolian Forest-Savanna Mosaic, and the Northwestern Congolian Lowland Forest, has probably contributed to its contemporary diversity.

Herkt *et al.* (2016) used predicted distribution models to show that centers of bat endemism in Africa are typically found in or near areas with significant elevational ranges, such as tropical

mountains, and the richness of bat species is often closely linked with high topodiversity at lower elevations. These models revealed a strong connection between high species richness and endemism in areas that are topographically varied and humid, lying close to significant elevational gradients. Specifically, the Mt. Cameroon area was recognized as one of Africa's six distinct regional hotspots and highlighted for its substantial overlap between species richness and endemism, consistent with its global ranking as a major center of endemism for numerous taxa (Brooks *et al.*, 2001; Linder, 2001; Jetz *et al.*, 2004; Ceballos and Ehrlich, 2006; Schipper *et al.*, 2008; Herkt *et al.*, 2016). This predicted high species richness and endemism associated with Mt. Cameroon and the Cameroon Volcanic Line, extend outward to the Mbam Minkom Massif, positioning it near the edge of this incredible biodiversity hotspot.

Tanshi *et al.* (2021, 2022) surveyed two Key Biodiversity Areas in Southeastern Nigeria—the Afi Mountain Wildlife Sanctuary and the Okwangwo Division of the Cross River National Park—both located within the predicted Mt. Cameroon hotspot and the Lower Guinean Forests, a recognized global biodiversity hotspot (Herkt *et al.*, 2016; Tanshi *et al.*, 2021, 2022). These surveys, conducted at elevations ranging from 150 to 1,700 meters above sea level, recorded 1,141 individual bats belonging to 36 species and nine families, with a sampling effort totaling

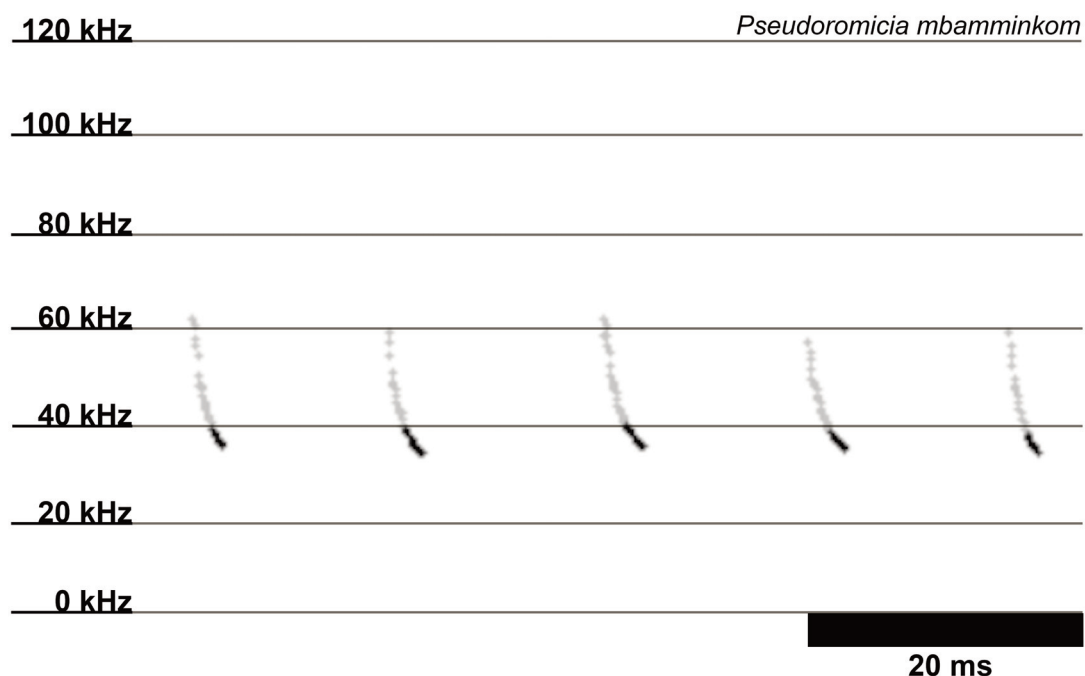


FIG. 7. Sonogram of acoustic pulses from a single *P. mbamminkom* (FNMH 241915) with an average peak frequency of 41.6 ± 2.4 kHz

11,503.2 m² capture hours. Remarkably, despite the proximity of the Mbam Minkom Massif to the edge of the hotspot and its lack of formal protection, it demonstrated comparable species richness. However, our sampling intensity (21,797.6 m² capture hours) was nearly double that of Tanshi *et al.* (2021).

