Journal of Mammalogy, 93(6):1440–1455, 2012

Phylogeny of the Emballonurini (Emballonuridae) with descriptions of a new genus and species from Madagascar

Steven M. Goodman,* Sébastien J. Puechmaille, Nicole Friedli-Weyeneth, Justin Gerlach, Manuel Ruedi, M. Corrie Schoeman, William T. Stanley, and Emma C. Teeling

Field Museum of Natural History, Department of Zoology, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA (SMG, WTS)
Association Vahatra, BP 3972, Antananarivo 101, Madagascar (SMG)
Department of Mammalogy and Ornithology, Natural History Museum of Geneva, Route de Malagnou 1, BP 6434, 1211 Geneva (6), Switzerland (NF-W, MR)
University Museum of Zoology Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom (JG)
School of Life, Biological Sciences Building, South Ring Road, Westville Campus, University of Kwa-Zulu Natal, Kwa-Zulu Natal 3630, South Africa (MCS)
School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland (SJP, ECT)

* *Correspondent: sgoodman@fieldmuseum.org*

Molecular phylogenetic studies suggest that the genus *Emballonura*, a member of the Old World tribe Emballonurini (Family Emballonuridae), is paraphyletic. This genus has a broad distribution across islands in the Indo-Pacific, southern Asia, and Madagascar. The paraphyly is the result of the genus *Coleura*, known from sub-Saharan Africa, portions of the Arabian Peninsula, Madagascar, and the Seychelles, being embedded between the Malagasy and Asian/Indo-Pacific clades of *Emballonura*, and the latter clade has priority for the use of the name. To resolve this situation, we propose a new genus for the Malagasy *Emballonura* clade. Furthermore, with greater molecular sampling of *Coleura* across portions of its range in association with morphological and bioacoustical characters, we are able to resolve aspects of the phylogenetic history and species limits of this genus. *Coleura* contains two well supported clades, including *C. afra* from mainland Tanzania and the offshore island of Pemba and a sister clade composed of *C.* cf. *afra* from Madagascar and *C. seychellensis* from the Seychelles. The average genetic distance between animals from Madagascar and the Seychelles is 6%, whereas Pemba/Tanzania and Madagascar is 10%. Because of the paraphyletic relationship of populations of *C. afra* with respect to *C. seychellensis*, we describe a new species of *Coleura* from Madagascar.

Key words: *Coleura*, *Emballonura*, Emballonurini, Madagascar, new genus, new species, paraphyly, taxonomy

© 2012 American Society of Mammalogists
DOI: 10.1644/11-MAMM-A-271.1

Recent systematic research on the bat fauna of Madagascar, at least in part based on molecular genetics, has revealed that a considerable portion of the locally occurring species was either previously unrecognized from the island or simply unknown to science. In a review of Malagasy bats by Peterson et al. (1995), 27 species were documented and as of June 2011, this figure has increased to 44 species (Goodman 2011; Goodman et al. 2011, 2012). This result stems from both molecular and morphological studies that have provided considerable insight into the evolutionary history, origins, and species diversity of the Malagasy and regional bat fauna.

The vast majority of Malagasy bats originated from Africa (e.g., Russell et al. 2008; Stadelmann et al. 2004; Trujillo et al. 2009), although based on current biogeographic distributions, two non-African genera appear to be Asian in origin and occur across a broad area from southeastern Asia to the Pacific and Indian oceans. The first case is that of the large and frugivorous genus *Pteropus* (family Pteropodidae), which is a strong flyer and presumably an excellent island hopper. However, at least on western Indian Ocean islands, the different *Pteropus* species have a complex history of leapfrog colonization (Chan et al. 2011; O'Brien et al. 2009).

The 2nd and less-studied case is that of the typically small (<5 g) and weak-flying insectivorous genus *Emballonura*

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

(family Emballonuridae). It is found on islands off New Guinea westward from mainland Southeast Asia (8 species) to Madagascar (2 species), with a distributional gap of 3,500 km across the Indian Ocean between the western-most Asiatic occurrence and Madagascar. This genus is a member of the subfamily Emballonurinae, in which the tribe Emballonurini occurs in the Old World and the tribe Diclidurini in the New World (McKenna and Bell 1997). Another member of the Emballonurini, *Coleura*, has a distribution across much of sub-Saharan Africa, portions of the Middle East, and islands in the western Indian Ocean. The other large radiation in this family, the subfamily Taphozoinae, has a broad Old World distribution from Africa, the Middle East, western Indian Ocean islands, mainland Asia, to the Indo-Pacific. Phylogenetic reconstruction indicates that the emballonurid radiation is African in origin, and during the mid-Eocene to the early Oligocene dispersed to different portions of the New and Old Worlds (Eick et al. 2005; Jones et al. 2002; Lim 2007; Teeling et al. 2005).

Recent molecular phylogenetic research on the Emballonurini, composed of the genera *Coleura*, *Emballonura*, and *Mosia*, has found this tribe to be paraphyletic, with the genus *Coleura* being placed between the Asiatic/Indo-Pacific and Malagasy clades of *Emballonura* (Ruedi et al. 2012). In contrast to *Emballonura*, *Coleura* occurs on the African mainland and offshore islands, as well as on the Arabian Peninsula (*C. afra* Peters, 1852), Madagascar (*C.* cf. *afra*), and the eastern portions of the Seychelles Archipelago (*C. seychellensis* Peters, 1868); the phylogenetic relationships between these genera and within *Coleura* have not been examined in any detail. Recent fieldwork with *Coleura* in the Seychelles has provided molecular genetic material of a previously unavailable taxon and an increased number of samples for other populations from Madagascar and Tanzania. In this paper, we critically examine the phylogenetic relationships between the genera *Emballonura* and *Coleura*, and address the problem of paraphyly in the former genus. Using molecular, morphological, and bioacoustical characters, we investigate the intrageneric relationships of certain *Coleura* populations, which resulted in the identification and description of a new species from Madagascar, named herein.

Materials and Methods

Extraction, amplification, and sequencing.—Total genomic DNA was isolated from tissue samples stored in a buffer containing NaCl-saturated 25% dimethyl sulfoxide and 250 mM ethylenediaminetetra-acetic acid *C. afra*) or stored in 75% ethanol (*Emballonura* sp. and sample originally preserved in formalin). Extraction followed a modified salt/chloroform extraction protocol (Miller et al. 1988), which included an additional chloroform/isoamyl alcohol (24/1) step after the addition of the saturated NaCl solution. For *C. seychellensis*, DNA was isolated from feces collected on Silhouette Island and desiccated in silica gel (Puechmaille and Petit 2007). Fecal samples were extracted in an ancient DNA lab using the QIAamp DNA Stool Mini Kit (Qiagen Ltd., West Sussex, United Kingdom) following the modifications as detailed in Puechmaille et al. (2007). The complete mitochondrial cytochrome *b* gene was amplified using the primers mitochondrial (mt)DNA-R3-F (5′-TGGCATGAAAAA TCACCGTTGT-3′—Puechmaille et al. 2011) and Cytb-H (5′-CTTTTCTGGTTTACAAGACCAG-3′—Weyeneth et al. 2008). For 2 *C. seychellensis* samples, only the first 450 base pairs (bp) of the cytochrome *b* gene were amplified with the primers mtDNA-R3-F and MVZ 04 (Smith and Patton 1991). All reactions were carried out in 25-μl simplex reactions containing 2 μl of DNA extract, 1× polymerase chain reaction (PCR) buffer minus Mg (Invitrogen, Bio Sciences Ltd., Dublin, Ireland), 1.5 mM $MgCl_2$, 0.4 μM each primer, 0.2 mM deoxynucleotide triphophates, and 1 U Platinum *Taq* DNA Polymerase High Fidelity (Invitrogen). Amplifications were carried out in a DNA Engine DYAD thermocycler (MJ Research, Quebec, Canada) with the following touchdown PCR profile: initial step 15 min at 95°C, then 10 cycles of 3 s at 95°C, 3 s at 60°C (with a reduction of 2°C every 2 cycles), 1 min at 72°C, followed by 30 cycles of 30 s at 95°C, 30 s at 50°C, and 1 min at 72°C and a final step of 10 min at 72°C. PCR products were purified and sequenced in both directions by Macrogen Inc. (Seoul, Korea) using the 4 PCR primers mentioned above. Complementary sequences were assembled and edited for accuracy using CodonCode Aligner 3.7.1 (CodonCode Corporation, Dedham, Massachusetts).

Phylogenetic analyses.—In addition to sequences generated for this study (Table 1), we included full cytochrome *b* sequences retrieved from Genbank (Goodman et al. 2006; Lim et al. 2008; Ruedi et al. 2012). These sequences included 2 New World Emballonuridae (tribe Diclidurini), 7 of the 9 currently recognized species of *Emballonura*, and the 2 known *Coleura* species (Simmons 2005). Phylogenetic reconstruction was independently undertaken using the Bayesian inference in BEAST (Drummond and Rambaut 2007) and maximum likelihood (ML) in PAUP* version 4.0b10 (Swofford 2003), using the general time-reversible + gamma-distributed rates among sites + proportion of invariable sites (GTR + Γ + I) substitution model as determined by the hierarchical likelihood ratio tests in ModelTest version 3.7 (Posada and Crandall 1998). For the Bayesian analysis, no outgroup was specified and the constant population size coalescent was used as a tree prior. The program was run for 10,000,000 generations and sampled every 500. The first 1,000,000 generations were discarded as burn-in. Two replicate analyses were performed to ensure convergence and the results were then pooled. Effective sample sizes for the estimated parameters and posterior probability as calculated with the program Tracer v1.4 (Rambaut and Drummond 2007) were higher than 500. ML analyses were performed with PAUP 4.0b10 (Swofford 2003) and node support was estimated with 100 bootstrap replicates. Starting trees were obtained via neighbor joining and analyses carried out using tree bisection and reconnection-based heuristic searches. We used the Shimodaira–Hasegawa test (Shimodaira and Hasegawa 1999) with full optimization and 1,000 bootstrap replicates to compare the statistical

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

Table 1.—Information on the samples used in the molecular analysis of Emballonurini and associated references from the museum collections of the American Museum of Natural History, New York (AMNH), the Field Museum of Natural History, Chicago (FMNH), Muséum d'histoire naturelle de la Ville de Genève, Geneva (MHNG), the Royal Ontario Museum, Toronto, Canada (ROM), the National Museum of Natural History, Washington, DC (formerly United States National Museum, USNM), and V, F. M. Catzeflis collection, Montpellier, France. PN is an abbreviation for Parc National.

