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A new species of horseshoe bat (Chiroptera: Rhinolophidae) from Mount Namuli, Mozambique

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The ecology of the high-altitude mountains of northern Mozambique is understudied in comparison to surrounding countries. A series of biological surveys have focused on filling this data gap, with Mount Namuli in Zambezia Province one of the focal sites of these expeditions. A biological survey of Mount Namuli in 2009 resulted in the collection of five specimens of a horseshoe bat species (Rhinolophidae) that is here described as a new species from Mozambique. Morphologically, the new species is very similar to *Rhinolophus maendeleo* Kock, Csorba and Howell, 2000 of the *adami*-group, but lacks some key morphological characters of this group (large ears, narrow skull, long palate). Molecular reconstructions clearly suggest the new species belongs to the *capensis*-group, but no members of the *adami*-group were included in this analysis (due to lacking data). It is thus unclear whether this unexpected phylogenetic position reflects morphological convergences between members of the *adami*- and *capensis*-groups, or whether the morphology-based *adami*-group should be reconsidered. The new species and *R. maendeleo* share similar external and craniodental measurements, but can be distinguished based on a number of key characters. These include the presence of a bony bar forming the interorbital foramena, rostrum shape, ear length and highly differing bacular morphologies. It also differs from the genetically closely related *R. denti* Thomas, 1904, *R. swinnyi* Gough, 1908 (including two recently described cryptic species) and *R. simulator* Andersen, 1904 by non-overlapping external and cranial measurements. The new species echolocates at a mean peak frequency of 76.9 kHz and shows an affinity to forest habitats, which are highly threatened in the surrounding region. It joins other coastal and montane forest endemics in defining the bat fauna of south-eastern Africa.

Key words: horseshoe bat, *Rhinolophus*, Chiroptera, Mount Namuli, Zambezia, Mozambique

INTRODUCTION

The ecology of the high-altitude mountains (> 1,000 m) of northern Mozambique has historically been overlooked until recently in comparison to other montane eco-regions in surrounding countries, mainly due to inaccessibility and human conflict. Over the last 20 years, a series of biological surveys has focused on filling this data gap. Mount Namuli, in Zambezia Province (Fig. 1), is one of the focal sites of these expeditions that has been relatively well sampled, both historically and recently, compared to the surrounding mountains. The first account of the area was carried out by the British Consul Henry O'Neill in 1883, shortly followed by J. T. Last in 1885 — a Victorian explorer reporting to the Royal Geographical Society. Almost 50 years passed before the next account of the area was published by the Ornithologist J. Vincent on his visit in 1932, which included some of the first photographs of Mount Namuli and the Ukalini forest (Vincent, 1933*a*, 1933*b*). Between 1937 and 1943, António Rocha da Torre collected approximately 90 plant specimens as part of a national survey, and again visited Namuli between 1966 and 1968. Mozambique experienced a war of independence (1964–1975) followed by the Mozambican civil war (1977–1992) which prevented further exploration of these northern mountains. Between 1998 and 2001 several bird expeditions were organised to Mount Namuli through the Percy Fitzpatrick Institute for Ornithology (Ryan *et al.*, 1999*a*, 1999*b*), followed

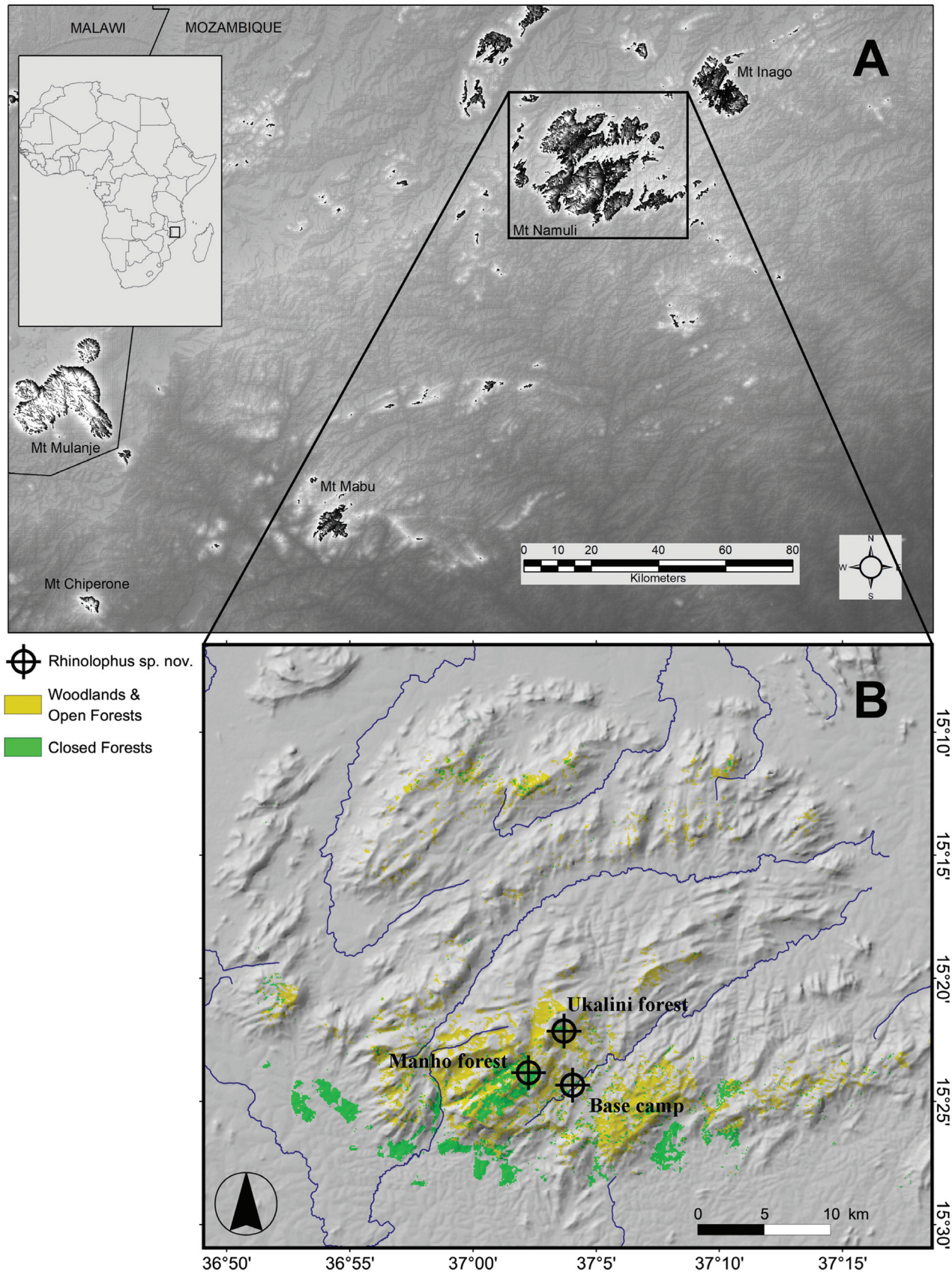

FIG. 1. Regional overview (A) and zoom in of the study area on Mount Namuli (B), showing specimen collection sites and extant montane forest and woodland cover, overlaid onto a hillshade DEM (SRTM, 90 m resolution)

by a 3-month collecting trip in 2003 by the Chicago Field Museum of Natural History (FMNH) focusing on birds and small mammals. In 2006, bats were collected from the lower slopes of Mount Namuli as part of a national bat survey (Monadjem *et al.*, 2010*a*).

Between 2007 and 2009 several expeditions visited Mount Namuli (Timberlake *et al.*, 2008) funded by the Darwin Initiative (UK) and organised through the Royal Botanic Gardens Kew, in collaboration with the Instituto de Investigação Agrária de Moçambique, and the Mulanje Mountain Conservation Trust (Malawi). In 2010, an expedition visited Mount Namuli funded by the African Butterfly Research Institute (ABRI), and since this time there have been several other expeditions to survey aspects of the ecology from Mount Namuli and in particular the herpetology (Portik *et al.*, 2013*a*; Farooq and Conradie, 2015; Conradie *et al.*, 2016). Most of these recent expeditions form part of an ongoing biological focus on the high-altitude mountains of northern Mozambique resulting in the discovery of the largest patch of contiguous rainforest in southern Africa at Mount Mabu (Bayliss *et al.*, 2014). To date several species new to science have been discovered from Mount Namuli (including endemic and shared endemic species), covering numerous taxonomic groups (Branch and Bayliss, 2009; Daniels and Bayliss, 2012; Portik *et al.*, 2013*b*; Branch *et al.*, 2014, 2019; Bayliss *et al.*, 2016, 2018, 2019; Kennerley and Peterhans, 2016; van Velzen *et al.*, 2016; Conradie *et al.*, 2018). Although the biological influences are not completely understood, evidence exists within certain taxonomic groups to suggest that the species assemblages across the Afromontane Archipelagos of southeast Africa are old in origin inferring a long period of forest isolation, particularly evident in the butterfly fauna (Congdon *et al.*, 2010). Within most of the taxonomic groups that have been even partially surveyed there is evidence of a significant influence from mountains to the north (in Tanzania) and to the west (Malawi), such as the Eastern Arc Mountains and Moreau's Tanganyika-Nyasa montane chain.

This region of Mozambique, and the country at large, has also seen many new geographic records and new descriptions of bat species over the past decade. As early as 2010, sampling of bats across Mozambique generated seven new species to the country checklist, including several notable records from central and northern Mozambique (Monadjem *et al.*, 2010*a*). These included a record of *Myonycteris relicta* Bergmans, 1980 from Chinizuia Forest near the coast of central Mozambique. This is a rare forest specialist known from the coastal forests of Tanzania (Bergmans, 1997), and was also recorded from mid-altitude forests on Mount Mulanje across the border in southern Malawi (Curran *et al.*, 2012). The region has yielded two new species of long-fingered bat (*Miniopterus*). The first, *Miniopterus mossambicus* (Monadjem *et al.*, 2013), was recorded at mid-to high altitude areas in northern Mozambique and western Zambia. The second, *Miniopterus wilsoni* (Monadjem *et al.*, 2020), was described from Mount Gorongosa, central Mozambique, but is likely spread more widely into the north of the country and southern Malawi. Within the family of horseshoe bats (Rhinolophidae), a resolution of the *hildebrandtii*-complex led to the descriptions of two new species, *Rhinolphus mabuensis* and *Rhinolophus mozambicus* (Taylor *et al.*, 2012). *Rhinolophus mabuensis* was recorded from Mount Inago and Mount Mabu, located ca. 50 km and 100 km of Mount Namuli, respectively and *R. mozambicus* from scattered records from lowland savanna in Mozambique and northwest Zimbabwe. A later study uncovered cryptic diversity within the *swinnyi-landeri* complex, describing a new species, *R. gorongosae* (Taylor *et al.*, 2018, 2019), from Gorongosa National Park in Central Mozambique (closely related to *R. swinnyi*). The same study also elevated *R. rhodesiae* Roberts, 1946 (previously a synonym of *R. swinnyi*) and *R. lobatus* Peters, 1952 (previously a synonym of *R. landeri* Martin, 1832) to full species status. *Rhinolophus rhodesiae* is distributed across Mozambique, Malawi and Zimbabwe (Taylor *et al.*, 2018, 2019), while *R. lobatus* appears more narrowly distributed across central and northern Mozambique.

The Darwin Initiative project 'Monitoring and Managing Biodiversity Loss on South-East Africa's Montane Ecosystems' visited the area in 2005, 2007, and 2009, resulting in the collection of a number of specimens of Rhinolophidae. These specimens closely resembled *Rhinolophus maendeleo* (Kock *et al.*, 2000), which is known from only three specimens collected in coastal and montane regions of Tanzania, eastern Africa. The specimens were listed as *R.* cf. *maendeleo* in the aforementioned inventory of the bats of Mozambique (Monadjem *et al.*, 2010*a*) but subsequent morphological and genetic analysis reveals that these specimens form an as yet undescribed species. In the following sections, we describe the specimens from Mount Namuli as a new species of horseshoe bat adding to existing knowledge on the Afrotropical bat fauna.