The Mpem and Djim National Park, located in the Centre Region, is recognized as a biodiversity hotspot in Cameroon. From July 2016 to January 2017, Atagana *et al.* (2018) surveyed 14 sites within the park, capturing 166 bats representing 14 species in 11 genera and five families. In particular, all 14 species identified within the park were also detected in or around the Mbam Minkom Massif, probably due to similar habitats in both locations, given their positioning in ecotones, and distinct floristic and faunal characteristics.

Although our study found a similar level of species richness to that of Waghiiwimbom *et al.* (2020) in their surveys of the Centre Region, species composition varied. They documented several species not observed in our study; notably many of these species were captured in traditional farms and savannah habitats. Specifically, species such as *Eidolon helvum*, *Hipposideros abae*, *H. caffer*, *Nycticeinops eisentrauti*, *N. grandidieri*, *Vansonia rueppellii*, *Mops leucogaster* (*Chaerephon nigr*), *M. nanulus*, *M. pumilus*, and *Cloeotis percivali* [Rhinonycteridae, a family not represented in our study] were documented by Waghiiwimbom *et al.* (2020) in traditional farms. In addition, they recorded four species in savannah environments not detected in our study: *Scotoecus albofuscus*, *Mops condylurus*, *M. nigeriae*, and *M. major*, with *Scotoecus hirundo* also found primarily in the savannah with a single capture in traditional farms.

On the contrary, our study identified several species not captured in the study by Waghiiwimbom *et al.* (2020), including *S. zenkeri*, *H. curtus*, *N. major*, *M. brachypterus leonis*, *M. spurrelli*, *M. thersites*, *G. argentata*, *M. bocagii*, *N. crassulus*, *N. hapdorum*, *P. mbamminkom*, *P. roseveari*, *P. sp. indet.*, and *Scotophilus nux*. This research, along with studies by Atagana *et al.* (2018) and Waghiiwimbom *et al.* (2020), underscores habitat-based structuring within bat assemblages in the region, despite geographical proximity, and highlights the distinct bat species composition near Mbam Minkom compared to other areas in the Centre Region.

Our findings suggest that the massif may play an important role in shaping the composition of nearby bat communities and highlight the massif's importance for regional bat diversity. These findings

emphasize the need to better understand and conserve these ecosystems from high-impact human activities. The area surrounding the massif is a mosaic of intact primary forests, secondary forest, cocoa plantations, and patches of early successional vegetation recovering from slash and burn agriculture. Agricultural encroachment has reduced the extent of undisturbed forest habitat, and timber extraction has reduced the quality of the remaining forest. Timber extraction is common practice in the area, although opposed by many community members concerned about temperature increases and decreases in water supply (Bikié *et al.*, 2000). The area is also affected by its proximity to Yaoundé.

In the 1960's, the urban center comprised about 1% of the total Centre Region forest basin area; this has expanded to an estimated 30–35% in 2019 (Jourdan *et al.*, 2019). Prior to urban expansion, beginning in the 1980's, the Centre Region consisted of dense tropical forest in the south transitioning to savanna in the north (Zogning Moffo *et al.*, 2011). Over the last few decades, more than 50% of forest cover has been converted from primary forest to secondary and degraded forest (Jourdan *et al.*, 2019). The key drivers of deforestation in the region are the expansion of agricultural land (cash crop and subsistence agriculture) and the extraction of wood (Apiapuh, 2014; Epule *et al.*, 2014; Njabe and Akwanga, 2014). Of particular concern are the effects of urbanization and forest degradation on regional water cycles, since the Mbam Minkom Massif is the source of the main tributaries of the catchment area that supply water to Yaoundé and numerous surrounding villages.