Sample reference	Sex	Taxon	Country	Geographic precision	GenBank	Reference
FMNH 213591	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213592	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213593	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213594	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213595	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213596	♂	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213597	♂	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213598	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213599	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213600	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213601	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213602	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 213603	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 183864	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 183865	♂	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 183866	♂	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
FMNH 183867	♀	*Coleura kibomalandy*	Madagascar	Province d'Antsiranana, PN d'Ankarana	JQ710748	This study
UADBA 43497	♂	*Coleura kibomalandy*	Madagascar	Province de Mahajanga, PN de Namoroka	JQ710749	This study
FMNH 192804	♂	*Coleura afra*	Tanzania	Pemba Island	JQ710750	This study
FMNH 192805	♀	*Coleura afra*	Tanzania	Pemba Island	JQ710751	This study
FMNH 192806	♂	*Coleura afra*	Tanzania	Pemba Island	HQ693721	Ruedi et al. (2012)
FMNH 192807	♀	*Coleura afra*	Tanzania	Pemba Island	HQ693721	Ruedi et al. (2012)
FMNH 198024	♂	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	JQ710752	This study
FMNH 198025	♂	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	JQ710752	This study
FMNH 198027	♀	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	JQ710752	This study
FMNH 198028	♀	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	JQ710752	This study
FMNH 198029	♂	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	HQ693720	Ruedi et al. (2012)
FMNH 198030	♂	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	HQ693720	Ruedi et al. (2012)
FMNH 198031	♂	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	JQ710752	This study
FMNH 198032	♂	*Coleura afra*	Tanzania	Tanga Region, Amboni Caves	JQ710752	This study
Csey3	?	*Coleura seychellensis*	Seychelles	Silhouette Island (roost B)	JQ710753	This study
Csey4	?	*Coleura seychellensis*	Seychelles	Silhouette Island (roost B)	JQ710753	This study
Csey5	?	*Coleura seychellensis*	Seychelles	Silhouette Island (roost B)	HQ693735	Ruedi et al. (2012)
Csey6	?	*Coleura seychellensis*	Seychelles	Silhouette Island (roost B)	HQ693735	Ruedi et al. (2012)
Csey7	?	*Coleura seychellensis*	Seychelles	Silhouette Island (roost B)	JQ710753	This study
Csey8	?	*Coleura seychellensis*	Seychelles	Silhouette Island (roost B)	JQ710753	This study
ROM 105746	?	*Cormura brevirostris*	Ecuador		EF584158	Lim et al. (2008)
V 1833	♀	*Saccopteryx leptura*	French Guyana		HQ693718	Ruedi et al. (2012)
USNM 580434	♂	*Emballonura semicaudata*	Palau Islands	Peleliu Island	HQ693708	Ruedi et al. (2012)
USNM 580435	♀	*Emballonura semicaudata*	Palau Islands	Peleliu Island	HQ693709	Ruedi et al. (2012)
USNM 590688	♀	*Emballonura alecto*	Malaysia	Borneo	HQ693710	Ruedi et al. (2012)
USNM 590689	♀	*Emballonura alecto*	Malaysia	Borneo	HQ693711	Ruedi et al. (2012)
UADBA 31936	♀	*Emballonura atrata*	Madagascar	Toamasina	HQ693734, HQ693745	This study
UADBA 31938	♂	*Emballonura atrata*	Madagascar	Fianarantsoa	HQ693731, HQ693739	This study
TK 20327	?	*Emballonura beccarii*	Papua New Guinea		EF584222	Lim et al. (2008)
USNM 586288	♂	*Emballonura dianae*	Papua New Guinea		HQ693716	Ruedi et al. (2012)
USNM 586289	♀	*Emballonura dianae*	Papua New Guinea		HQ693717	Ruedi et al. (2012)
MHNG 1970.038	♀	*Emballonura monticola*	Malaysia	Peninsular Malaysia	HQ693714	Ruedi et al. (2012)
MHNG 1970.044	♀	*Emballonura monticola*	Malaysia	Peninsular Malaysia	HQ693715	Ruedi et al. (2012)
FA447	?	*Emballonura raffrayana*	Papua New Guinea		EF584224	Lim et al. (2008)
USNM 580434	♂	*Emballonura semicaudata*	Palau Islands	Peleliu Island	HQ693708	Ruedi et al. (2012)
USNM 580435	♀	*Emballonura semicaudata*	Palau Islands	Peleliu Island	HQ693709	Ruedi et al. (2012)
FMNH 176360	♂	*Emballonura tiavato*	Madagascar	Antsiranana	DQ178257, HQ693738	Goodman et al. (2006), this study
FMNH 184026	♂	*Emballonura tiavato*	Madagascar	Mahajanga	HQ693724, HQ693737	This study
AMNH 275979	?	*Emballonura* sp.	Solomon Islands		JQ710754	This study

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

significance of the monophyly versus paraphyly of species belonging to *Emballonura*.

Morphological comparisons and analyses.—In the handling of wild animals, we followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Details on the morphology and genetics of the Malagasy and Asian/Pacific clades of *Emballonura* have been presented elsewhere (Goodman et al. 2006; Ruedi et al. 2012). To further evaluate morphological and associated taxonomic relationships of *Coleura*, we examined 66 specimens of *C. afra* from the African mainland, 37 specimens of *C. seychellensis* from the Seychelles (Appendix 1), and 19 specimens of *C.* cf. *afra* from Madagascar (see holotype and paratype entries in the species description below). These specimens are housed in the following institutions: the Natural History Museum, London (BMNH; formerly British Museum of Natural History); Field Museum of Natural History, Chicago (FMNH); Muséum national d'Histoire naturelle, Paris (MNHN); National Museum of Kenya, Nairobi (NMK); Université d'Antananarivo, Département de Biologie Animale, Antananarivo (UADBA); and Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin (ZMB, formerly Zoologisches Museum Berlin). Only adult specimens were used in the morphological comparisons and these were defined on the basis of the fusion of the basisphenoid–basioccipital suture and the complete eruption of the adult dentition. We examined the holotypes of *C. silhouettae* [=*C. seychellensis*] (BMNH 6.3.18.2), *C. gallarum* [=*C. afra*] (BMNH 11.8.2.4), and *C. nilosa* [=*C. afra*] (BMNH 15.3.6.76), as well as the cotypes of *C. afra* (BMNH 7.1.1.703 and 58.6.18.12).

Six external measurements in millimeters of recently collected specimens of *Coleura* from Madagascar and Tanzania were recorded before preparation and included: total length, tail length, hind foot length, ear length, tragus length, and forearm length. Mass in grams was also recorded using a spring balance. For Malagasy specimens collected by SMG the hind foot length does not include the claw and for Tanzanian specimens obtained by WTS this measurement includes the claw.

SMG measured 5 cranial and 4 dental characters from specimens using digital calipers accurate to the nearest 0.1 mm. The measurements and their definitions are: occipitocanine length—from posterior-most part of occiput to anterior buccal alveolar border of canines; condylocanine length—from posterior-most part of occipital condyle to anterior buccal alveolar border of canines; greatest zygomatic breadth—width across zygomatic arches at widest point; postorbital breadth—dorsal width at most constricted part of skull; breadth braincase—greatest breadth across skull at mastoid processes; maxillary tooth row (C-M3)—crown length from the anterior buccal alveolar border of the canine to the posterior buccal margin of the third upper molar; mandibular tooth row (c-m3)—crown length from the anterior buccal alveolar border of the canine to the posterior buccal margin of the third lower molar; width M3—greatest width of third upper molar; and width m3—greatest width of third lower molar.

Definitions of operational taxonomic units (OTUs).—Current geographic patterns of *C. afra* on mainland Africa have not been studied in detail, although it has a broad distribution across the southern portion of the continent. Several different forms have been named that are considered synonyms of *C. afra* (Dunlop 1997; Koopman 1994; Simmons 2005). Although the subject of a portion of the current study is the relationship of Malagasy *Coleura* to other western Indian Ocean and east African populations, the question of patterns of variation in the mainland African populations could not be completely neglected. To assess geographic variation, we have assigned animals from different regions of the African continent to an OTU system, which is defined as follows: OTU 1—*C. afra* from the type locality of Tete, Mozambique; OTU 2—*C. afra* from coastal Kenya and Tanzania; OTU 3—*C.* "*gallarum*" Thomas, 1915 from "Zeyla" [=Zeila or Zaylac], extreme northern Somaliland and includes specimens from Djibouti and Berbera; OTU 4—*C.* "*nilosa*" Thomas, 1915 from Bahr-el-Zeraf, Sudan.

Statistical tests associated with morphology.—Univariate statistical analyses were conducted for each of the measured morphological and craniodental variables and no evidence of sexual dimorphism was found. Hence, in all of the comparisons presented herein the sexes of each species or population are combined. To assess differences in morphology of different species and populations of *Coleura*, we conducted a principal component analysis (PCA) using the statistical package Systat (Systat 2004). Data were log transformed and the unrotated option was used. Three factors were extracted from the correlation matrix.