Materials and Methods

Field Sampling

We employed monofilament mist nets of both 6 m and 9 m length and 3 m height (black nylon, with 70 denier/2-ply netting, and five shelves; Avifaunistische Untersuchungen GmBh, Germany) and two custom made 2-tiered harp traps (M. Obrist, Swiss Federal Institute for Forest, Snow and Landscape Research) in an opportunistic manner. Nets and traps were placed over small streams, paths and along the forest edge. Sampling effort, expressed in 6 m net hour equivalents (i.e. one hour of a 9 m net counts as 1.5-hour equivalents of a 6 m net), totalled 8.125, 44.25 and 6 net hour equivalents at the Base camp, Ukalini forest, and Manho forest sites, respectively. Additionally, 53.5 and 9.5 trap hours were sampled at the Base camp and Ukalini forest site, respectively, with an additional 10.5 canopy net hours at the Ukalini forest (height of ca. 10 m at top pocket). In total, we recorded 14 individuals of the new *Rhinolophus* species distributed across the three sampling sites. We collected five voucher specimens preserved in 70% alcohol after being soaked in 90% alcohol for 48 hours. Three of the specimens (MHNG 1971.067, MHNG 1971.068 and MHNG 1971.069) were deposited at the Museum of Natural History of Geneva (MHNG), while two (DM 10833 and DM 10839) were deposited at the Durban Natural Science Museum (DM). All bats were handled according to the standard methods in mammalogy (Sikes *et al.*, 2011). The five specimens were captured over small to medium sized streams and riverbeds within montane forest understorey and along forest edges at altitudes between 1,200 and 1,700 m on Mount Namuli, from the 20th to 27th November 2008. Collecting permission was given through the permission granted to the Darwin Initiative project (Award 15/036) by the Government of Mozambique to undertake a series of biodiversity surveys across the high-altitude mountains of northern Mozambique.

Comparative Material

We compared specimens of *Rhinolophus* sp. nov. to preserved reference material from two closely related species: *R. maendeleo* and *R. simulator*. Three specimens of *R. maendeleo* were examined from the Senckenberg Museum Frankfurt (SMF): SMF 79.643 (Holotype, male, formalin fixed, alcohol preserved, separate skull, baculum), SMF 66.960 (Paratype, female, formalin fixed, alcohol preserved, separate skull) and SMF 93.354 (male, alcohol preserved, separate skull). Five specimens of *R. simulator* were examined from the MHNG and National Museums of Malawi, Blantyre (MoM): MHNG 1971.064 (male, alcohol preserved, separate skull), MHNG 1971.065 (female, alcohol preserved, separate skull), MHNG 1971.066 (male, alcohol preserved, separate skull), MoM MW179 (MoM accession number unknown, field reference number used), MoM MW273 (MoM accession number unknown, field reference number used). One specimen each of *R. capensis* and *R. adami* were examined from the MHNG: MHNG 1973.095 (*R. capensis*; male, alcohol preserved, separate skull), and MHNG 1129.084 (*R adami* paratype; male, alcohol preserved, separate skull). Detailed comparisons were conducted with *R. maendeleo*, because the two species show striking morphological similarity. The new species was attributed to the relevant group of the genus *Rhinolophus* using the key of Csorba *et al.* (2003: 1–3), paying particular attention to the features that define the *adami*-group containing *R. maendeleo*.

The *adami*-group also represents an interesting comparative case, due to it being a relatively recently established group of only two species (*R. maendeleo* and *R. adami*) and defined based on morphology alone (Kock *et al.*, 2000). Due to a lack of available genetic material (the few existing specimens were initially preserved in formalin), neither member of the *adami*-group was included in a recent revision of the molecular phylogeny of Afrotropical horseshoe bats (Demos *et al.*, 2019). According to Kock *et al.* (2000), the combination of the following morphological characters differentiates the *adami*-group from the *capensis*-group (and other Afrotropical species): very large ears and sella, straight-sided or rounded (but not hastate) lancet, three well-defined mental grooves in the lower lip, narrow skull (mastoid width subequal or greater than zygomatic width), more bulbous narial swellings, small second premolar in the toothrow, and a long palate. Following the genetic analysis (detailed below) we also compared external and craniodental measurements with literature accounts of *R. denti* and *R. swinnyi* (including the recently described cryptic species *R. gorongosae* and *R. rhodesiae*), which were revealed to be closely related genetically to *R.* sp. nov. (see Results section).

Character Measurements

External measurements were made using digital callipers and rounded to the nearest 0.1 mm. Cranial and dental dimensions were measured under a stereo-microscope using digital callipers with 0.01 mm accuracy. Measurements were taken according to the descriptions in Csorba *et al.* (2003: xxvi) with the same abbreviations used unless otherwise stated. For external measurements, these were: BM (body mass), HB (head and body length), Tail (tail length), HS (horseshoe breadth), Ear (ear length), FA (forearm length), Tib (tibia length) and HF (hind foot length including claws). For craniodental measurements, these were: SL (skull length), MW (mastoid width), ZW (zygomatic width), M3M3 (rostral width), CM3 (upper toothrow length), IOB (interorbital breadth), ML (mandible length), cm3 (lower toothrow length), ALSW (greatest width of the anterior lateral swellings), AMSW (anterior median swellings width), PL (palate length). The following external and craniodental measurements were included that are not described by Csorba *et al.* (2003): 3Met (metacarpal length on third digit), 3Ph1 (first phalanx length on third digit), 3Ph2 (second phalanx length on third digit), 4Met (metacarpal length on forth digit), 4Ph1, (first phalanx length on forth digit), 4Ph2 (second phalanx length on forth digit), 5Met (metacarpal length on fifth digit), 5Ph1 (first phalanx length on fifth digit) and 5Ph2 (second phalanx length on fifth digit), CC (width between outer crowns of upper canines), BcH (height of the braincase, measured from between the bullae to the top of the skull, including the sagittal crest), PB (palate breadth, measured as the smallest distance between the first molars), Ang1 (the angle, in lateral view, between a hypothetical line 1, drawn from the posterior most point of the skull to the tip of the rostral inflation, and line 2, drawn from the same origin to the front/crowns of the canines), Ang2 (the angle, in dorsoventral view, between a hypothetical line 1, drawn from the posterior most point of the rostral depression and the right side of the rostral inflation, and line 2, drawn from the same starting point to the left side of the rostral inflation). Throughout the text, we use capitalized letters to refer to

upper teeth (i.e. CM3) and lower case letters for lower teeth (i.e. cm3).

The protocol for preparation of the baculum of *R.* sp. nov. was modified following White (1951): The penis was severed close to the body and incised dorso-ventrally; the baculum was located under a stereomicroscope, removed and lightly cleaned; the retrieved baculum and adjoining tissue was then stained with alzarin red in a 2% KOH solution for about 48 hours to make the baculum more visible, and macerate the surrounding tissue. The baculum was then briefly (ca. 1 min) boiled in distilled water to further soften the tissue before being cleaned by hand under a microscope and photographed. In addition to describing the shape of the baculum, we recorded its total length, greatest lateral width of the basal cone and greatest dorsoventral width of the basal cone.

Echolocation

Hand-held reference calls were recorded from seven individuals of the new species (two females and five males), including MHNG 1971.067 and DM 10833. For each individual bat, a call sequence of 1.7 seconds was recorded using a Pettersson D240x ultrasound detector (Pettersson Electronik AB, Uppsala, Sweden), expanded 10 times, and transferred to a Cowon iAudio X5L mp3 player (Cowon Electronics, http://www.cowon.ch/index.html). The iAudio had a sampling rate of 48 kHz and bit rate of 320 kbps ('lossless' mp3 format). Calls were analysed using the software Raven Pro 1.3 (Cornell Lab of Ornithology, Bioacoustics Research Program, http://birds.cornell.edu/). Audio data was transferred to Raven Pro with a sampling frequency of 44 kHz, which translated to an effective sampling rate of 440 kHz, and 8 bits per sample, when calculating frequency grid spacing or resolution (because Raven Pro accounts for the 10× time expansion factor embedded in the recording from the D240x). This corresponded to a frequency grid spacing (i.e. the frequency resolution of the spectrogram) of 431 Hz, or roughly half a kHz. Spectrograms were generated by a Fast Fourier Transformation (FFT) using 1024 samples, a 3 dB Filter Bandwidth of 1239 Hz and a Hanning-Window. To ensure that the identity of released individuals could be traced back to a voucher specimen from the same location, biopsies of wing tissue were collected from all released individuals. A full analysis of this tissue data has not been carried out, but the material is available with permission from MC. Peak frequency (PF; frequency with highest amplitude, i.e. highest energy) was measured from the highest quality calls within the call sequence (up to 10 calls per sequence). The mean peak frequency of the selected calls measured in the sequence was then calculated. This gave mean peak frequency for each individual bat. The species mean and range was then calculated from these individual means to avoid pseudo-replication.

Morphometric Analyses

Statistical analyses and graphs were performed using the open-source software R, ver. 3.6.3 (R Development Team 2011; www.r-project.org), primarily using the packages 'FactoMineR' (Husson *et al.*, 2020) for Principal Component Analysis (PCA) and 'factoextra' (Kassambara and Mundt, 2020) for visualization. PCA was performed on log-transformed measurement data, separately for external (HS, Ear, FA, 3Met, 3Ph1, 3Ph2, 4Met, 4Ph1, 4Ph2, 5Met, 5Ph1, 5Ph2, Tib and HF) and craniodental (SL, MW, ZW, BcH, CC, M3M3, CM3, IOB, cm3, ALSW, AMSW, PL, PB). Elliptical confidence intervals were overlaid onto biplots for each species groups based on the mean and standard deviation of the respective PC (dimension) scores. All image preparation and manipulation for external, cranial and bacular features was carried out using the open-source software 'GNU Image Manipulation Program' (GIMP), ver. 2.6. (www.gimp.org).

Genetic Analyses

We extracted DNA from the ethanol-preserved biopsy samples of 24 African *Rhinolophus* specimens from eight distinct species (Table 1), which include most specimens used for the morphologic comparisons. Genomic DNA was extracted with the Qiagen DNeasy blood and tissue kit. We amplified the mitochondrial cytochrome *b* gene (abbreviated hereafter CYT-B) with the primer pair Molcit-F/Cyt-b-H (Ibáñez *et al.*, 2006; Weyeneth *et al.*, 2008) with a touch-down PCR procedure including a decreasing annealing temperature (by 0.5°C) from the initial temperature at 50°C during the first 10 cycles; the annealing temperature was then set to 45°C for the last 30 cycles. The PCR were carried out in 25 µl reactions containing 4 µl of genomic DNA and were run with negative controls to monitor possible contaminants. PCR products were cleaned using the ExoSAP Kit (Thermo Fisher Scientific, Switzerland) and sent to Macrogen Europe Inc. (the Netherlands) for Sanger sequencing. Amplicons were sequenced in both directions. Chromatographs were checked visually, assembled, and edited using Sequencher version 4.8 (Gene Codes Corp., USA). For the four specimens designated as the type series for the new species, we also sequenced part of the mitochondrial cytochrome oxidase *c* subunit 1 (*COI*), which is a useful barcode gene for species identifications (Francis *et al.*, 2010). Amplification conditions and primers (UTyr/C1L705) were the same as described in Hassanin *et al.* (2012). All new sequences generated in this study were deposited in the GenBank under accession numbers MZ936285–MZ936312.

Phylogenetic Reconstructions

To place the newly sequenced individuals in a phylogenetic framework, we downloaded from the GenBank 28 Eurasian and 49 African sequences of CYT-B (see SupplementaryAppendix S1) representing all available major clades of Rhinolophidae from the World, following the nomenclature of Csorba *et al*. (2003) and Demos *et al*. (2019). These previously sequenced individuals included notably five *Rhinolophus* of the *capensis* group collected in Malawi, Mozambique and Tanzania and vouchered in the collections of the FMNH. These bats could not be identified to the species level by Demos *et al*. (2019) and were labelled as '*R.* cf. *denti/simulator*' and referred here as *R.* sp. nov. (GenBank numbers MN025579–MN025583; SupplementaryAppendix S1).