Despite anthropogenic threats to the region, the Mbam Minkom Massif still supports a diverse bat population, and remains an area of enormous natural value. Our surveys revealed a high species richness, with an estimated 84% sample completeness suggesting that, although we identified a considerable portion of the area's bat diversity, several species, likely uncommon, may have remained undetected. Additional research would help compile a more comprehensive checklist of bats in the area. As anthropogenic pressures intensify, so does the need for effective conservation strategies to protect bat populations in the region. Incorporating strategies that involve bats could enhance outcomes, considering the pivotal role bats play in maintaining tropical forest biodiversity and aiding in the regeneration of disturbed habitats (van Toor *et al.*, 2019; Beilke and O'Keefe, 2023). Bats are highly productive seed dispersers and pollinators. They are vital to pest

management as predators of defoliating insects, and are important initiators of top-down trophic cascades (Kalka and Kalko, 2006; Kalka *et al.*, 2008; van Toor *et al.*, 2019; Frick *et al.*, 2020; Atagana *et al.*, 2021; Beilke and O’Keefe, 2023). Despite their benefits to forest health and functioning, as well as suppressing insect populations in agricultural ecosystems, bats are often excluded from conservation programs due to a lack of ecological research, their nocturnal lifestyle, and popular superstitions and fears (Bakwo Fils *et al.*, 2014; Waghiwimbom *et al.*, 2019; Tuneu-Corral *et al.*, 2023). Conservation of the Mbam Minkom Massif and surrounding forest will preserve unique foraging and roosting sites and maintain microclimatic conditions that increase the availability and predictability of water and food safeguarding regional bat diversity (Mares, 1997; Argoitia *et al.*, 2021).

The present research and other baseline studies are essential for documenting species distributions and patterns of community assemblage upon which conservation strategies can be based. However, further research and understanding of local interests and perceptions of conservation is necessary to inform any sustainable management strategy and to avoid furthering the gap between research and implementation (Yousefpour *et al.*, 2022). Given the complex dynamics at the intersection of biodiversity conservation and human development, conservation efforts could be strengthened by including local communities and all stakeholders of the Mbam Minkom Massif and surrounding areas to determine the sensitive reasons underlying forest decline and how to develop a long-term sustainable conservation and management strategy for the area (Ocampo-Ariza *et al.*, 2023). Conservation of the Mbam Minkom Massif is vital to the preservation of the region’s biodiversity as well as to the stability of its neighboring communities. The contribution of tropical inselbergs, such as Mbam Minkom, to the diversity of species on local, regional and global scales, as well as to the overall health of their surrounding ecosystems, warrants further attention and collaborative efforts from all stakeholders.

SUPPLEMENTARY INFORMATION

Contents: Supplementary Fig. S1. Phylogeny of African bats based on maximum likelihood analysis of *cyt-b* based on 158 individuals. Supplementary Information is available exclusively on BioOne.

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AUTHOR CONTRIBUTION STATEMENT

ALG: research concept and design, collection and assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; TCD: data analysis and interpretation, writing, critical revision, and final approval of the article; PJA: research concept and design, collection of data, critical revision and final approval of the article; CMV: collection and assembly of data, data analysis and interpretation, writing and final approval of the article; AM: data analysis and interpretation, critical revision and final approval of the article; FPMO: collection of data, critical revision and final approval of the article; YN: collection of data; RTM: data analysis and interpretation; IB: collection of data, and final approval of the article; KDA: data analysis and interpretation, and final approval of the article; EEK: data analysis and interpretation, and final approval of the article; AT: collection of data; EMBF: collection of data, critical revision and final approval of the article; BDP: data analysis and interpretation, critical revision and final approval of the article; DJB: critical revision and final approval of the article; LAR: research concept and design, collection of data, writing, critical revision and final approval of the article.

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