Bioacoustics.—We recorded the echolocation calls of *Coleura* as they emerged from the Grotte d'Ambatoharanana (Crocodile Cave; 12.9883°S, 49.0217°E, 20 m above sea level [asl]). Echolocation calls were recorded with an Avisoft Ultrasound 116 bat detector (Avisoft Bioacoustics, Berlin, Germany) connected to an ASUS EEE 1005HA netbook (ASUSTek Computer Inc., Taiwan). The recording equipment was placed 10 m inside the cave on a sandbank ~15 m away from the edge and 1.8 m above the surface of the Mananjeba River. The microphone was placed at a 10° angle pointing toward the river. The river flows 2.7 km into the 18.3-km-long cave (Wilson 1987). For at least 100 m from the entrance, the width and height of the cave was >30 m and 5 m, respectively. Assuming that the maximum detection range of *Coleura* calls was similar to that of the emballonurid *Cormura brevirostris* (10–17 m—Surlykke and Kalko 2008), the recording context could be considered open space. In addition, we recorded the echolocation calls of 3 individuals of this population that were released in a flight cage measuring 1.8 × 1.4 × 5.4 m.

For all recordings, the sampling frequency was set at 500 kHz (16 bits, mono), with a threshold of 16. The resultant wave files were analyzed with Batsound Pro (version 3.31b, Pettersson Elektronik AB, Uppsala, Sweden). We also measured the echolocation calls of *Coleura afra* from Kenya that were recorded by Taylor et al. (2005) in open habitat. One signal pulse with a high signal-to-noise ratio (at least 3 times

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

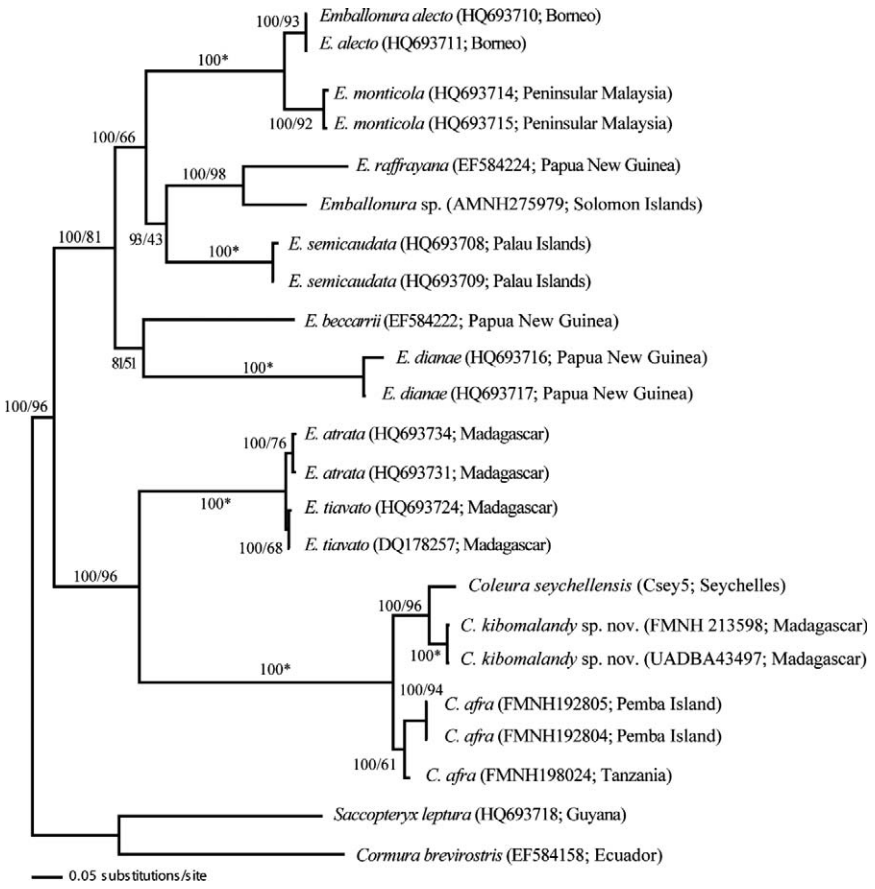

Fig. 1.—Maximum likelihood tree (GTR + Γ + I substitution model) showing the phylogenetic relationship among 23 complete cytochrome *b* sequences (1,140 base pairs) of Emballonurini. Percentage of posterior probabilities from a Bayesian analysis and bootstrap support from a maximum likelihood analysis are shown near each branch with 100* indicating 100% support in both analyses. Tip labels are composed of species names followed in brackets by specimen reference or GenBank accession number and geographic origin of the sample.

stronger than the background noise) for each bat was selected to avoid pseudoreplication. The dominant harmonic from each call was taken from the fast Fourier transform (FFT) power spectrum (size 512). A Hanning window was used to eliminate effects of background noise. Peak echolocation frequency (PF) was measured from the peak of the power spectrum, bandwidth (BW) of call was measured at ±18 dB from the PF on the FFT power spectrum, and interpulse interval (IPI) and duration of call (Dur) were measured from the time-amplitude display (Schoeman and Jacobs 2008). We used *t*-tests with separate variance estimates (Welch t—Blalock 1972) to compare the call parameters between *Coleura* in the cave and in the flight cage and *C. afra* in open habitat.

Results

Description of nucleotide data.—Cytochrome *b* sequences were generated for 31 samples of 3 taxa: 26 individuals of *C. afra* or *C.* cf. *afra* including those from Madagascar ($n = 18$), mainland Tanzania ($n = 6$), and the offshore island of Pemba ($n = 2$), 4 samples of *C. seychellensis* from Silhouette Island, and 1 sample of "*Mosia*" sp. from the Solomon Islands. These sequences supplemented those previously generated from 7 of the 9 currently recognized species of *Emballonura* (Goodman et al. 2006; Lim et al. 2008; Ruedi et al. 2012; Simmons 2005). Individuals sharing the same haplotype were only represented by 1 sequence in the phylogenetic reconstructions, resulting in only 1 sequence for *C. afra* from mainland Tanzania and *C. seychellensis* from the Seychelles, and 2 sequences for *C.* cf. *afra* from Madagascar and *C. afra* from Pemba. The final data set consisted of 23 unique sequences (Table 1).

Phylogenetic analyses within the Emballonurini.—Bayesian and ML phylogenetic reconstructions on the basis of the mtDNA data recovered 2 well-supported clades that separated species distributed in the Asiatic/Indo-Pacific region from those distributed in Africa, Madagascar, and the Seychelles (Fig. 1). All the *Emballonura* species distributed in the Asiatic/Indo-Pacific region form a monophyletic clade, whereas *Emballonura* from Madagascar are more closely related to species belonging to the genus *Coleura*. *Emballonura* paraphyly was significantly better supported than *Emballonura* monophyly (Shimodaira–Hasegawa test; *Emballonura* paraphyly: –ln L = 7627.98, *Emballonura* monophyly: –ln L = 7636.93, $P = 0.045$). Pair-wise ML-corrected genetic distances between *Emballonura* species from each of the 2 clades ranged between 27.3 and 34.3%.

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

Table 2.—Selected morphological characters of the genus *Coleura* and the Malagasy clade of *Emballonura* (*E. atrata* and *E. tiavato*), here named as *Paremballonura* gen. nov. Several of these characters distinguish these 2 genera.

Character	*Coleura*	Malagasy *Emballonura* (*Paremballonura*)
Lower lip	Prominent median groove	No median groove
Rhinarium	Dark and naked	Dark flesh tones and naked
Tragus	Simple structure, longer than broad	Convex, longer than broad
Gular throat pouch	Absent	Absent
Forearm length	>47 mm	<41 mm
Radiometacarpal pouch	Absent	Absent
Wing membrane	Translucent or dark	Dark
Calcar	Equal or slightly shorter than tibia	Shorter than tibia
Occipitocanine length	>16.0 mm	<13.8 mm
Premaxillary	Delicate, not united, curved inwardly	Delicate, not united, curved inwardly
Nasal bones	Notably concave	Slightly concave
Postorbital crest	Developed, confluent with sagittal crest	Moderately developed, not confluent with sagittal crest
Basiosphenoid pits	Deep, single basin with partial septum or completely absent	Moderate, rounded, with at least moderately absent developed septum
Number upper incisors	One pair	Two pairs
Upper toothrows	Converging anteriorly	Largely parallel
Lower incisors	No diastema before canine	Diastema before canine

On the basis of the molecular analyses presented above, as well as in Ruedi et al. (2012), the genus *Emballonura* is paraphyletic, forming 2 distinct nonsister groups. The 1st of these is Asiatic/Indo-Pacific in distribution and composed of at least 7 taxa (Simmons 2005): *E. alecto* Eydoux and Gervais, 1836; *E. beccarii* Peters and Doria, 1881; *E. dianae* Hill, 1956; *E. furax* Thomas, 1911; *E. monticola* Temminck, 1838; *E. raffrayana* Dobson, 1879; and *E. semicaudata* Peale, 1848. The other clade is composed of 2 species restricted to Madagascar: *E. atrata* Peters, 1874 and *E. tiavato* Goodman, Cardiff, Ranivo, Russell, and Yoder, 2006. On the basis of publication date, the type species within the genus *Emballonura* is *E. monticola* and, hence, the generic name *Emballonura* is associated with the Asiatic/Indo-Pacific clade. Two options can be proposed to resolve the problem of paraphyly—transfer *Coleura* to *Emballonura* or put *E. atrata* and *E. tiavato* in a separate genus. Interestingly, when Peters originally named *afra*, he placed it in *Emballonura* (Peters 1852), but subsequently created the genus *Coleura* (Peters 1868), where he transferred *afra* on the basis of notable morphological differentiation between the 2 genera. We create a separate genus for *E. tiavato* and *E. atrata* to reflect aspects of the evolutionary history of this portion of the tribe Emballonurini. No alternative genus name has been previously published for Malagasy *Emballonura* (see African Chiroptera Report 2010; McKenna and Bell 1997) and, hence, we propose:

Paremballonura gen. nov.