Phylogenetic relationships were estimated with maximum likelihood (ML) and Bayesian inferences (BI) using the programs MrBayes v3.2 (Ronquist *et al.*, 2012) and iQ-TREEv 2.0 (Nguyen *et al.*, 2015; Chernomor *et al.*, 2016), respectively. All analyses were done with a fully partitioned model, the best-fitting model for these partitions being evaluated with Modelfinder (Kalyaanamoorthy *et al.*, 2017) and the Akaike Information Criterion. We inferred the ML tree using the edge-linked partition model and obtained branch supports with 1000

TABLE 1. Species name, voucher accession (DM = Durban Natural Science Museum; MHNG = Muséum d'Histoire Naturelle de Genève; NMK = National Museum of Kenya, MoM = National Museums of Malawi) and corresponding GenBank numbers, and geographic origin of the 24 African *Rhinolophus* samples newly sequenced in this study. CYT-B and *COI* abbreviations stand for the cytochrome *b* and cytochrome oxidase *c* subunit 1, respectively. * — field collection number, museum accession number unknown

Species name	Voucher	GenBank no.		Province/Locality	Country	Latitude (dec)	Longitude (dec)	Altitude (m a.s.l.)
		CYT-B	*COI*					
R. blasii	MHNG 1971.051	MZ936285	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. blasii	MHNG 1971.052	MZ936286	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. blasii	MHNG 1971.053	MZ936287	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. blasii	MHNG 1971.050	MZ936288	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. blasii	MHNG 1971.049	MZ936289	–	Zambesia Province, Mt. Mabu, MB Large River	Mozambique	-16.284861	36.398028	1,000
R. blasii	MoM MZ286*	MZ936290	–	Zambesia Province, Mt. Mabu, MB Large River	Mozambique	-16.284861	36.398028	1,000
R. damarensis	MHNG 1972.092	MZ936291	–	Western Cape, S of Goodhouse, old mines	South Africa			
R. clivosus keniensis	MHNG 1971.058	MZ936292	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. c. keniensis	MHNG 1971.057	MZ936293	–	Mulanje District, Mt. Mulanje, Minunu plateau	Malawi	-15.92479	35.63852	2,010
R. clivosus	MHNG 1971.059	MZ936294	–	Zambesia Province, Mt. Namuli, NL Ukalini Forest	Mozambique	-15.36925	37.061361	1,650
R. clivosus	MHNG 1971.054	MZ936295	–	Zambesia Province, Mt. Mabu, MB Large River	Mozambique	-16.284861	36.398028	1,000
R. clivosus	MHNG 1971.055	MZ936296	–	Zambesia Province, Mt. Mabu, MB Large River	Mozambique	-16.284861	36.398028	1,000
R. clivosus	NMK 180824	MZ936297	–	Aberdare, Nyandoma forest, Kikuyu Escarpment	Kenya	-0.94751	36.71133	2,290
R. darlingi	MHNG 1971.063	MZ936304	–	Mulanje District, Mt. Mulanje, Illingworth forest	Malawi	-16.02775	35.522139	700
R. fumigatus	MHNG 1971.060	MZ936298	–	Mulanje District, Mt. Mulanje, MMCT Guesthouse	Malawi	-16.0219	35.5157	730
R. mabuensis	MHNG 1971.061	MZ936299	–	Zambesia Province, Mt. Mabu, MB Base Camp	Mozambique	-16.305806	36.424222	550
R. lobatus	MHNG 1971.062	MZ936300	–	Zambesia Province, Mt. Mabu, MB Large River	Mozambique	-16.284861	36.398028	1,000
R. simulator	MHNG 1971.064	MZ936301	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. simulator	MHNG 1971.066	MZ936302	–	Mulanje District, Mt. Mulanje Foothills, Tea Research Foundation Forest	Malawi	-16.0992	35.6245	630
R. simulator	MHNG 1971.065	MZ936303	–	Mulanje District, Mt. Mulanje, Ruo Gorge	Malawi	-15.9715	35.6548	900
R. sp. nov.	DM 10833	MZ936305	MZ936309	Zambesia Province, Mt. Namuli, NL Base Camp	Mozambique	-15.405933	37.067006	1,200
R. sp. nov.	MHNG 1971.068	MZ936306	MZ936310	Zambesia Province, Mt. Namuli, NL Ukalini Forest	Mozambique	-15.36925	37.061361	1,650
R. sp. nov.	MHNG 1971.069	MZ936307	MZ936311	Zambesia Province, Mt. Namuli, NL Ukalini Forest	Mozambique	-15.36925	37.061361	1,650
R. sp. nov.	MHNG 1971.067	MZ936308	MZ936312	Zambesia Province, Mt. Namuli, NL Base Camp	Mozambique	-15.405933	37.067006	1,200

ultrafast bootstraps (Hoang *et al.*, 2018). For the BI, we run four parallel MCMC chains for 4 million generations. The chains were checked for convergence and appropriate effective sample size (ESS>200) with TRACER v.1.5 (Rambaut and Drummond, 2009). The initial 10% of sampled trees were discarded as burn-in. Posterior probabilities (PP) were subsequently computed from the consensus of the remaining trees. According to previous studies (e.g. Demos *et al.*, 2019), we used European *Rhinolophus hipposideros* as an outgroup to root all tree reconstructions of the Rhinolophidae.

Results

The morphometric results indicate that the collected *Rhinolophus* specimens constitute a new species with distinct characteristics that differentiate it from its closest relatives. This conclusion is based on a comparison of craniodental and external characteristics and phylogenetic reconstructions across a large number of *Rhinolophus* species.

The morphological comparisons concentrated on the two most similar species, *R. maendeleo* (*adami*-group) and *R. simulator* (*capensis*-group) and showed distinct positions occupied by each species. These results are summarized in PCA biplots of external and craniodental measurements (Fig. 2). *Rhinolophus* sp. nov. differs from *R. maendeleo* in several craniodental characters, namely the presence of bony bars at the infraorbital foramina, skull length, rostrum shape and rostral inflation. It also differs in external features, possessing a shorter tail and ears, along with differences in the horseshoe structure and wing bone dimensions. Compared to *R. simulator*, *R.* sp. nov. is larger overall (forearm length, skull measurements) and echolocates at a lower peak frequency. *Rhinolophus* sp. nov. differs from *R. adami* across features that are shared with *R. maendeleo*, such as smaller overall size (reflected in external and craniodental measurements) and baculum shape (Kock *et al.*, 2000). In common with species of the *adami*-group, the new species has three well-defined mental groves and bulbous narial swellings. Following the phylogenetic analysis based on CYT-B sequences, the morphological comparison was extended to *R. denti* and *R. swinnyi,* which were revealed to be close relatives alongside *R. simulator* (see below). Based on comparisons with published measurements, *R.* sp. nov. is much larger than both *R. denti* and *R. swinnyi* and echolocates at a different frequency to both of these species (Table 2). Details on these and other comparisons can be found in the Comparisons section below.

Molecular reconstructions based on the CYT-B gene and Bayesian or maximum likelihood criteria were very similar and returned very similar node

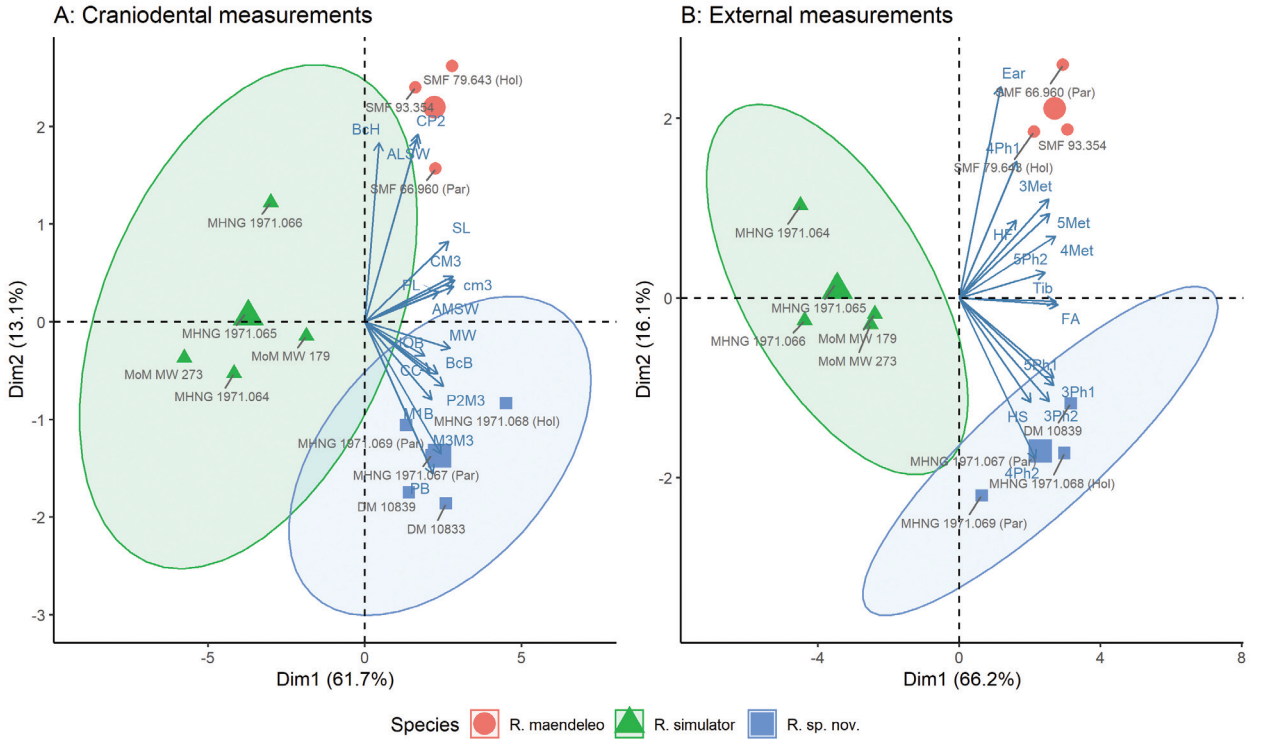

Fig. 2. PCA biplot for selected (A) craniodental and (B) external measurements. Ellipses represent 95% confidence intervals around each species group (not possible for *R. maendeleo* due to the low sample size). Large symbols represent the species mean value. Percentage values on each axis are the variances explained. For specimen accession numbers and input data, see Tables 3 and 4

TABLE 2. Key comparative characteristics and measurements reported in the literature (or observed by the authors) that distinguish *R. namuli* sp. nov. from morphologically similar or genetically closely related species. FA = forearm length; PF = peak frequency; SL = skull length. Measurements for Taylor *et al.* (2018) are provided separately for male and female specimens, which were combined in this analysis (via weighted average using sample size as weight)

Species	FA mean (mm)	FA range (mm)	PF mean (kHz)	SL mean (mm)	SL range (mm)	Coloration	Source
Rhinolophus namuli sp. nov.	48.3	47.3–49.5	~77	18.0	17.8–18.3	beige-brown	Authors' observations, n = 5 (FA), 4 (SL)
R. maendeleo	48.5	47.6–49.1	–	18.6	18.5–18.7	pale grey to beige-brown	Authors' observations, n = 3, and Kock *et al.* (2000) for coloration
R. simulator	43.8	42.0–45.3	~86	16.9	16.7–17.2	light to reddish-brown	Authors' observations, n = 5 (FA) and 5 (SL)
	44.6	42.0–48.0	~84	16.8	16.2–17.8		Taylor *et al.* (2010), n = 70 (FA), 44 (SL), 6 (PF)
R. denti	43.1	42.0–45.0	~111	15.1	14.0–15.6	pale grey to cream	Taylor *et al.* (2010), n = 25 (FA), 29 (SL)
	–	37.0–44.0	–	–	–		Csorba *et al.* (2003), no mean or sample size provided
R. swinnyi	43.6	41.7–45.0	~106	17.7	16.8–18.0	grey to pale-brown	Taylor *et al.* (2018), n = 9 (FA), 10 (SL) and 6 (PF)
	42.0	37.0–44.0	~106	15.7	16.2–17.8		Taylor *et al.* (2010), n = 37 (FA), 16 (SL) and 10 (PF)
	–	40.0–44.5	–	17.4	17.0–18.2		Csorba *et al.* (2003), no mean or sample size provided
R. gorongosae	41.3	38.5–44.5	~106	–	–	grey to pale-brown	Taylor *et al.* (2018), n = 15 (FA) and 16 (PF)
R. rhodesiae	44.2	43.0–45.0	~100	17.8	17.2–18.6	–	Taylor *et al.* (2018), n = 20 (FA), 13 (SL) and 8 (PF)

support values. Hence, only the ML tree issued from iQtree is shown here (Fig. 3). As most sequences were already included in a broader phylogenetic context of Afrotropical Rhinolophidae, relationships recovered in our analyses are strongly concordant with those reported in Demos *et al.* (2019), including the strong support (100%) for a monophyletic *capensis*-group, or paraphyletic relationships for the *euryale*- and *ferrumequinum*-groups. Within the *capensis*-group, *R. denti* and *R.* cf. *denti* (a central-equatorial lineage of this otherwise eastern and southern African taxon, Demos *et al*., 2019) appear as sister species, albeit with low support (< 75%), and are closely related to species in the *simulator-gorongosae-rhodesiae* species complex. The five previously unidentified lineages labelled *R.* cf. *denti/simluator* (Demos *et al*., 2019) form a strongly supported (100%) monophyletic group with the four newly sequenced *R.* sp. nov. from Mozambique (this study). The maximum Kimura 2-parameter (K2P) distance within this monophyletic unit is 0.8% whereas each member differs by at least 4.6% from other members within the *capensis*-group or by over 9% compared to members of other species groups. According to these mitochondrial and previous analyses based on multiple nuclear genes (Demos *et al*., 2019), all molecular reconstructions support that this unknown taxon is a deeply diverged and unique clade embedded within the African radiation of *Rhinolophus*. As none of the previously identified African Rhinolophidae fit with this taxon, we describe it hereafter as a new species.

Description of New Species

Family Rhinolophidae Gray, 1825
Genus *Rhinolophus* Lacépède, 1799
Rhinolophus namuli sp. nov.
Curran, Kopp, Ruedi, and Bayliss, 2022
Common name: Namuli Horseshoe Bat

2009 *Rhinolophus* sp. — Timberlake *et al.* (2008): Mount Namuli, Mozambique: biodiversity and conservation. Report produced under the Darwin Initiative Award 15/036. Pp. 60 and 110.

2010 *Rhinolophus* cf. *maendeleo* — Monadjem *et al.* (2010*b*): Act. Chiropterol., 12: 371–391 — partim: Mount Namuli.

2010 *Rhinolophus maendeleo* — Monadjem *et al.* (2010*b*): Bats of Southern and Central Africa: a biogeographic and taxonomic synthesis. Wits University Press, Johannesburg: 220–223, 560 — partim: Mount Namuli.

2019 *Rhinolophus* cf. *denti/simulator* — Demos *et al.* (2019). Molecular phylogenetics of the African horseshoe bats (Chiroptera: Rhinolophidae): expanded geographic and taxonomic sampling of the Afrotropics. BMC Evolutionary Biology, 19: 166.

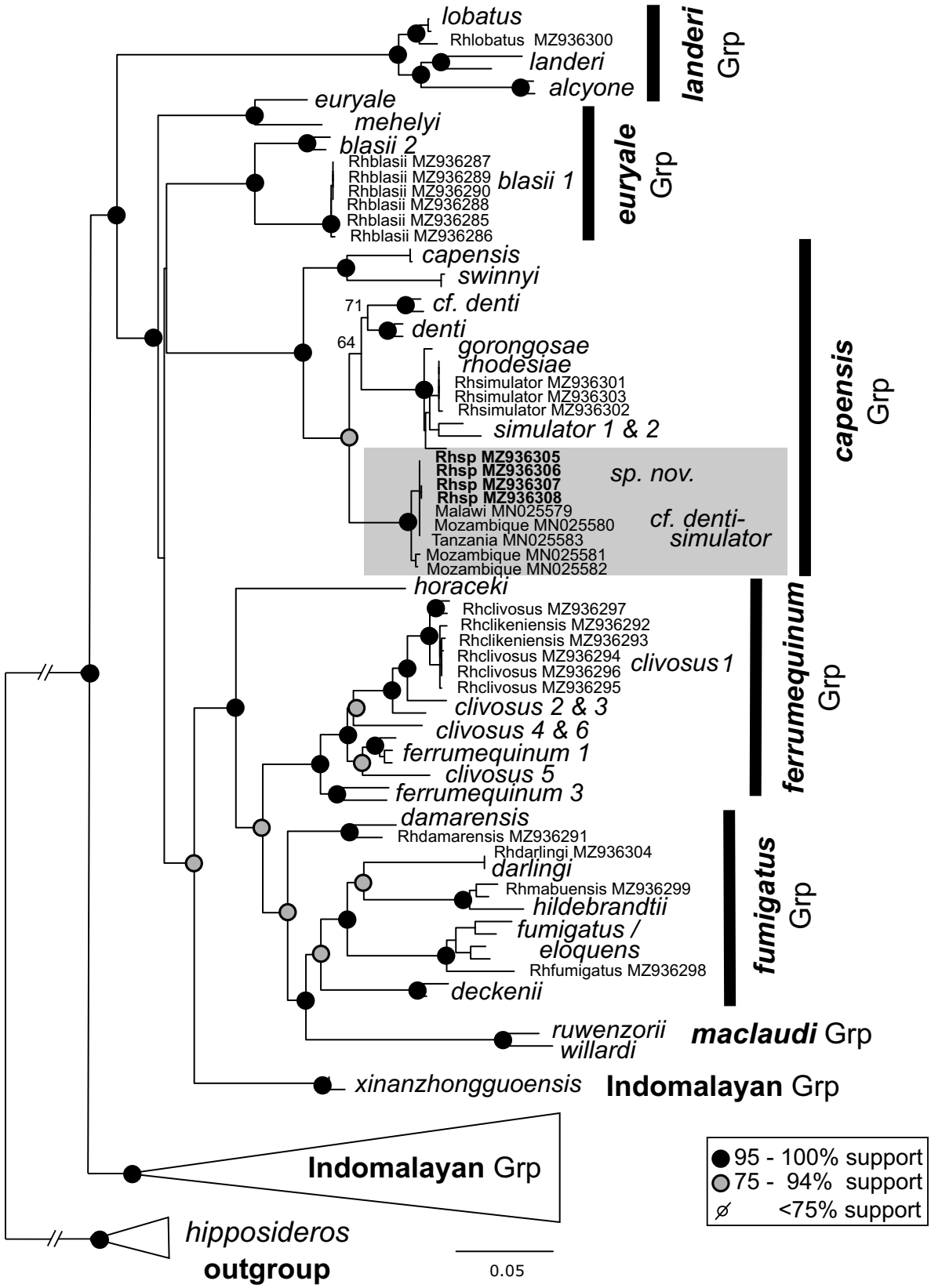

FIG. 3. Maximum likelihood tree based on CYT-B sequences and reconstructed with IQ-tree. Sequences of *R. hipposideros* were used as outgroups. Bootstrap support levels are explained in the box; the scale indicates nucleotide substitutions per site. Newly sequenced taxa are associated with their GenBank accession numbers (see Table 2 and Supplementary Appendix S3 for more details), while the species groups to which they belong appear to the right of the tree. The clade representing the new species (sp. nov.) is highlighted in grey

Holotype.—Male adult (alcohol preserved, skull, baculum preserved in glycerol), MHNG 1971.068 (field collection number MZ 120). Mozambique, Zambezia Province, Mount Namuli, Ukalini saddle forest, below mountain peak, 15.369250°S, 37.061361°E ca. 1650 m a.s.l., 21 November 2008. Captured in 2-tiered harp trap set over a small stream leading to large clearing in montane forest, at ca. 18h00. Reference sequences of the mitochondrial CYT-B and *COI* genes issued from the holotype are deposited in the GenBank under accession numbers MZ936306 and MZ936310, respectively.

Paratypes.—Male adult (alcohol preserved, skull, baculum preserved in glycerol), MHNG 1971.069 (field collection number MZ257). Mozambique, Zambezia Province, Mount Namuli, Ukalini saddle forest, below mountain peak, 15.369250°S, 37.061361°E, ca. 1650 m a.s.l., 21 November 2008. Captured in 2-tiered harp trap over small stream leading to large clearing in montane forest, ca. 18h00. Female adult (alcohol preserved, skull), MHNG 1971.067 (field collection number MZ261). Mozambique, Zambezia Province, Mount Namuli, camp on mountain plateau, 15.405933°S, 37.067006°E, ca. 1,200 m a.s.l., 20 November 2008. Mist netted over river in fragment of mid-altitude forest on mountain plateau, ca. 18:45 h. Reference sequences of the mitochondrial CYT-B and *COI* genes issued from these paratypes are deposited in the GenBank under accession numbers MZ936305–MZ936308 and MZ936309–MZ936312, respectively.

Referred material.—Female adult (alcohol preserved, skull), DM 10839. Mozambique, Zambezia Province, Mount Namuli, Manho Plateau Forest, 15.3975°S, 37.0372°E, ca. 1,734 m a.s.l., 20 November 2008. Mist netted over small stream in forest clearing at approximately 18:30 h. Male adult (alcohol preserved, skull, baculum preserved in glycerol), DM 10833 (field collection number MZ099). Mount Namuli, base camp on mountain plateau, 15.405933°S, 37.067006°E, ca. 1,200 m a.s.l., 20 November 2008. Mist netted over river in remnant fragment of mid-altitude forest on mountain plateau, ca. 18:00 h. Other referred material are five specimens previously reported as *R.* cf. *denti/simulator* by Demos *et al.* (2019), which also proved to belong to *R. namuli* sp. nov. based on very similar CYT-B lineages. These specimens were collected approximatively 8 km north and 8 km east of Gurue, Mozambique (FMNH 17708–177110), in the Zovo Chipolo Forest, Nyika National Park, Malawi (FMNH 191585), and in the Ndundulu Forest, 9 km east of Udekwa Udzungwa Mts, in Tanzania.

Type locality and distribution.—Mount Namuli (15.369250°S, 37.061361°E, ca. 1,650 m a.s.l.), ca. 10 km north-west of Gurue, Zambezia Province, north-central Mozambique (central Mozambique). Recorded in montane evergreen forest and nearby forest clearings on the high plateau and below the peak of the mountain at altitudes ranging 1,220 to 1,650 m.

Etymology

The species epithet *namuli* is a noun in apposition and is a derivative of the type locality Mount Namuli, Zambezia Province, Mozambique.

Nomenclatural statement.—A life number was obtained for the new species *Rhinolophus namuli*: urn:lsid:zoobank.org:act:7A9806D9-CCC6-41A2-B898-6DCDEFFFBB51.

Diagnosis

Medium sized bat (forearm length 47.2–49.5 mm) with medium sized ears and three well-defined mental groves on lower lip (Supplementary Appendix S2 Fig. A1). Horseshoe and sella wide (Fig. 4), lancet concave with a narrow tip (hastate), connecting process high and rounded, with scattered hairs present along its ridge (Fig. 5, Supplementary Appendix S2 Fig. A2 and A3). Elongated first phalanx of third digit relative to metacarpal (Table 3). Bony bar forming the infraorbital foramen is present and slender, inflated nasal swellings (Fig. 6 and Supplementary Appendix S2 Fig. A4), length of palatal bridge 36% of upper toothrow length (Table 4). Minute pm3 either present or absent in the lower toothrow, with pm2 and pm4 not making contact (Fig. 7). Baculum medium-sized, dorsal and ventral parts of the basal cone subequal in size with dorsal and ventral incision shallow (Fig. 8). In lateral view, baculum shaft narrows towards tip, undulating in shape and forms an evenly rounded ventrally bent tip. In dorsoventral view, shaft straight with shallow constriction at inflection point of spatulated tip (Supplementary Appendix S2 Fig. A5). *Rhinolophus namuli* sp. nov. echolocates at a mean peak frequency of 76.9 kHz, SD = 0.8, range = 75.9–78.0 (Fig. 9 and Table 5). Phylogenetically, this species belongs to the *capensis*-group.