Type species.—*Emballonura atrata* Peters, 1874.

Description.—This genus contains 2 species, *Paremballonura atrata* and *P. tiavato*. Bats are of small size, with *P. tiavato* having a forearm length of 35–41 mm and occipitocanine length of 12.2–13.6 mm, whereas these measurements in *P. atrata* are 40–41 mm and 12.8–13.8 mm, respectively (Goodman et al. 2006). Both species have long and slightly shaggy dorsal pelage, which ranges in color from a uniform pale to medium grayish brown in *P. tiavato* to brownish black in *P. atrata*. The 2 taxa have notably long rounded ears (11–14 mm in *P. tiavato* and 15–19 in *P. atrata*) with the inner portion of tragus convex and with a distinct hatchet-shaped anterior projection. In both species, the calcar is slightly shorter in length than tibia, nasal bone hourglass in shape and with distinct central sulcus, basisphenoid pits distinctly rounded and of medium depth and separated by median septum, and with a relatively narrow diastema between PM1 and PM2. All of these characters are discussed and in some cases illustrated in Goodman et al. (2006).

Genetics.—Phylogenetic reconstructions on the basis of cytochrome *b* had 2 well-supported clades for the Emballonurini (Fig. 1). The 1st clade is represented by Asiatic/Indo-Pacific region members of the genus *Emballonura* and the 2nd clade by members of the genera *Coleura* and *Emballonura* found in Africa, Madagascar, and the Seychelles. Hence, *Emballonura* is paraphyletic and the two Malagasy species are renamed as *Paremballonura*.

Diagnosis and comparisons.—*Paremballonura* contains 2 species, *P. atrata* and *P. tiavato*. *Paremballonura* is differentiated from the genus *Coleura* by having no median groove in the lower lip, calcar shorter than the tibia, convex tragus, dark and nontranslucent wing membranes, and diminutive size. See Table 2 for a list of additional characters that separate *Paremballonura* from *Coleura* (Dobson 1878; Goodman et al. 2006, 2008; Miller 1907).

Etymology.—The generic name *Paremballonura* gen. nov. is derived from the Greek prefix *para-*, meaning close to or besides, and the genus *Emballonura* Temminck, 1838.

Distribution.—Restricted to Madagascar.

Phylogenetic relationships.—All *Coleura* sequences form a well-supported monophyletic group sister to the genus *Paremballonura* (Fig. 1). The *Coleura* clade is further divided into 2 well-supported subclades matching the geographic origin of samples with *C. afra* from mainland Tanzania and the offshore island of Pemba grouping together and forming a sister clade to *C.* cf. *afra* from Madagascar and

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

Table 3.—External measurements (mm) and mass (g) of adult *Coleura* specimens from Madagascar, the Seychelles, and Amboni Caves in Tanzania. Descriptive statistics presented are mean ± standard deviation followed by minimum–maximum and sample size (*n*). Measurements from Madagascar and Tanzania were made by SMG and WTS, respectively, and in the case of the hind foot length, SMG excludes the claws and WTS includes the claws. No sexual dimorphism was found in any of the variables with the exception of mass in the Madagascar sample, as most of the females had large embryos.

Locality	Total length	Tail length	Hind foot length	Ear length	Tragus length	Forearm length	Mass length
Coleura kibomalandy, FMNH 213598							
♀ Holotype	79	16	7	16	7	51	11.5
Type series	79.1 ± 2.01	15.1 ± 2.26	6.8 ± 0.73	15.9 ± 1.04	6.9 ± 0.49	50.6 ± 1.07	9.7 ± 1.08
	75–81, n = 17	11–18, n = 17	6–9, n = 17	14–18, n = 13	6–8, n = 13	48–52, n = 21	8.4–12.5, n = 11[a]
Coleura seychellensis			9.6 ± 0.47	14.7 ± 1.02[b]		54.5 ± 1.29	11.1 ± 0.3 ♀♀[c]
			8.5–10.3, n = 16	14.0–15.9, n = 3		51.9–56.4, n = 21	10.2 ± 0.2 ♂♂
Coleura afra, Amboni Caves Tanzania	73.7 ± 3.25	14.2 ± 1.87	10.2 ± 0.46	16.4 ± 0.50	6.4 ± 0.51	49.6 ± 1.50	8.0 ± 0.70
	70–80, n = 25	10–17, n = 25	9–11, n = 26	16–17, n = 26	6–7, n = 25	47–52, n = 26	6.7–9.3, n = 26

[a] Descriptive statistics do not include females with embryos greater than 9 mm and $t = 2.48$, $d.f. = 8$, $P = 0.04$.

[b] Measured from fluid-preserved specimens.

[c] Mass taken from Nicoll and Suttie (1982).

C. seychellensis from the Seychelles. If the Malagasy bats are assigned to *C. afra*, this topology indicates that this species is paraphyletic. The ML-corrected genetic distance between *C.* cf. *afra* from Madagascar and *C. seychellensis* is 6%, whereas the distance between *C. afra* from Pemba and mainland Tanzania is 3.7%. A 9.6–10.4% genetic distance separates *C.* cf. *afra* from Madagascar and *C. afra* from mainland Tanzania and Pemba. Under the framework of the genetic species concept (Bradley and Baker 2001), there is strong evidence that these bats from Madagascar represent an unrecognized species, which we describe herein.

Coleura kibomalandy, sp. nov.

syn. *Coleura afra* Goodman 2011
syn. *Coleura afra* Monadjem et al. 2010
syn. *Coleura afra* Goodman et al. 2005
syn. *Coleura afra* Goodman et al. 2008

Holotype.—Adult female, FMNH 213598 (field number SMG 16954), collected 2 November 2010 by SMG and MCS. The specimen was preserved in 12% formaldehyde and subsequently transferred to 70% ethanol. Before preservation, the skull was removed via small incisions on both sides of the mouth, conserved in approximately 60% ethanol, and then cleaned by dermestid beetles. Samples of pectoral muscle from the individual were collected and saved in lysis buffer. The specimen has a full adult dentition and the basisphenoid–basioccipital suture is completely fused. Postorbital processes are partially broken, whereas the delicate premaxillaries and upper incisors remain attached. When collected, the animal was in an active reproductive state, with a single embryo in the right oviduct measuring 24 mm in crown–rump length. External measurements (in millimeters) are total length 79, tail length 16, hind foot length (without claws) 7, ear length 16, tragus length 7, forearm length 51, and mass 11.5 g (Table 3).

Type locality.—Madagascar: Province d'Antsiranana, Parc National d'Ankarana, 2.2 km ESE d'Amboandriky, Grotte d'Ambatoharanana (Crocodile Cave), 12.9883°S, 49.0217°E, 20 m asl.

Paratypes.—Madagascar: Province d'Antsiranana, Parc National d'Ankarana, 2.2 km ESE d'Amboandriky, Grotte d'Ambatoharanana (Crocodile Cave), 12.9883°S, 49.0217°E, 20 m asl, FMNH 183864–183867 (fluid preserved with skull removed), 183907 (skull only; S. G. Cardiff), 213591–213597 (fluid preserved with skull removed), 213599–213603 (fluid-preserved specimen; SMG and MCS); Madagascar: Province de Mahajanga, Parc National de Namoroka, Anjohimbovonomby, 16.4692°S, 45.3481°E, 115 m asl, UADBA 43497 (R. B. Jenkins).

Geographic distribution.—*Coleura kibomalandy* is only known from 2 sites on Madagascar, the Parc National d'Ankarana and Parc National de Namoroka, both of which are karstic limestone massifs (Fig. 2).

Etymology.—The name *kibomalandy* is derived from a northern Malagasy dialect and means white (*malandy*) and belly (*kibo*) and refers to this species' distinctive underside, which distinguishes it from other described species of *Coleura*, *Paremballonura*, and *Emballonura*.

Common name.—Madagascar Sheath-tailed Bat, Emballonure de Madagascar.

Diagnosis.—*Coleura kibomalandy* is a moderately sized species of Emballonuridae (forearm 48–52 mm), similar in external measurements to *C. afra* (forearm 47–52 mm) and *C. seychellensis*, but the latter species has on average a longer forearm (forearm 52–56 mm; Table 3). *Coleura kibomalandy* is easily distinguished from other *Coleura* by its dark brown dorsum and throat, primarily white underside, and dark wings with translucent patches (Fig. 3). Tragus is proportionately wide. No pronounced diastema between PM1 and PM2 (Fig. 4). Genetically, *C. kibomalandy* has unique cytochrome *b* sequences differing by at least 6% from *C. afra* and *C. seychellensis*.