Description

Dorsal pelage near uniform beige brown, slightly darker towards head, turning near rusty on both sides of the muzzle. Ventral fur paler than dorsal. Hair

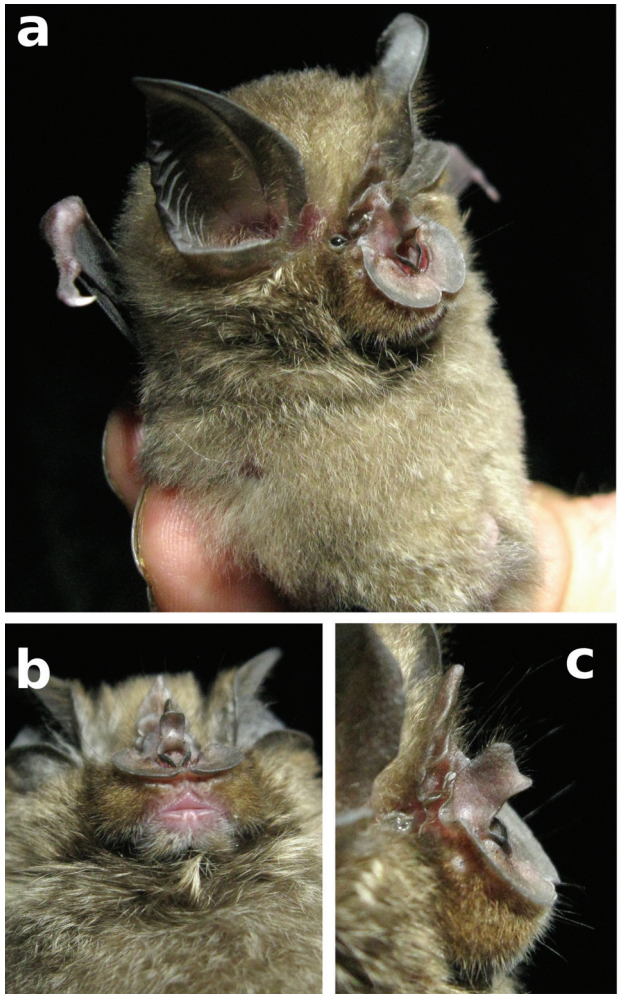

FIG. 4. Live photographs of *R. namuli* sp. nov. in the field (♀, MHNG 1971.067), illustrating pelage colour and features of the (a) head and ears, (b) sella and lips and (c) connecting process

length ca. 7 mm, with dark base becoming lighter towards tips causing slight shimmering effect. At time of capture, both male and female live animals exhibited musky and somewhat unpleasant smell.

Head.—Ears medium sized, just reaching tip of muzzle when laid forward, tips pointed in holotype but bluntly rounded in both paratypes, 8–9 ear folds. Three well-developed mental grooves on the lower lip, both lips devoid of hair (Fig. 4 and Supplementary Appendix S2 Fig. A1). The mental grooves were diagnosed according to Csorba *et al.* (2003: Fig. vi, p. xxviii) and are shown in close-up in Supplementary Appendix S2 (Fig. A1). Noseleaf completely covers muzzle, horseshoe wide and secondary noseleaf absent. Sella naked, wide at base, slightly constricted in the middle but otherwise almost parallel sided with rounded tip (Fig. 5 and Supplementary Appendix S2 Fig. A2). Internarial cup rather well developed. Internarial septum is not markedly expanded. Connecting process somewhat hairy, high and rounded, basal part rises near parallel to sella. Tip of the lancet is hastate, with concave sides and a pointed, tapering tip. The hastate lancet differentiates *R. namuli* sp. nov. from *R. maendeleo* and other members of the *adami*-group (Fig. 5 and Supplementary Appendix S2 Fig. A2), more closely resembling members of the *capensis*-group (see Supplementary Appendix S2 Fig. A3 for a comparison of lancet shape with *R. simulator*).

Wing bones.—Metacarpal of the 4th and 5th digit subequal in length, always longer than the 3rd digit (Table 3). Length of the 1st phalanx greatest in 3rd digit, followed by 5th, then 4th digit. Length of the 2nd phalanx greatest in 3rd digit, followed by 4th, then 5th digit. 2nd phalanx of 4th digit greater than twice the length of 1st phalanx.

Cranium.—Skull is narrow (mastoid width exceeds zygomatic width) in MHNG 1971.068 (holotype, male), MHNG 1971.069 (paratype, female), and DM 108333 (referred material, male), but robust (zygomatic width exceeds mastoid width) in MHNG 1971.067 (♂) and DM 10839 (referred material, ♀). Differences are slight, indicating within-species variation in skull shape (Table 4). Weakly developed sagittal crest extends roughly three quarters along the length of the braincase from well-developed supraorbital crest (sagittal crest equally developed in both male and female). Posterior-most point of skull (meeting point of lambdoid and sagittal crest) positioned markedly above the lateral plane formed by the zygomatic arches. Anterior nasal swelling inflated, moderately wide and high, angled forward and protruding anteriorly in lateral view (Fig. 6 and Supplementary Appendix S2 Fig. A4). Anterior median and lateral nasal swellings well-developed but posterior median swellings deflated. Moderate rostral depression between supraorbital ridges creates a concave rostral profile. Posterior-most point of rostral depression reaches, but does not extend beyond, constriction point between the orbits (Fig. 6). The infraorbital foramena are enclosed by a bony bar on both sides in all specimens collected, which is illustrated in close-up in Supplementary Appendix S2 (Fig. A4). Note that in specimen DM 10833, initial inspection concluded the bar was absent on the left side (as reported by Monadjem *et al.*, 2010*a*), but subsequent investigation confirms it presence on both sides (L. Richards, personal communication). Length of the palatal bridge moderate, about one third CM3 length (34.1–37.3%).

Teeth.—Dental formula I 1/2, C 1/1, PM 2/2, M 3/3. Upper canines moderately well developed,

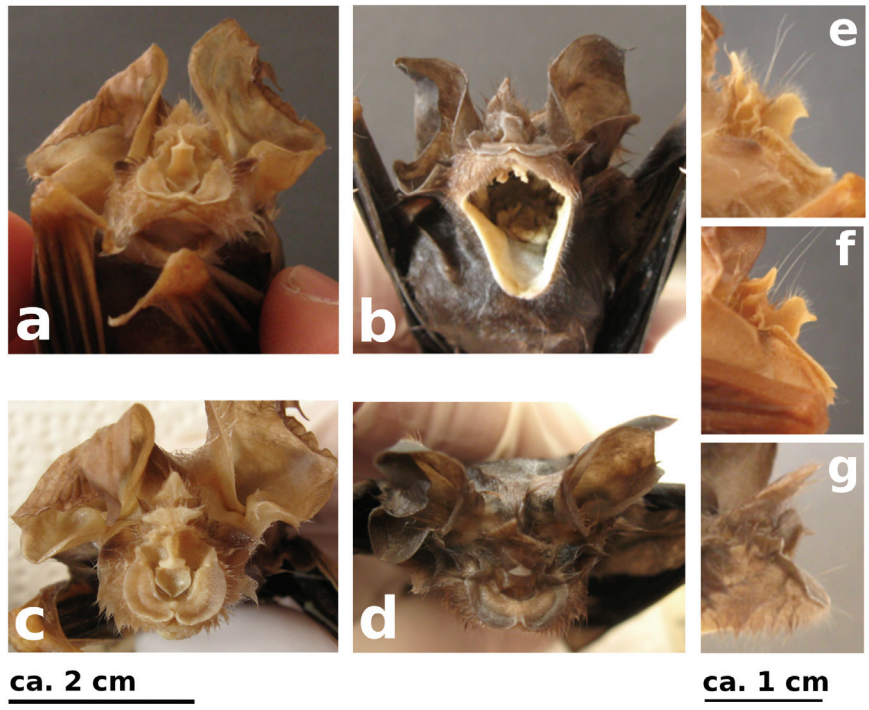

FIG. 5. Head shape (a and b) and noseleaf (c and d) of holotypes of *R. maendeleo* SMF 79.643 and *R. namuli* sp. nov. MHNG 1971.068, respectively; connecting process of *R. maendeleo* SMF 79.643 (e), SMF 99.760 (f), and of *R. namuli* sp. nov. MHNG 1971.068 (g)

extending about twice the length of PM4 (Fig. 6). PM2 small, slightly extruded, separating C1 and PM4 and present on both sides. Minute pm3 present on left side and partly hidden by crown of pm2, lacking on right side, with pm2 and pm4 separate on both sides (Fig. 7).

Baculum.—The baculum is medium-sized with a total baculum length of 2.85 mm (range ca. 2.8–2.95 mm), greatest lateral width of basal cone of 0.78 mm and greatest dorsoventral width of basal cone of 0.87 mm (Fig. 8 and Supplementary Appendix S2 Fig. A5). The basal cone occupies about 20% of the total length, with dorsal and ventral parts subequal in size, neither exhibiting a relative proximally projection. Both ventral and dorsal incisions of the basal cone are shallow. In lateral view, the baculum shaft constricts gradually, before reaching a constant width at about half the length to the tip. The shaft is not straight, but rather undulating. The tip is evenly rounded and distinctively curves ventrally at an angle of about 30° from the proximal-distal axis. In dorsoventral view, the shaft extends from the basal cone largely straight, unflattened and of equal width almost along its entire length. At the inflection point where the tip begins to curve ventrally (about 4/5th along the total baculum length), there is a shallow constriction in the shaft when viewed from a dorsoventral perspective. The tip thus appears spatulated and rounded (Fig. 8 and Supplementary Appendix S2 Fig. A5).

Echolocation.—Calls recorded from seven individuals had a mean peak frequency of 76.9 kHz and a range of 75.9–78.0 kHz (Fig. 9 and Table 5).

Comparisons

Taxonomic position.—The connecting process is well-developed, high and rounded, but is neither continuously arched (*pearsoni*-group, *ferrum-equinum*-group or *fumigatus*-group), low and rounded (*hipposideros*-group), low and poorly developed (*maclaudi*-group) nor sharply triangular (*landeri*-group) (Csorba *et al.*, 2003). The sella is naked and constricted in the middle rather than hairy (*fumigatus*-group) and/or parallel-sided (*euryale*-group). Three mental groves are well developed (Supplementary Appendix S2 Fig. A1), not partly obliterated like in members of *capensis*-group. These features, in addition to the characters described above, indicate *R. namuli* sp. nov. bears most resemblance morphologically to *R. maendeleo*, which was moved, with *R. adami,* from the *capensis*-group into a newly created *adami*-group by Kock *et al*. (2000). Regarding the defining characters of the *adami*-group, *R. namuli* sp. nov. has a large sella,

TABLE 3. External measurements of specimens of *R. namuli* sp. nov., *R. maendeleo* and *R. simulator*. Measurement with an asterisk in the header have non-overlapping ranges between *R. namuli* sp. nov. and *R. maendeleo*. DM = Durban Natural Science Museum; MHNG = Muséum d'Histoire Naturelle de Genève; MoM = National Museums of Malawi; SMF = Senckenberg Museum Frankfurt. * = accession numbers unknown for MoM, field codes used. Abbreviations are explained in the methods under 'Character measurements'

Collection no.	Sex	BM	HB	Tail*	HS	Ear*	FA	Tib	HF	3Met*	3Ph1	3Ph2*	4Met	4Ph1*	4Ph2*	5Met	5Ph1	5Ph2
R. namuli sp. nov.																		
MHNG 1971.067 (Paratype)	♀	10.0	49.2	19.8	8.9	19.6	48.3	19.0	8.9	30.7	15.1	26.3	34.4	7.5	16.5	33.7	11.3	13.3
MHNG 1971.068 (Holotype)	♂	9.5	48.2	23.6	9.3	19.5	49.5	19.3	8.1	31.5	15.6	26.3	35.4	8.0	16.3	34.7	11.3	12.5
MHNG 1971.069 (Paratype)	♂	9.0	49.1	19.0	9.3	20.1	47.3	18.9	8.4	29.8	14.9	26.3	33.6	7.3	15.4	31.9	10.5	12.3
DM 10833	♂	10.0	46.3	18.9	8.7	19.7	47.5	19.2	–	–	–	–	–	–	–	–	–	–
DM 10839	♀	–	–	–	8.4	19.6	48.9	19.8	9.0	31.0	15.3	26.5	34.8	7.6	16.9	35.5	11.5	13.3
Mean	–	9.6	48.2	20.3	8.9	19.7	48.3	19.2	8.6	30.7	15.2	26.3	34.5	7.6	16.3	33.9	11.1	12.9
Range	–	9.0–10.0	46.3–49.2	18.9–23.6	8.4–9.3	19.5–20.1	47.3–49.5	18.9–19.8	8.1–9.0	29.8–31.5	14.9–15.6	26.3–26.5	34.4–35.4	7.3–8.0	16.3–16.9	31.9–35.5	10.5–11.5	12.3–13.3
R. maendeleo																		
SMF 79.643 (Holotype)	♂	–	–	26.2	8.8	24.2	47.6	19.6	8.4	32.5	14.6	24.2	35.1	8.1	14.5	34.5	10.4	13.0
SMF 66.960 (Paratype)	♀	–	–	25.8	8.5	23.5	49.1	19.1	8.8	33.0	14.5	25.2	36.3	8.2	14.2	36.9	10.3	13.3
SMF 93.354	♂	–	–	25.7	8.8	22.9	48.8	19.5	9.4	32.1	14.9	24.5	36.0	8.1	14.1	35.1	11.0	13.0
Mean	–	–	–	25.9	8.7	23.5	48.5	19.4	8.9	32.5	14.7	24.6	35.8	8.1	14.3	35.5	10.6	13.1
Range	–	–	–	25.7–26.2	8.5–8.8	22.9–24.2	47.6–49.1	19.1–19.6	8.4–9.4	32.1–33.0	14.5–14.9	24.2–25.2	35.1–36.3	8.1–8.2	14.1–14.5	34.5–36.9	10.3–11.0	13.0–13.3
R. simulator																		
MHNG 1971.064	♂	8.0	38.5	25.5	8.0	19.8	43.1	17.3	8.4	28.6	13.4	21.8	31.9	7.9	12.7	31.1	9.0	11.4
MoM MW179°	♀	8.0	45.9	25.1	8.4	19.7	44.5	17.8	8.0	30.5	13.7	22.9	32.8	7.4	14.0	31.7	9.5	12.7
MHNG 1971.066	♂	7.5	42.9	20.9	8.2	20.4	42.0	17.8	8.2	27.9	13.5	22.6	30.7	7.3	13.3	31.1	9.5	11.9
MHNG 1971.065	♀	7.5	39.8	22.8	8.0	20.0	45.3	17.0	8.6	29.0	13.8	21.5	32.6	6.9	13.6	32.4	9.4	12.0
MoM MW273°	♀	8.5	42.2	27.3	8.5	19.8	44.2	17.6	8.2	29.5	14.0	23.2	32.8	7.8	14.4	32.2	9.6	11.4
Mean	–	7.9	41.9	24.3	8.2	19.9	43.8	17.5	8.3	29.1	13.7	22.4	32.1	7.4	13.6	31.7	9.4	11.9
Range	–	7.5–9.0	38.5–45.9	20.9–27.3	8.0–8.5	19.7–20.4	42.0–45.3	17.0–17.8	8.0–8.6	27.9–30.5	13.4–14.0	21.5–23.2	30.7–32.8	6.9–7.9	12.7–14.4	31.1–32.4	9.0–9.6	11.4–12.7