Description and comparisons.—The relatively long and slightly shaggy fur on the back and head of *C. kibomalandy*

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

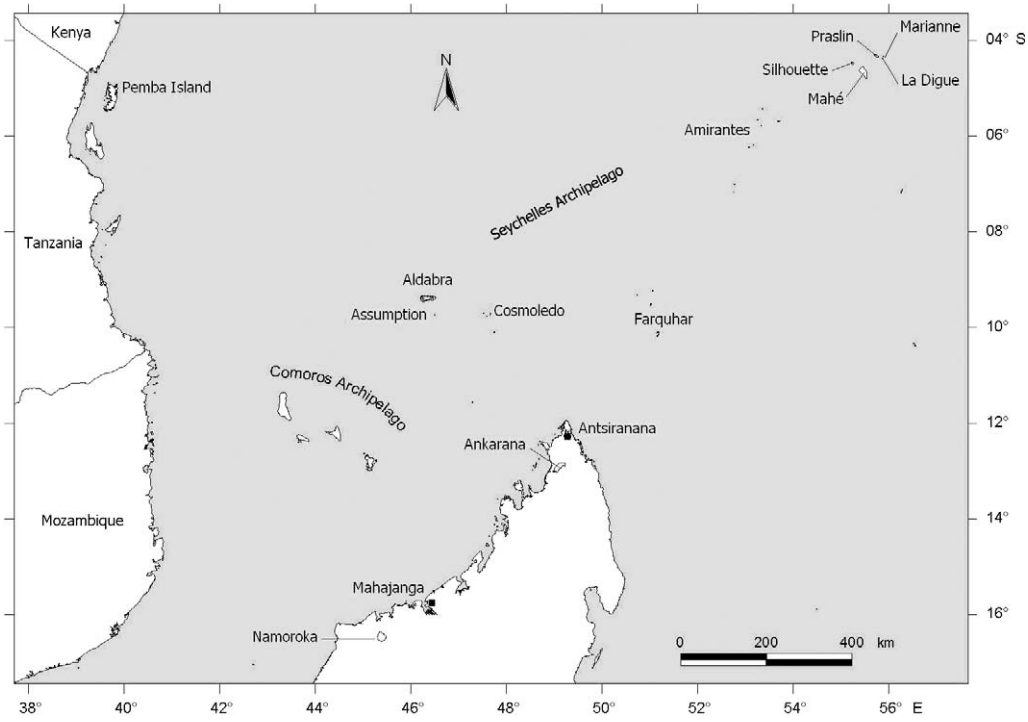

Fig. 2.—Map of the western Indian Ocean showing localities of Emballonurini mentioned in the text from eastern and southeastern Africa, Madagascar, and the Seychelles. Black squares are provincial capitals on Madagascar.

is blackish brown (Fig. 3A). The underside is grayish cream to pure white, often with the underfur having gray bases (Fig. 3B). In contrast, the back and head of *C. afra* is distinctly lighter, varying between medium to a slightly deep brown, often with a grayish tinge, and the underparts are similar in coloration, only slightly paler (Fig. 5A). In a few individuals of *C. afra*, the lower belly is distinctly lighter than the upper portion but not approaching the mainly white underside of *C. kibomalandy*. The dorsal and head pelage of *C. seychellensis* is similar to that of *C. kibomalandy,* but the venter is without any markedly paler fur and similar in coloration to *C. afra* (Fig. 5B). The wing membranes of both *C. kibomalandy* and *C. afra* are light to medium brown and often with relatively large translucent patches, whereas the wings in *C. seychellensis* are blackish brown and without the translucent areas. *Coleura kibomalandy*, as in other members of this genus, does not have radiometacarpal or gular throat pouches. Among the 3 species of *Coleura*, the tragus in *C. kibomalandy* is the largest in width and length (see figure 2 in Goodman et al. 2008), that of *C. afra* is approximately the same shape but smaller, and *C. seychellensis* has a distinctly diminutive tragus with a tapered margin and narrow distal tip.

The animals from Madagascar are almost overlapping in all external measurements with those from Tanzania (Amboni Caves; Table 3). The foot measurements of *C. kibomalandy* from Madagascar were made by SMG and *C. afra* from Tanzania by WTS (excluding or including claw, respectively). The only variable that showed a significant difference between species was hind foot length. In addition, the external measurements of *C. seychellensis* were largely comparable with the African and Malagasy populations, but as different field-workers were responsible for these measurements, the ranges tend to be large and comparisons more difficult to make. Most notable is the average forearm length in *C. seychellensis*, which is larger than the other 2 taxa.

In *C. seychellensis*, there is a pronounced diastema between the minute PM1 and larger PM2, which is notably more prominent than in *C. kibomalandy* and *C. afra*. The nasal depression in *C. seychellensis* tends to be more rectangular than *C. afra* and has a medial furrow (Goodman et al. 2008). A reassessment of these characters using a larger sample size has found them to be variable and not species diagnostic. Both *C. kibomalandy* and *C. seychellensis* have a partial medial septum traversing the anterior portion of the basisphenoid pit, and this septum is absent in *C. afra*.

The cranial (Table 4) and dental measurements (Table 5) of *C. kibomalandy* and *C. afra*, particularly from the type locality (OTU 1) and animals from the Kenyan and Tanzanian coastal region (OTU 2), are similar, whereas those of *C. seychellensis* are distinctly smaller and in some cases exhibit no overlap with *C. kibomalandy* and *C. afra* (OTUs 1 and 2). The samples of *C. afra* from OTUs 3 and 4 were smaller than those from OTUs 1 and 2, approaching the size of *C. seychellensis*.

To examine differences in the craniodental variables between different populations of *Coleura* on continental Africa (separated into 4 OTUs), Madagascar, and the Seychelles, we conducted a PCA. The first 2 unrotated PCs accounted for 70%

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

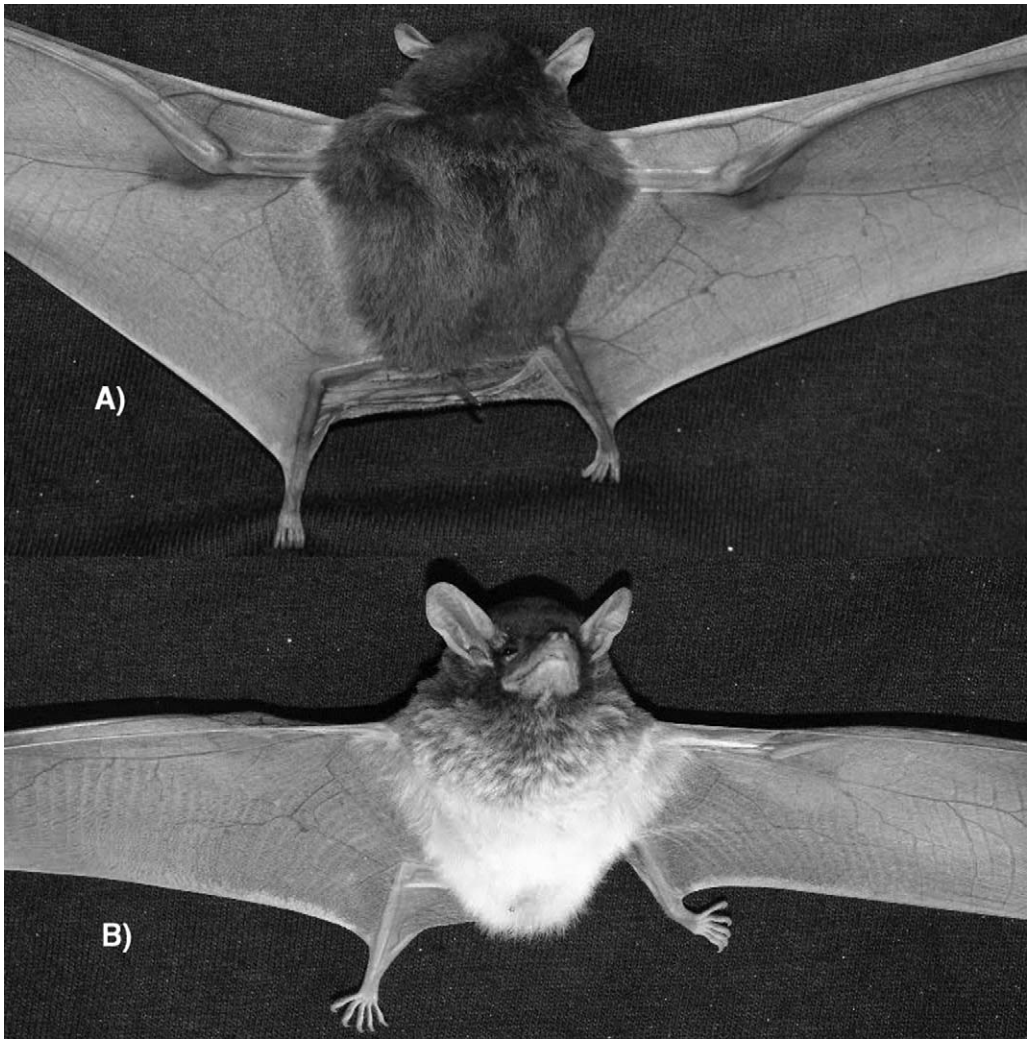

Fig. 3.—Photographs of adult male *Coleura kibomalandy* (FMNH 183865) captured at the Grotte d'Ambatoharanana, the type locality of this species. Note the distinctive dark back and head on the dorsum A) and largely white underparts on the ventrum B), characteristics that are diagnostic of this species with regard to other members of the genus. (Photographs by Scott G. Cardiff.)

of the total variance in craniodental morphology (Table 6), and there was broad overlap between specimens of *C. afra* from the type locality (OTU 1), *C. afra* from coastal Kenya and Tanzania (OTU 2), and *C. kibomalandy* from Madagascar (Fig. 6). In contrast, a separate cluster of points represent the specimens forming part of the type series of *C. gallarum* (OTU 3) from Zeyla in northern Somaliland and surrounding areas, *C. nilosa* (OTU 4) obtained at Bahr-el-Zeraf in Sudan, and animals referable to *C. seychellensis* from the Seychelles. Four of the variables had high loadings on PC1 (occipitocanine length, condylocanine length, C-M3, and c-m3), but only 1 variable (width m3) exhibited a high loading on PC2 and high negative loading on PC3 (postorbital breadth).

Multivariate patterns recovered from the PCA are not good indicators of phylogenetic relationships. The molecular phylogeny has *C. kibomalandy* and *C. seychellensis* as sister species, but they do not overlap in the PC projections. Furthermore, *C. kibomalandy* and *C. afra* from southeastern and eastern Africa show broad morphological overlap, but are genetically divergent. We did not have access to fresh tissue samples of animals obtained in northern Somaliland (OTU 3) and southern Sudan (OTU 4), but they appear smaller and morphologically divergent from *C. afra* from southeastern and eastern Africa and these differences require further investigation. Our study did not take into account patterns of molecular or morphological variation in *Coleura* in central and western Africa.

Bioacoustics.—Coleura kibomalandy produced low-duty-cycle echolocation calls with a prominent quasi-constant frequency component, where most of the energy was concentrated in a narrow frequency band (always in the 2nd harmonic) and a small frequency-modulated portion (Fig. 7). Echolocation calls consisted of monotonous frequency sequences with low PF (<35 kHz), narrow BW (<7 ms), and short Dur (<6 ms; Table 7). Although the overall call structure was similar in the 2 recordings, there were significant

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

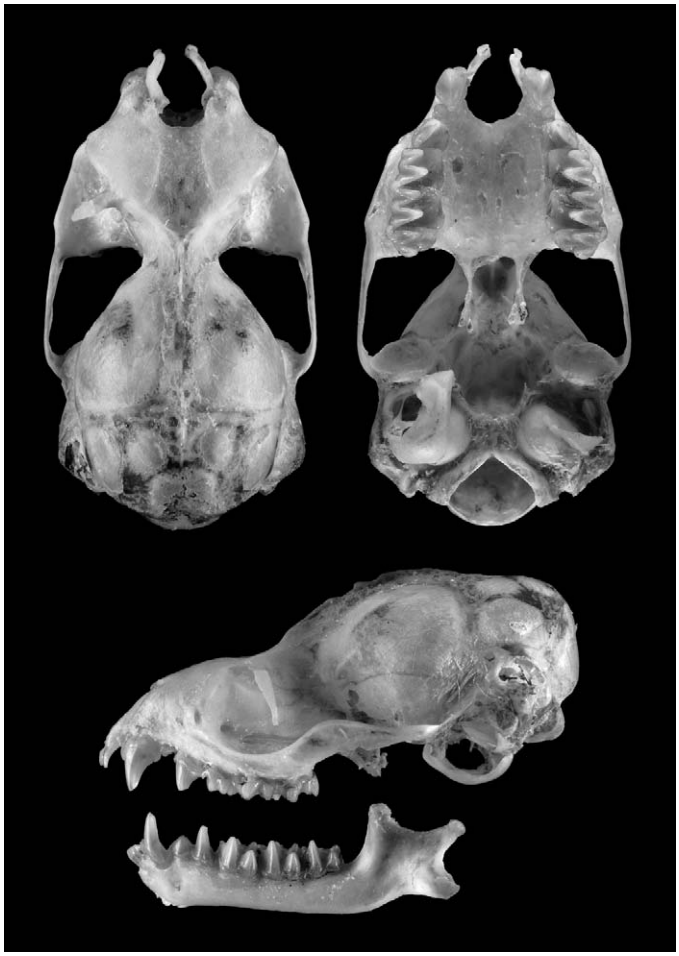

Fig. 4.—Different views of skull and mandible of the holotype of adult female *Coleura kibomalandy* (FMNH 213598) collected in the Grotte d'Ambatoharanana: upper row (left), dorsal view of cranium; upper row (right), ventral view of cranium; lower row, lateral view of cranium and mandible. The condylocanine length is 16.0 mm. (Photograph by John Weinstein, Field Museum image number Z94556_11d.)

differences in Dur ($t = 4.73$, $d.f. = 2.07$, $P = 0.039$) and IPI ($t = 4.53$, $d.f. = 2.23$, $P = 0.037$). Search signals that are dominated by a narrowband portion improve detection of flying insects, and lower call frequencies indicate a long-range detection strategy.

The echolocation calls of *C. kibomalandy* in the Grotte d'Ambatoharanana were similar to the orientation and foraging calls of *C. seychellensis* in the Seychelles and *C. afra* in Kenya (Gerlach 2009a; Taylor et al. 2005; Table 7). There was no significant difference in echolocation call parameters between *C. kibomalandy* and *C. afra* (all $P > 0.05$). We were not able to statistically compare the call parameters of *C. kibomalandy* with those of *C. seychellensis* because most of the call data for the latter species were recorded with a frequency-division (ANABAT) bat detector (Gerlach 2009a), which may not be comparable with time expansion data (Fenton et al. 2001). Furthermore, the oscillographs of the time-expanded recordings of *C. seychellensis* (Gerlach 2009a) indicate that these calls were amplitude clipped (Fenton et al. 2011), hence with a high number of artificial harmonics. Nonetheless, the PF, BW, and Dur of *C. kibomalandy* appear to be markedly lower, broader, and longer, respectively, than those of *C. seychellensis*.

Natural history and conservation status.—Given that *C. kibomalandy* is only known from 2 sites on Madagascar and fewer than 20 specimens, little information is available on its natural history. Scott G. Cardiff visited the Grotte d'Ambatoharanana, the type locality, during the 1st week of July 2004 and his observations on this species are presented in Goodman et al. (2008). Among the animals he handled, at least 3 females showed signs of recent reproduction, including relatively large mammae and remnant lactation tissue. Two adult males collected during this period had enlarged testes and the epididymes were convoluted.

The 2nd visit was in early November 2010, just at the start of the rainy season, by SMG and MCS. Of the 13 individuals handled, 2 were males that had abdominal testes, both measuring 6 × 3 mm, and with convoluted epididymes. Of the 11 females, 10 had single embryos, 8 of which had crown–rump lengths of 22 to 24 mm, one 18 mm, and one 3 mm. An individual with a 24-mm embryo was lactating, and probably approaching parturition. The nongravid female, which was lactating, had a single placental scar. These data suggest a synchrony in the breeding season of these animals at Ankarana. In East Africa, the reproductive period of *C. afra* is associated with the rainy seasons and there is some evidence of delayed maturation after implantation (McWilliam 1987). Although similar reproductive strategies may be in practice in Madagascar, current data are insufficient to draw any clear conclusion.

As in *C. afra* and *C. seychellensis*, *C. kibomalandy* occupies caves for day roost sites. In Kenya, colonies of *C. afra* can reach up to 50,000 individuals (McWilliam 1987), whereas the endangered *C. seychellensis* reaches about 40 individuals (Gerlach 2011). In the case of *C. kibomalandy*, few details are available, but in July 2004, Cardiff estimated that about 500 individuals occupied the Grotte d'Ambatoharanana, and were divided into subgroups, 2 numbering fewer than 100 individuals and another of at least 300 individuals (Goodman et al. 2008). At Ankarana, a massif with a large assortment of caves that have been surveyed for bats, they prefer day roost sites near running water and a permanent river flows through the Grotte d'Ambatoharanana (Cardiff 2006). We do not have any information on the population living in Anjohimbovonomby, Parc National de Namoroka.

Coleura kibomalandy is only known from 2 cave sites on Madagascar in Parc National d'Ankarana and Parc National de Namoroka, which are separated by approximately 550 km (Fig. 2). Within each park, this species has only been found in a single cave, although numerous other cave systems have been explored and surveyed for bats (Cardiff 2006; Goodman et al. 2005). Even though the Grotte d'Ambatoharanana and Anjohimbovonomby are not subject to human exploitation at

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

Fig. 5.—Photographs of A) adult *Coleura afra* (Field Museum of Natural History 192804) from Pemba Island (photograph by William T. Stanley), and B) *C. seychellensis* from Silhouette Island, Seychelles. (Photograph by Justin Gerlach.)

this time and *C. kibomalandy* is not known to be gathered for bush meat, given its limited distribution and the apparent limited number of individuals at the 2 known sites, it should be considered a species of conservation concern. More detailed information is needed on aspects of *C. kibomalandy*'s distribution, ecology, life history, and population size to have its conservation status properly assessed.

Discussion

On the basis of molecular analyses, the genus *Emballonura* was found to be paraphyletic, with the genus *Coleura* nested between the Asiatic/Indo-Pacific clade, which has priority for the generic name *Emballonura*, and the Malagasy clade. To resolve this nomenclatural conflict, we propose to place the Malagasy species in a new genus, *Paremballonura*. The unidentified cf. *Emballonura* specimen (American Museum of Natural History [AMNH] 275979) sequenced herein from the Solomon Islands, originally catalogued as *Mosia,* was divergent from its closest species, *E. raffrayana*, on the basis of sequences presented in Colgan and Soheili (2008) of voucher specimens in the Australian Museum (M23380, M23382). Tissue samples of a few recognized species of *Emballonura* and definitively identified *Mosia* were not available for this study and further investigations are needed to determine if AMNH 275979 represents an undescribed species of Emballonurini.

Table 4.—Cranial measurements (mm) of *Coleura* specimens from Madagascar, the Seychelles, and operational taxonomic units (OTUs) in eastern Africa. Descriptive statistics presented are mean ± standard deviation followed by minimum–maximum, and sample size (*n*).

	Occipitocanine length	Condylocanine length	Zygomatic breadth	Breadth braincase	Postorbital minimum breadth
Coleura kibomalandy, FMNH 213598					
♀ Holotype	17.2	16.0	10.0	9.0	2.6
Type series	17.5 ± 0.39	16.2 ± 0.37	10.0 ± 0.19	9.0 ± 0.14	2.9 ± 0.20
	17.0–18.3, n = 13	15.7–16.9, n = 13	9.7–10.4, n = 11	8.7–9.3, n = 11	2.6–3.3, n = 12
Coleura seychellensis	16.6 ± 0.30	14.9 ± 0.23	9.6 ± 0.24	8.6 ± 0.35	2.9 ± 0.12
	16.1–17.0, n = 8	14.5–15.2, n = 8	9.3–10.0, n = 8	7.8–9.1, n = 9	2.8–3.1, n = 9
Coleura afra					
OTU 1	17.3, 17.4	15.8, 16.2	10.2	8.9, 9.3	2.8, 3.2
OTU 2[a]	17.6 ± 0.33	16.0 ± 0.31	10.1 ± 0.19	9.1 ± 0.21	3.0 ± 0.12
	17.0–18.3, n = 28	15.5–16.6, n = 27	9.7–10.4, n = 27	8.7–9.6, n = 28	2.7–3.2, n = 29
OTU 3	16.6 ± 0.33	15.4 ± 0.31	9.6 ± 0.25	8.7 ± 0.15	2.9 ± 0.16
	16.1–17.0, n = 6	14.9–15.8, n = 6	9.2–9.9, n = 6	8.5–8.9, n = 6	2.7–3.1, n = 7
OTU 4	16.6 ± 0.27	15.3 ± 0.15	9.7 ± 0.30	8.8 ± 0.21	3.0 ± 0.25
	16.3–16.8, n = 3	15.1–15.4, n = 3	9.4–10.0, n = 3	8.6–9.0, n = 3	2.8–3.3, n = 3

[a] Includes the specimens from Amboni Caves used in the molecular analysis.