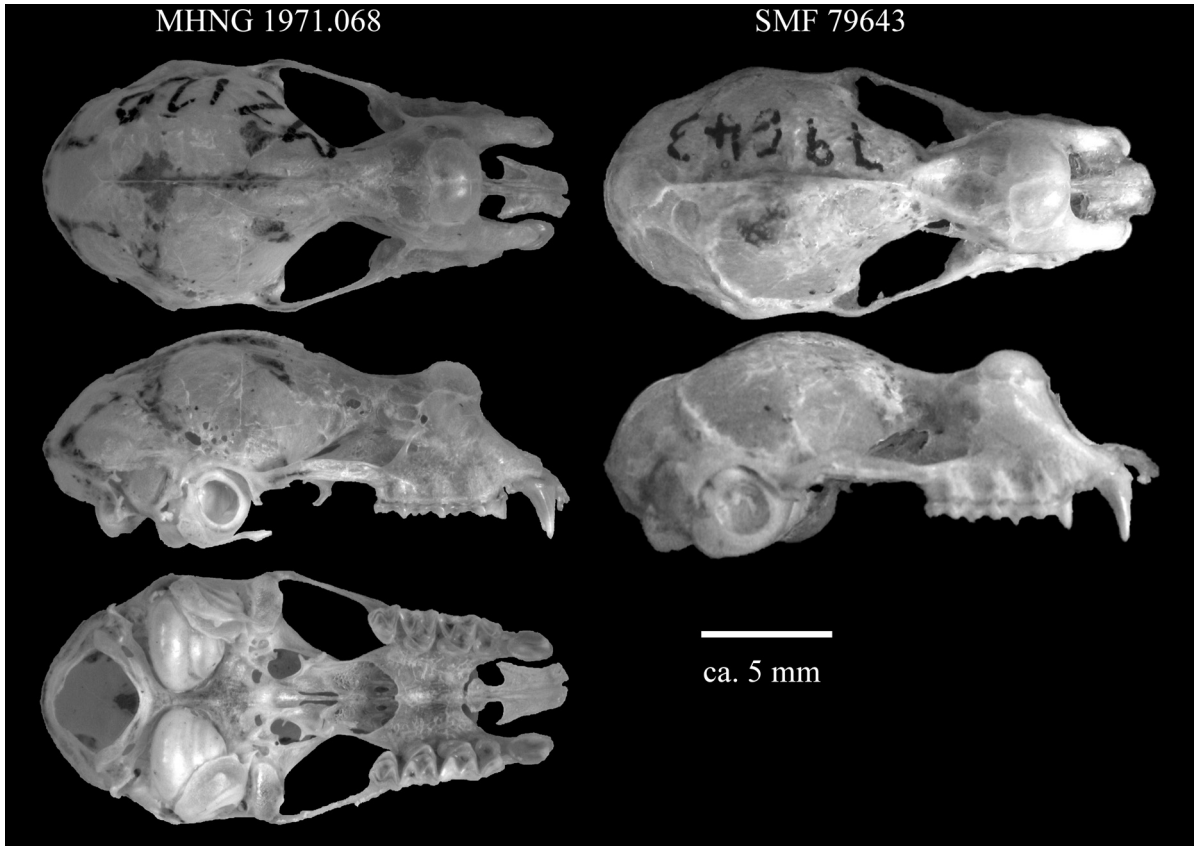

FIG. 6. Cranium in dorsoventral (top), lateral (middle) and ventrodorsal (bottom; only for MHNG 1971.168) views of holotypes of *R. namuli* sp. nov. (left) and *R. maendeleo* (right)

straight-sided or rounded lancet, three well-defined mental grooves, small second premolar in the toothrow and more bulbous narial swellings. The nasal swellings are pronounced and clearly align to species of the *adami*- rather than *capensis*-group when *R. namuli* sp. nov., *R. capensis*, *R. simulator* and *R. adami* are compared side-by-side (see Supplementary Appendix S2 Fig. A6). However, the ear length of *R. namuli* sp. nov. is medium rather than large, only three of the five specimens of *R. namuli* sp. nov. have a narrow skull, and all have a moderate palate (36% of CM3 in *namuli* sp. nov. against > 40% in *adami*-group). Furthermore, when viewed in profile, *namuli* sp. nov. has a high and rounded connecting process, which is lower and regularly arched in the *adami*-group (Csorba *et al.*, 2003). Morphologically, *R namuli* sp. nov. should therefore be retained within the *capensis*-group. Our genetic analysis confirms this, with a robust positioning of *R namuli* sp. nov. in the *capensis*-group alongside *R. simulator*, *R. swinnyi* and *R. denti* as closest relatives (Fig. 3). Unfortunately, as no genetic sequences for *R. maendeleo* or *R. adami* are currently available, we cannot assess formally their phylogenetic position within the Rhinolophidae radiation. We therefore leave open the question of the validity of the *adami*-group and whether the striking morphological similarities shared between *maendeleo* and *namuli* sp. nov. represent convergences or true synapomorphies.

Specific status.—*Rhinolophus namuli* sp. nov. appears morphologically most similar to *R. maendeleo*, although these two species are currently placed in two separate groups (*capensis*-group and *adami*-group, respectively). Due to this mismatch, *R. maendeleo* is used as the primary comparison to assign specific status, while other members of the *adami* and *capensis* groups are considered under 'Similar species' below. In comparison to *R. maendeleo*, *R. namuli* sp. nov. shares several similar external and craniodental measurements, including overlapping forearm length, horseshoe width, metacarpal length of 4th and 5th digit, length of 1st phalanx of 3rd and 5th digit, length of 2nd phalanx of 5th digit, Tib, HF, MW, ZW, BcH, CC, CM3, IOB, ML, cm3, AMSW, PL (Table 3). The two species also exhibit a similar overall cranial shape and size (Fig. 6). However, *R. namuli* sp. nov. is

TABLE 4. Craniodental measurements of specimens of *R. namuli* sp. nov., *R. maendeleo* and *R. simulator*. Measurement with an asterisk in the header have non-overlapping ranges between *R. namuli* sp. nov. and *R. maendeleo*. DM = Durban Natural Science Museum; MHNG = Muséum d'Histoire Naturelle de Genève; MoM = National Museums of Malawi; SMF = Senckenberg Museum Frankfurt. * = accession numbers unknown for MoM, field codes used. Abbreviations are explained in the methods under 'Character measurements'

Collection no.	Sex	SL*	MW	ZW	BcH	CC	M3M3*	CM3	IOB	ML	cm3	ALSW*	AMSW	PL	PB*	Ang1*	Ang2
R. namuli sp. nov.																	
MHNG 1971.067 (Paratype)	♀	19.09	9.30	9.29	5.79	4.78	6.90	7.08	2.51	12.67	7.43	3.34	4.97	2.64	3.01	16.11	19.46
MHNG 1971.068 (Holotype)	♂	19.60	9.56	9.64	6.01	5.10	7.07	7.19	2.51	12.95	7.56	3.31	5.17	2.59	3.25	15.97	17.95
MHNG 1971.069 (Paratype)	♂	19.27	9.25	9.18	5.82	4.84	6.72	7.04	2.33	12.75	7.33	3.21	4.85	2.46	3.13	15.70	17.66
DM 10833	♂	19.39	9.65	9.41	5.64	4.89	6.77	7.08	2.64	12.84	7.44	3.27	5.03	2.60	3.27	–	–
DM 10839	♀	19.48	9.40	9.53	5.7	4.70	6.96	7.03	2.51	12.74	7.35	3.29	4.88	2.48	2.98	16.38	18.45
Mean	–	19.37	9.43	9.41	5.79	4.86	6.88	7.08	2.50	12.79	7.42	3.28	4.98	2.55	3.13	16.04	18.38
Range	–	19.09–19.60	9.25–9.65	9.18–9.64	5.64–6.01	4.70–5.10	6.72–7.07	7.03–7.19	2.33–2.61	12.67–12.95	7.33–7.56	3.21–3.34	4.85–5.17	2.46–2.6	2.98–3.27	15.7–16.38	17.66–19.46
R. maendeleo																	
SMF 79.643 (Holotype)	♂	19.96	9.39	9.39	6.06	4.74	6.60	7.25	2.54	–	7.61	3.51	5.03	2.73	2.87	17.56	18.4
SMF 66.960 (Paratype)	♀	19.99	9.43	9.38	5.78	4.76	6.55	7.20	2.43	13.16	7.41	3.65	4.99	2.54	2.79	16.72	17.88
SMF 93.354	♂	19.91	9.42	9.21	6.02	4.59	6.46	7.10	2.49	12.89	7.48	3.48	5.05	2.64	2.68	17.69	19.26
Mean	–	19.95	9.41	9.33	5.95	4.70	6.54	7.18	2.49	13.03	7.50	3.55	5.02	2.64	2.78	17.32	18.51
Range	–	19.91–19.99	9.39–9.43	9.21–9.39	5.78–6.06	4.59–4.76	6.46–6.60	7.10–7.25	2.43–2.54	12.89–13.16	7.41–7.61	3.48–3.65	4.99–5.05	2.54–2.73	2.68–2.87	16.72–17.69	17.88–19.26
R. simulator																	
MHNG 1971.064	♂	18.08	8.85	–	5.71	4.70	6.25	6.71	2.27	–	6.88	3.04	4.63	2.25	2.67	–	–
MoM MW179°	♀	18.59	9.07	9.12	5.72	4.56	6.56	6.73	2.51	11.94	7.00	3.38	4.66	2.55	2.76	–	–
MHNG 1971.066	♂	18.41	8.80	8.90	5.87	4.87	6.38	6.76	2.16	–	7.06	3.40	4.74	2.22	2.81	–	–
MHNG 1971.065	♀	18.09	9.00	8.79	6.04	4.35	6.35	6.63	2.54	11.29	6.90	3.26	4.59	2.07	2.72	–	–
MoM MW273°	♀	18.17	8.89	8.52	5.79	4.35	6.26	6.36	2.19	11.10	6.69	3.08	4.38	2.34	2.60	–	–
Mean	–	18.27	8.92	8.83	5.83	4.57	6.36	6.64	2.33	11.44	6.91	3.23	4.60	2.29	2.71	–	–
Range	–	18.08–18.59	8.80–9.07	8.52–9.12	5.71–6.04	4.35–4.87	6.25–6.56	6.36–6.76	2.16–2.54	11.10–11.94	6.69–7.06	3.04–3.40	4.38–4.74	2.07–2.55	2.60–2.81	–	–

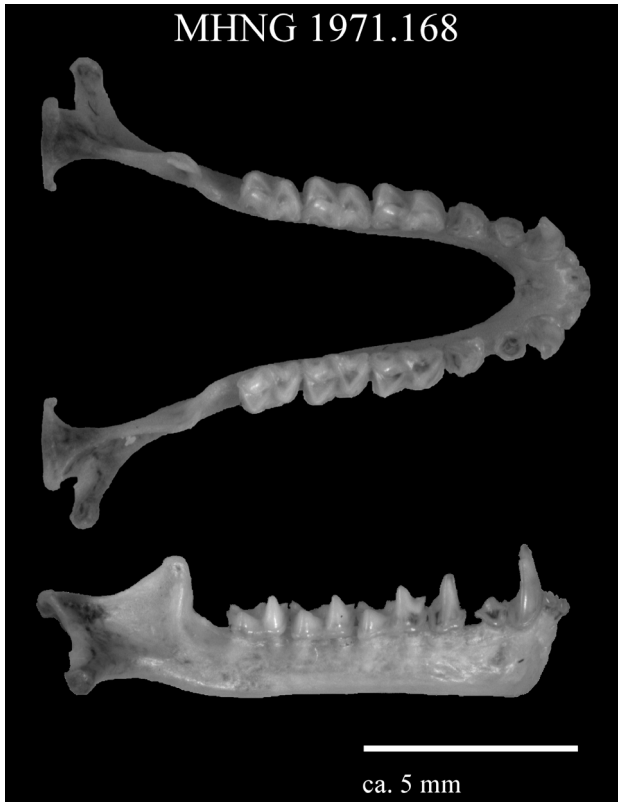

FIG. 7. Mandibles of the holotype of *R. namuli* sp. nov.

distinguished from *R. maendeleo* by a number of key characters. The characteristic feature of *R. maendeleo,* an absence of the bony bars forming the infraorbital foramena (Kock *et al.*, 2000), is not shared in *R. namuli* sp. nov, where the bony bars forming the infraorbital foramena are present in all collected specimens (Supplementary Appendix S2 Fig. A4). *R. namuli* sp. nov. can also be distinguished from *R. maendeleo* by a number of non-overlapping craniodental measurements that indicate a slightly shorter overall skull length (SL — Table 4), a slightly wider and shorter rostrum (M3M3 and PB — Table 4) and subtle differences in rostral and narial inflation shape (Fig. 6). *R. maendeleo* also bears a deeper and longer rostral depression whose posterior most point extends beyond the constriction point between the orbits. In *R. namuli* sp. nov. the depression is shallower, and does not extend as far back between the orbits (Fig. 6). These differences in rostrum shape, inflation angle and depression are captured in the two angle measurements (Ang1, Ang2), of which the first is non-overlapping between the species (Table 4).

The two species also differ completely in bacular morphology (Fig. 8 and Supplementary Appendix S2 Fig. A5). In lateral view, the baculum of *R. maendeleo* narrows gradually from the basal cone to the tip, the shaft being straight and flattened dorsoventrally, especially towards the distal end (Kock *et al.*, 2000). In contrast, the baculum of *R. namuli* sp. nov. is undulating, uncompressed, and is distinctively downturned (ventrally angled) at the tip. The inflations forming the basal cone of the baculum of *R. maendeleo* are unequal with the dorsal inflations protruding proximally relative to the ventral. This is in contrast to *R. namuli* sp. nov., which bears subequal inflations with no clear protrusion. The species also differ in the extent of the ventral incision in the basal cone, which is deep in *R. maendeleo* and shallow in *R. namuli* sp. nov. (Supplementary Appendix S2 Fig. A5).

Externally, the two species are distinguished by the length of the tail, size of the ears and differences in horseshoe structure, and in the dimensions of the wing bones (Table 3). At a mean length of 25.9 mm,

TABLE 5. Echolocation call parameters of *R. namuli* sp. nov. and species with similar echolocation peak frequency from nearby localities. Table highlights mean peak frequency (PF), standard deviation (SD), range and number of individuals recorded (*n*). Data collected by M. Curran and M. Kopp (unpublished material). MZ = Mozambique, MW = Malawi

Species	Location	PF (kHz)			*n*
		Mean	SD	Range	
R. landeri	Mount Mabu, MZ	102.2			1
R. blasii	Mount Namuli, MZ	94.0	1.1	93.2–94.7	2
	Mount Mabu, MZ	94.9	0.8	93.8–95.5	4
	Mount Mulanje, MW	93.9	1.0	92.2–96.0	17
R. simulator	Mount Mulanje, MW	86.0	0.8	84.0–86.7	13
R. clivosus	Mount Namuli, MZ	81.2	0.3	81.0–81.4	2
	Mount Mabu, MZ	80.5	0.5	79.8–81.0	4
	Mount Mulanje, MW	81.3	0.8	79.9–82.6	15
R. namuli sp. nov.	Mount Namuli, MZ	76.9	0.8	75.9–78.0	7
R. fumigatus	Mount Mulanje, MW	58.4	0.4	58.1–59.0	4
R. mabuensis	Mount Mabu, MZ	38.1	0.3	37.5–37.9	2
	Mount Mulanje, MW	37.7	0.3	37.9–38.3	2

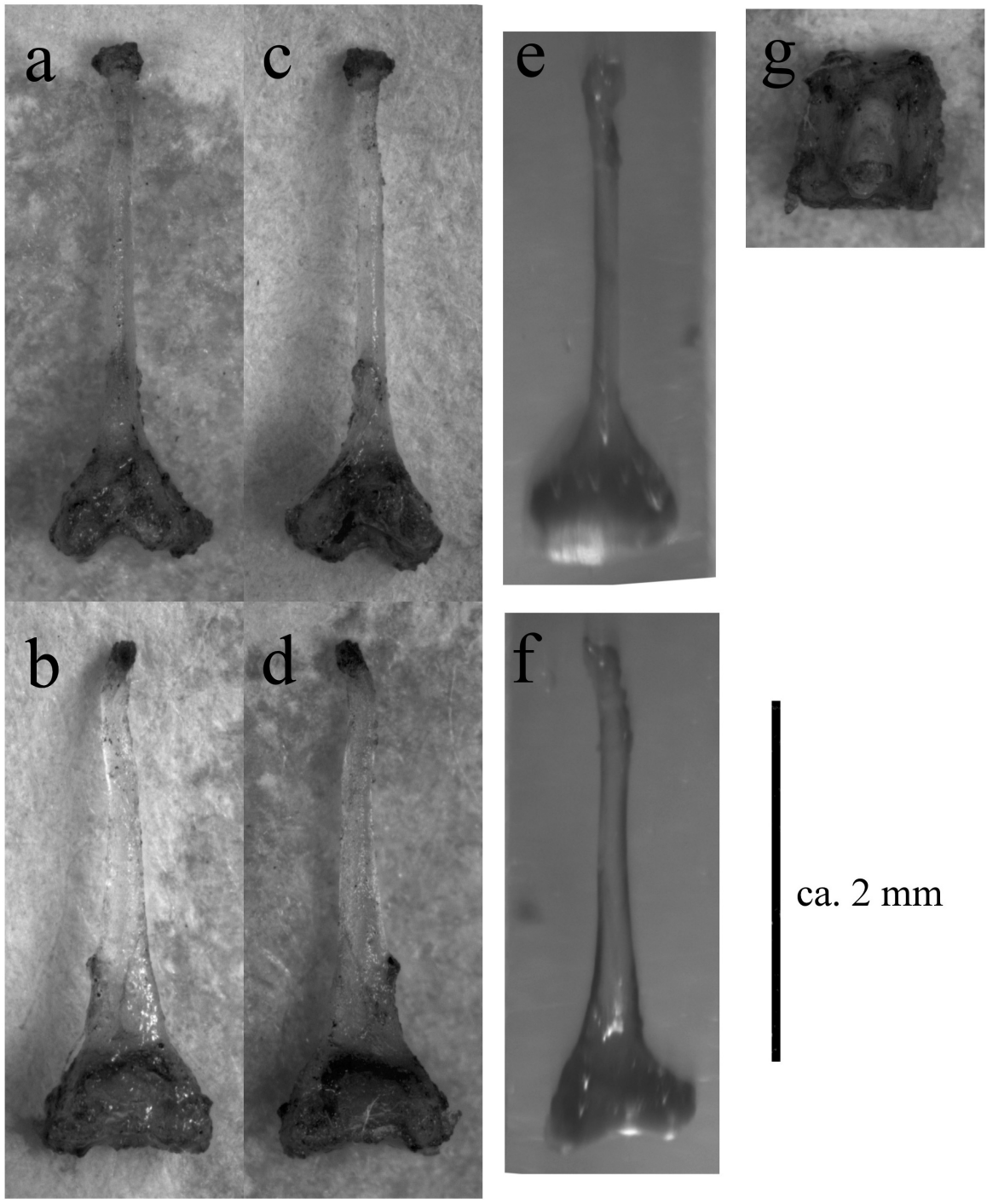

FIG. 8. Baculum of the holotype (MHNG 1971.168) of *R. namuli* sp. nov. in dorsal-ventral (a), ventral-dorsal (c), lateral (b and d) and proximal-distal (g) views. Baculum of the DM 10833 also shown in dorsal-ventral (e) and lateral (f) view. For the holotype (MHNG 1971.168), total baculum length is ca. 2.85 mm, greatest lateral width of basal cone is 0.78 mm and greatest dorsoventral width of basal cone is 0.87 mm

the tail of *R. maendeleo* is markedly longer than that of *R. namuli* sp. nov. (mean of 20.3 mm). Ear length follows a similar pattern (means of 23.5 mm versus 19.3 mm in *R. maendeleo* and *R. namuli* sp. nov., respectively). The connecting process of *R. namuli* sp. nov. is high and rounded, not continuously arched as in *R. maendeleo*, and with a more pronounced constriction in the sella (Figs. 4 and 5, and Supplementary Appendix S2 Fig. A2). Within the wing bones, measurements of metacarpal and phalanx length illustrate differences between the species, particularly in the 3rd and 4th digits (Table 3).

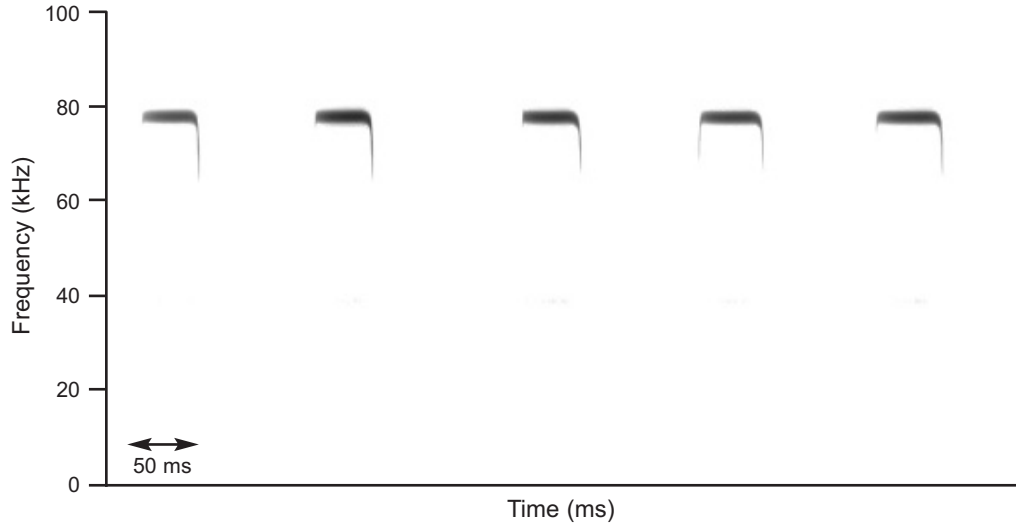

FIG. 9. Echolocation call of *R. namuli* sp. nov. (♀, MHNG 1971.067; recorded at Mount Namuli, Zambesia Province, Mozambique, -15.405933 / 37.067006, ca. 1,200 m a.s.l.)