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

Table 5.—Dental measurements (mm) of *Coleura* specimens from Madagascar, the Seychelles, and different operational taxonomic units (OTUs) across the eastern portion of Africa. Descriptive statistics presented are mean ± standard deviation followed by minimum–maximum, and sample size (*n*).

	C-M3	Width M3	c-m3	Width m3
Coleura kibomalandy, FMNH 213598				
♀ Holotype	7.1	2.1	7.4	1.0
Type series	7.1 ± 0.17	2.0 ± 0.09	7.4 ± 0.13	1.0 ± 0.05
	6.8–7.4, n = 13	1.9–2.2, n = 12	7.2–7.6, n = 13	0.9–1.0, n = 13
Coleura seychellensis	6.6 ± 0.18	1.8 ± 0.07	6.8 ± 0.12	0.8 ± 0.04
	6.2–6.8, n = 10	1.7–1.9, n = 10	6.6–7.0, n = 10	0.8–0.9, n = 10
Coleura afra				
OTU 1	7.0, 7.1	2.1, 2.0	7.3, 7.5	1.0, 1.0
OTU 2[a]	7.1 ± 0.21	2.1 ± 0.11	7.2 ± 0.11	1.0 ± 0.09
	6.7–7.5, n = 28	1.9–2.3, n = 29	6.8–7.2, n = 30	0.9–1.2, n = 30
OTU 3	6.7 ± 0.13	1.9 ± 0.05	7.0 ± 0.15	1.0 ± 0.05
	6.5–6.9, n = 7	1.9–2.0, n = 7	6.8–7.2, n = 7	1.0–1.1, n = 7
OTU 4	6.6 ± 0.17	1.9 ± 0.00	6.8 ± 0.17	1.1 ± 0.05
	6.4–6.8, n = 4	1.9–1.9, n = 4	6.6–6.9, n = 4	1.0–1.1, n = 4

[a] Includes the specimens from Amboni Caves used in the molecular analysis.

The genus *Coleura*, as recognized by Simmons (2005), contains 2 species: *C. seychellensis* from the Seychelles, as well as a dubious record from Zanzibar (Koopman 1993; Thomas 1915), and *C. afra* occurring across areas of Africa from Sudan south to Mozambique and west to portions of the Democratic Republic of the Congo, Angola, West Africa, and the Arabian Peninsula (Dunlop 1997; Monadjem et al. 2010). Subspecies of *C. afra* and *C. seychellensis* have also been described, but these are poorly defined and may not warrant recognition (Koopman 1975), although as shown herein, the forms *gallarum* and *nilosa* are smaller than typical *afra*.

Even though the karstic cave systems of the Ankarana Massif have been the subject of numerous bat inventories (Cardiff 2006; Goodman et al. 2005; Hutcheon 1997; McHale 1987; Wilson 1987), it was not until 2004 when Cardiff found the first evidence of the genus *Coleura* in the area, or for that matter on Madagascar. Between 2001 and 2011, over 25 caves were explored for bats in the Ankarana and this genus was only found in the Grotte d'Ambatoharanana (Cardiff 2006; Goodman et al. 2005). On the basis of 4 *Coleura* samples that were collected in 2004 and morphological comparisons with museum specimens of *C. afra* from mainland Africa and *C. seychellensis* from the Seychelles, Goodman et al. (2008) concluded that the Malagasy material was best referred to *C. afra*, although these authors noted several differences between Malagasy and East African members of this genus. On the basis of molecular phylogenetic analyses, it is clear that Tanzanian *C. afra* and the Malagasy population, named herein as *C. kibomalandy*, are different species, and the latter is sister to *C. seychellensis*. With the description of *C. kibomalandy*, the bat fauna of Madagascar now consists of 44 species, of which 34 (77%) are endemic to the island (Goodman 2011; Goodman et al. 2011, 2012).

Table 6.—Factor loadings, eigenvalues, and % variation from a principal component analysis (PCA) of cranial and dental characters of *Coleura* spp. from continental Africa, Madagascar, and the Seychelles. The greatest zygomatic breadth variable was removed to maximize the number of specimens used in the analysis.

	PC 1	PC 2	PC 3
Occipitocanine length	0.931	0.036	0.054
Condylocanine length	0.938	−0.004	0.103
Breadth braincase	0.774	0.063	−0.209
Postorbital breadth	0.377	0.240	−0.857
C-M3	0.931	0.013	−0.004
Width M3	0.725	−0.194	0.086
c-m3	0.846	−0.046	0.331
Width m3	−0.002	0.957	0.260
Eigenvalue	4.595	1.019	0.976
% total variation explained	57.4	70.1	82.3

The only islands in the western Indian Ocean that are known to have populations of *Coleura* are Madagascar and the granitic Seychelles in the eastern portion of the archipelago (Fig. 2). *Coleura seychellensis* was historically restricted to populations on 4 islands but is now only present on 2 (Mahé and Silhouette). Habitat degradation has reduced the population to extremely low levels, with colony sizes varying from 2 to 40 individuals. The total population size is estimated to be fewer than 100 individuals (Gerlach 2009b, 2011). On the African continent and its offshore islands, *C. afra* has a broad distribution, and this species occurs on the Arabian Peninsula (Harrison and Bates 1991). We did not have access to tissue samples from the Arabian Peninsula and the specific status of these animals cannot be addressed, but the Arabian Peninsula populations are presumably derived from Africa.

The biogeographic scenario that seems most concordant with current data is that the most recent ancestor of *C. kibomalandy* and *C. seychellensis* was from Africa and sequentially colonized and differentiated on Madagascar and then the eastern granitic Seychelles, where areas of exposed rock with small shelters and caves are not uncommon. The distance between the northern tip of Madagascar, close to the Ankarana

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

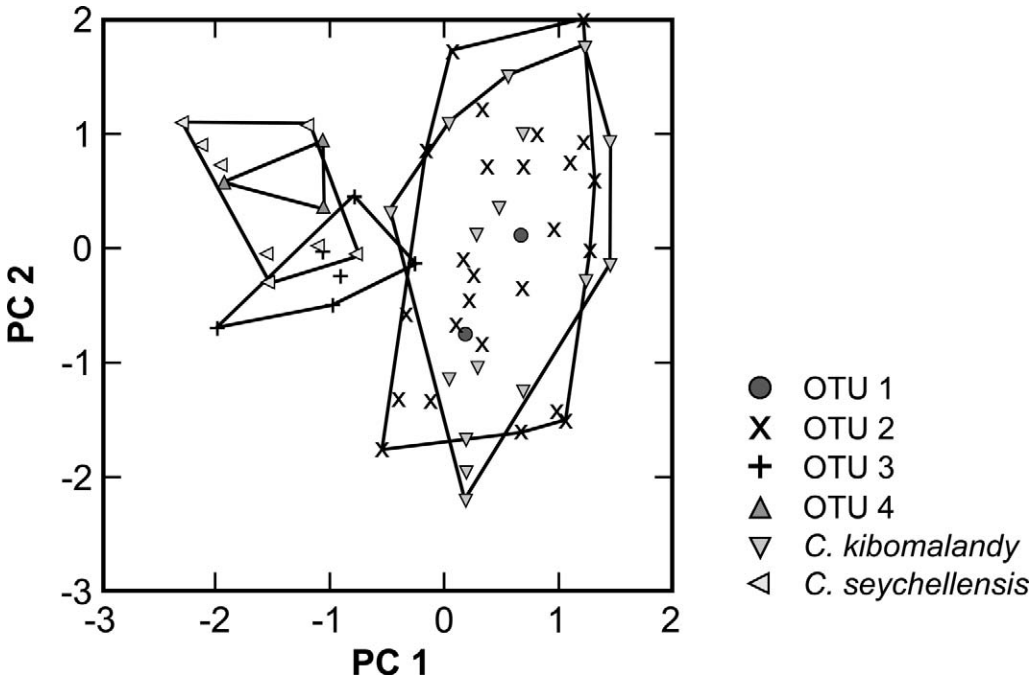

Fig. 6.—Projection based on the craniodental variables (excluding greatest zygomatic breadth) of principal component (PC) factors 1 and 2 for *Coleura kibomalandy* from Madagascar, *C. afra* from the type locality in Mozambique (operational taxonomic unit [OTU] 1), *C. afra* from lowland Kenya and Tanzania (OTU 2), *C.* "*gallarum*" from "Zeyla" in northern Somaliland and adjacent areas (OTU 3), and *C.* "*nilosa*" Thomas, 1915 from Bahr-el-Zeraf, Sudan (OTU 4). See Table 6 for numerical aspects of the PCA analysis.