Similar species.—Kock *et al.* (2000) compare *R. maendeleo* to the morphologically similar *R. adami*, illustrating a set of characters that differ between the species. We confirmed that *R. namuli* sp. nov. possesses many of the same distinguishing characters. Specifically, both *R. maendeleo* and *R. namuli* sp. nov. can be distinguished from *R. adami* by a smaller and concave-sided lancet, a less arched connecting process, a near-parallel sided interpterygoid groove, differing bacular morphologies, external and craniodental measurements, including palate length and inflation breadth (Kock *et al.*, 2000).

When compared to members of the *capensis*-group, *R. namuli* sp. nov. is larger than *R. simulator*, with non-overlapping forearm, tibia and wing bone lengths (Table 3) and several non-overlapping craniodental measurements, such as greatest skull length, mastoid width, zygomatic width and lower toothrow length (Table 4). Based on a comparison of published measurements of *R. denti, R. swinnyi*, *R. gorongosae* and *R. rhodesiae*, *R namuli* sp. nov. is much larger and more robust as highlighted by non-overlapping forearm length and greatest skull length. It also echolocates at a much lower frequency that any of these species (Table 2). *R. namuli* sp. nov. has more inflated anterior nasal swellings than members of the *capensis*-group (Supplementary Appendix S2 Fig. A6). Finally, the bacular morphology of *R. namuli* sp. nov. sets the species apart from all potentially similar species from the *adami* and *capensis* groups to which it bears closest morphological affinity.

Summarizing the differences highlighted above, the PCA results comparing *R. namuli* sp. nov. to both *R. maendeleo* and *R. simulator* (the two most similar species from the *adami* and *capensis* groups, respectively) illustrate the distinct position of the three species (Fig. 2). While 95% confidence intervals (CIs) for the first two PCs overlap slightly between *R. namuli* sp. nov. and *R. simulator*, such uncertainty is to be expected given the small sample size. For *R. maendeleo*, the sample size was too small to estimate CIs. The first two PCs explained a large amount of variance in the data, with a cumulative 76% for craniodental measurements and 82.2% for external measurements.

Phylogenetic reconstructions based on the CYT-B gene (Fig. 3) demonstrate that *R. namuli* sp. nov. belong to the *capensis*-group with strong support. Compared to the closely related and sympatric *R. simulator, R. namuli* sp. nov. is genetically distinct, confirming the morphological differences presented above. In the future, additional studies on the phylogenetic relationships between the species of the *adami*- and *capensis*-group would be desirable to ascertain relationships or test their taxonomic validity.

Rhinolophus namuli sp. nov. echolocates at a frequency that is not shared by other species in the region (Table 5). At a mean frequency of 76.9 kHz, the calls of *R. namuli* sp. nov. differs markedly from *R. simulator* (86 kHz), *R. clivosus* (80.5–81.3 kHz) and *R. fumigatus* (58.4 kHz), the three most similarly echolocating species in our dataset for the region (Table 5).

Discussion

In this paper, we describe a new species of *Rhinolophus* from Mount Namuli in northern Mozambique. Both morphological and genetic analyses were used to differentiate *R. namuli* sp. nov. from similar candidate species. Our morphological analysis suggests that *R. namuli* sp. nov. share with *R. maendeleo* some diagnostic features (bulbous anterior nasal swellings, three well-defined mental grooves, first small upper premolar in toothrow) of the *adami*-group (Kock *et al.*, 2000; Csorba *et al.*, 2003). However, other key external and craniodental characters differ between the two, including the shape of the ears, sella and connecting process, and palate length. Such a combination of morphological characters in *R. namuli* sp. nov. questions the validity of the diagnosis of the *adami*-group. Similarities in morphology between *R. namuli* sp. nov. and *R. maendeleo* could potentially be due to morphological convergence between members of the *adami*- and *capensis*-groups, or could indicate that the *adami*-group should be reconsidered and included within the *capensis*-group. Furthermore, genetic analyses based on mitochondrial (Fig. 3) or several independent nuclear genes (Demos *et al.*, 2019) clearly place *R. namuli* sp. nov. within the firmly established *capensis*-group. If members in the *adami*-group prove to be also phylogenetically nested within the *capensis*-group, this would render it paraphyletic. Until genetic sequences from members of the *adami*-group become available, and are included in a wider revision of African horseshoe bats (building on the work of Demos *et al.*, 2019), we are unable to test this hypothesis and leave final systematics conclusions for further studies.

The individuals described herein were captured in moist evergreen forest at and above 1,200 m on the Mount Namuli massif (Fig. 1). The species was relatively abundant in the two main sampling localities on the mountain, comprising two of the 12 individuals (across all species) recorded (17%) at the Base Camp site (1,200 m) and 11 of the 54 individuals (across all species) recorded (20%) at the Ukalini Forest site (1,650 m). The third site (Manho forest) was only opportunistically sampled; therefore, no statistics are provided. The species was captured in harp traps and nets set across small to medium-sized streams and riverbeds in the forest interior, and in openings and edge habitat bordering forest clearings. It was not recorded in a canopy net set at ca. 10 m height at highest pocket at Ukalini forest, although this net was only open for two nights. Of the five additional records of this species contained in Demos *et al*. (2019), three are from a cave North-East of Gurue (latitude -15.39933, longitude 37.04283), which borders Mount Namuli and is at a similar altitude to our own sites (ca. 1,750 m a.s.l.), and considered as the same site (Mount Namuli). The other two originate from Nyika National Park in Malawi (-10.5808, 33.7128; ca. 2,200 m a.s.l.), and the Udzungwa Mountains in southern Tanzania (-7.75195, 36.46338: ca. 1,900 m a.s.l.). Assuming that the species' habitat preferences match its presence across montane (> 1,000 m a.s.l.) forests or wooded areas in the region, its area of occupancy is likely to be relatively small and highly fragmented. The range enclosed by existing specimens extends over three countries and about a 1,000 km north-south and 350 km east-west. Remarkably, *R. namuli* sp. nov. is now the eighth new bat species described over the past decade with the majority of their range in Mozambique (Taylor *et al.*, 2012, 2018, 2019; Monadjem *et al.*, 2013, 2020), and contributes to a burgeoning country checklist (Monadjem *et al.*, 2010*a*). This is likely due to a historic absence of intense ecological studies in the past (due to a long-running civil war), favourable biogeographic conditions to support speciation and diversity and a host of new ecological surveys during a recent period of political stability (Timberlake *et al.*, 2008; Bayliss *et al.*, 2014).

Based on the existing records from this study and documented in Demos *et al.* (2019), *R. namuli* sp. nov. appears to be affiliated with Afromontane forested areas. It joins others, such as *R. maendeleo*, *R. mabuensis*, *Kerivoula africana* Dobson, 1878 and *Mops bakarii* Stanley, 2008, as an East African coastal and montane forest endemic (Cockle *et al.*, 1998; Kock *et al.*, 2000). Although we did not sample below 1,200 m, we suspect that the species could be a high-altitude specialist because it was not recorded by A. Monedjem, who sampled the foothills of the mountain in 2006, and did not record *R. namuli* sp. nov. (Monadjem *et al.*, 2010*a*). Within-site patterns in capture frequency tend to indicate an affinity to the forest understory, as the species was not recorded in the canopy fixture (although canopy sampling was limited and we did not sample in completely open habitat to further investigate this assertion). Assuming that the species represents a forest specialist with core requirements for breeding, roosting and foraging limited to montane forest habitat within the study region, the current state and projected future trends in forest cover on Mount Namuli and elsewhere in the region are of interest from a conservation perspective.

The current forest cover pattern on Mount Namuli is the result of the ongoing anthropogenic driving forces of habitat clearance, habitation and cultivation (Timberlake *et al.*, 2008). This has given rise to significant amounts of secondary derived grassland and non-forest vegetation. Historical imagery indicates forest cover in 1972 was about 1250 ha across the massif. When the specimens were first captured between 2007 and 2009, over 1000 ha of moist evergreen forest remained, of which about 90% was found between 1600 and 1900 m (ca. 135 ha between 1200 and 1600 m and almost nothing below 1200 m). Since 2009, Namuli has suffered a significant loss in its wet forest. Current remote sensing analysis provides a 2016 forest cover of 771 ha. The period from 2013 to 2016 shows an average annual deforestation of 98 ha/year, 17 times greater than the period from 2006 to 2013. The total deforestation from 1972 to 2016 is 479 ha which represents a 38% loss in wet forest (Legado, 2017). At current rates of loss, the forest would disappear entirely by 2025.

It is presumed that significant areas of lowland forest did exist in the Malema valley at lower altitudes, but have since been cleared. The remaining mid-altitude forests may serve as a refuge for species once found in these lowland forests. Mount Namuli is currently unprotected and there is a dense human population and high unemployment in the surrounding area. The nearby town of Gurue has been rejuvenating its tea industry in recent years, with previously fallow tea plantations being brought back under intensive management. The mid-altitude plateau (the Malema valley) is also populated by an estimated 7,000 people (Fig. 1). The main threats to the mountain's habitats will continue to arise from encroachment from within the Malema valley due to an increasing population, the cultivation of 'Irish potatoes' in the Ukalini and Manho forest patches, and the over-grazing of upland grassland species by cattle, pigs, and goats (Timberlake *et al.*, 2008). A conservation action plan, including conservation agriculture, is required urgently for Mount Namuli in order to address these unsustainable destructive threats, safeguard the biological riches of the mountain, and protect and conserve the remaining forest habitat. Similar conservation efforts across the presumed range of *R. namuli* sp. nov. (spanning montane forests from Mozambique to southern Tanzania), along with a formal assessment of the conservation status of the species, should be prioritized to prevent any emerging threats of extinction.

Supplementary Information

Contents: Supplementary appendices: Appendix S1. GenBank references for all samples used in the phylogenetic reconstructions. Table A. References of the 77 cytochrome *b* gene (CYT-B) sequences mined from the GenBank and used in phylogenetic reconstructions. The last five specimens, noted as sp. nov., pertain to the new species described in this manuscript, and were referred originally as *Rh*. cf. *denti-simulator*. Appendix S2. Additional morphological and craniodental features and comparisons. Fig. A1. Close-up of the lower lip of the holotype of *R. namuli* sp. nov. (MHNG 1971.068), showing three well-defined mental grooves (marked with arrows). Fig. A2. Close-up of the lancet (a) and sella (b and c) for *R. maendeleo* (left, holotype, SMF 79.643) and *R. namuli* sp. nov. (right, holotype, MHNG 1971.068). The lancet of *R. namuli* sp. nov. is concave with a narrower, rounded tip (hastate) in comparison to *R. maendeleo*, which bears a near straight-sided lancet and tapered pointed tip. Fig. A3. Comparison of noseleaf structure, in particular the shape of the lancet (marked with arrows), in living examples of *R. namuli* sp. nov. (left; female, MHNG 1971.067) and *R. simulator* captured on Mount Mulanje in Malawi (right; female above, field number ML 378, male below, museum accession number MHNG 1971.066). *R. simulator* bears a hastate lancet characteristic of the *capensis*-group (concave, narrow rounded tip), which *R. namuli* sp. nov. shares (as opposed to a non-hastate lancet in the *adami*-group). Fig. A4. Close-up of the bony bar (marked with an arrow) forming the interorbital foramena of the holotype of *R namuli* sp. nov. (MHNG 1971.068). Picture also illustrates the bulbous nasal swellings. Fig. A5. Comparison of the bacular morphology of *R. namuli* sp. nov. and *R. maendeleo*. Lateral view shown in the upper row (a, c, e), ventral view in the bottom row (b, d, f). Specimens used for the illustrations are the *R. namuli* sp. nov. holotype MHNG 1971.168 (a and b) and paratype MHNG 1971.069 (c and d), and the holotype of *R. maendeleo* SMF 79643 (e and f). Illustration of *R. maendeleo* is reproduced from Kock *et al*. (2000). Fig. A6. Comparison of the skull shape in dorsoventral view between *R. capensis*, *R. namuli* sp. nov. and *R. adami* (a) and between *R. simulator* and *R. namuli* sp. nov. (b), and frontal view of the rostral inflation for the two groups (c and d, respectively). Appendix S3. Estimates of Average Evolutionary Divergence over Sequence Pairs within Groups. The number of base substitutions per site from averaging over all sequence pairs within each group are shown. Analyses were conducted using the Kimura 2-parameter model [1]. This analysis involved 101 nucleotide sequences. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There were a total of 1,140 positions in the final dataset. Evolutionary analyses were conducted in MEGA X [2]. Supplementary Information is available exclusively on BioOne.

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