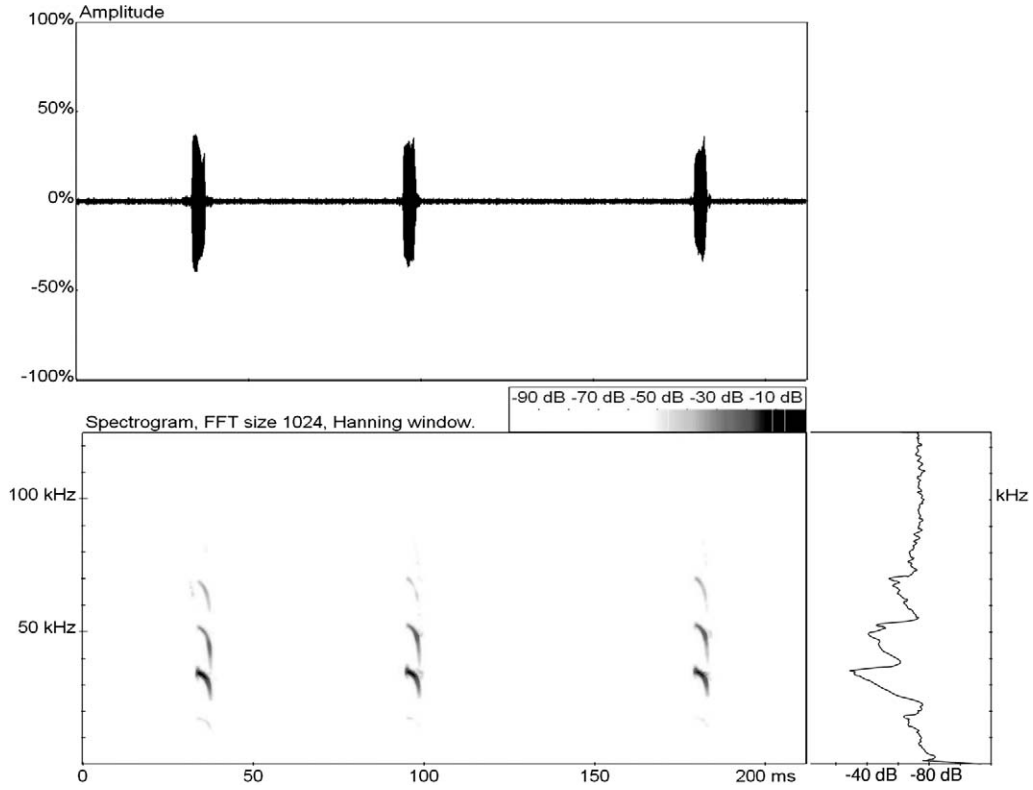

Fig. 7.—Oscillogram (top), spectrogram (bottom left), and power spectrum (bottom right) of echolocation calls emitted during search flight in *Coleura kibomalandy* at the Parc National d'Ankarana, Madagascar.

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

Table 7.—Echolocation parameters of *Coleura* species from Madagascar, Seychelles, and Kenya recorded in different contexts. PF: peak echolocation frequency, BW: bandwidth, Dur: duration, IPI: interpulse interval. Descriptive statistics presented are mean ± standard deviation followed by minimum–maximum, n = number of bats (* = number of pulses).

Species	Recording context	PF	BW	Dur	IPI	Source
C. kibomalandy	Cave entrance	33.8 ± 1.30 30.6–35.9, n = 45	2.9 ± 0.51 2.0–3.9, n = 45	4.3 ± 0.37 3.5–5.3, n = 45	113.1 ± 23.15 83.8–202, n = 45	This study
C. kibomalandy	Flight cage	33.3 ± 0.58 32.6–33.7, n = 3	4.7 ± 0.2 4.5–4.9, n = 3	2.4 ± 0.33 2.1–2.8, n = 3	34.1 ± 11.13 23.8–45.9, n = 3	This study
C. afra	Open habitat	33.4 ± 1.04 32.6–34.8, n = 3	6.2 ± 3.89 2.0–9.6, n = 3	4.5 ± 2.45 3.9–8.3, n = 3	102.0 ± 15.71 85–116, n = 3	Taylor et al. (2005)
C. seychellensis	Open habitat	39.2 ± 0.03 37.9–40.4, n = 29*	0.5 ± 0.13 N/A	4.4 ± 1.55 N/A	199.5 ± 40.85 N/A	Gerlach (2009a)
C. seychellensis	Foraging	41.1 ± 0.07 N/A, n = 141*	0.9 ± 0.16 N/A	1.4 ± 0.27 1.03–4.32	105.6 ± 5.13 100.0–121.0	Gerlach (2009a)

Massif, and the eastern Seychelles is approximately 1,100 km, with few intermediate islands and associated potential roosting or foraging areas for members of this genus to use as stepping-stones. Given the notably reduced long-distance flight capacity of members of this genus, how they physically crossed this considerable expanse of ocean remains enigmatic.

One of the aspects of the current study, as compared with the conclusions of Goodman et al. (2008) based exclusively on morphology, is that molecular markers were highly informative about the patterns of speciation in *Coleura*. This example is 1 of many among bats, where classical morphological studies do not provide sufficient insight into patterns of cladogenesis, particularly at the species level, and associated molecular data indicate convergence of morphology in the evolutionary history of certain species complexes (e.g., Clare et al. 2006; Mayer and Von Helversen 2001).

Résumé

Le genre *Emballonura* appartient à la tribu des Emballonurini (famille Emballonuridae), propre à l'Ancien Monde, et couvre une vaste aire de distribution comprenant des îles de la région Indo-Pacifique, l'Asie du Sud et Madagascar. Les études moléculaires montrent que ce genre est paraphylétique en raison de la position du genre *Coleura* qui vient s'insérer parmi les espèces d'*Emballonura*, entre les clades malgache et asiatique/indo-pacifique de ce dernier. Le clade asiatique/indo-pacifique d'*Emballonura* a la priorité nomenclaturale pour porter ce nom. Pour résoudre cette paraphylie, nous proposons de créer un nouveau genre pour les espèces d'*Emballonura* de Madagascar. Grâce à un échantillonnage moléculaire accru du genre *Coleura*, notamment avec l'inclusion de séquences de Tanzanie, des Seychelles et de Madagascar, ainsi que par l'utilisation de caractères morphologiques et bioacoustiques, nous décrivons les relations phylogénétiques et précisons la limite entre les espèces du genre *Coleura*. Ce dernier se subdivise en deux clades bien soutenus, l'un comprenant *C. afra* du continent et de l'île de Pemba, et l'autre *C.* cf. *afra* de Madagascar et *C. seychellensis* des Seychelles. La distance génétique ML entre les individus de Madagascar et des Seychelles est de 6%, alors que ceux de Pemba et Tanzanie diffèrent des malgaches de 9.6-10.4%. La *Coleura* de Madagascar est par conséquent décrite ici en tant qu'espèce nouvelle.

Acknowledgments

We thank the Direction des Eaux et Forêts and Association Nationale pour la Gestion des Aires Protégées (Madagascar) for providing authorizations for the capture, collection, and exportation of animals under a protocol of collaboration between the Département de Biologie Animale at the Université d'Antananarivo, Association Vahatra, and the FMNH. For help in the field we are grateful to Scott G. Cardiff and Beza Ramasindrazana. We also acknowledge the authorities in the Seychelles for permission to collect and export the scat samples. For access to specimens in their care, we are grateful to the curators of the following institutions (acronyms defined in the methods section): BMNH—P. Jenkins; MNHN—M. Tranier and J.-Marc Pons; NMK—P. W. Webala; UADBA—D. Rakotondravony and V. Soarimalala; and ZMB—F. Mayer. This project was supported by financial help from Center for Applied Biodiversity Science (CABS) of Conservation International, the John D. and Catherine T. MacArthur Foundation, the National Geographic Society (6637–99 and 7402-03), and the Volkswagen Foundation. Genetic analyses were supported by a Science Foundation Ireland grant (RFP GEN0056). Permission to conduct research on bats in Tanzania was granted by the Tanzania Commission for Science and Technology, the Tanzania Wildlife Research Institute, and the Ministry of Natural Resources and Tourism. We are grateful to the following individuals for providing or help with figures: M. H. Rakotondratsimba (Fig. 2), S. Cardiff (Fig. 3), J. Weinstein (Fig. 4), and R. Banasiak (Fig. 6). A. Newton provided advice on aspects of nomenclature. We thank P. Taylor for providing us with the wave files of Kenyan *Coleura afra*. J. Eger, B. K. Lim, and an anonymous reviewer provided helpful comments on an earlier version of the paper.

Literature Cited

African Chiroptera Report. 2010. African Chiroptera Project. Pretoria. http://www.Africanbats.org. Accessed 20 June 2011.

Blalock, H. M. 1972. Social statistics. 2nd ed. McGraw-Hill, New York.

Bradley, R. D., and R. J. Baker. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

CARDIFF, S. G. 2006. Bat cave selection and conservation at Ankarana, northern Madagascar. Masters thesis, Columbia University, New York.

CHAN, L. M., S. M. GOODMAN, M. NOWAK, D. W. WEISROCK, AND A. D. YODER. 2011. Increased population sampling confirms low genetic divergence among *Pteropus* (Chiroptera: Pteropodidae) fruit bats of Madagascar and other western Indian Ocean islands. PLoS Currents: Tree of Life. 2011. Feb 21 [revised 2011 Mar 21]:PMC3064450.

CLARE, E. L., B. K. LIM, M. D. ENGSTROM, J. L. EGER, AND P. D. N. HEBERT. 2006. DNA barcoding of Neotropical bats: species identification and discovery within Guyana. Molecular Ecology Notes 7:184–190.

COLGAN, D. J., AND S. SOHEILI. 2008. Evolutionary lineages in *Emballonura* and *Mosia* bats (Mammalia: Microchiroptera) from the southwestern Pacific. Pacific Science 62:219–232.

DOBSON, G. E. 1878. Catalogue of the Chiroptera in the collection of the British Museum. British Museum (Natural History), London.

DRUMMOND, A. J., AND A. RAMBAUT. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214.

DUNLOP, J. 1997. *Coleura afra*. Mammalian Species 566:1–4.

EICK, G. N., D. S. JACOBS, AND C. A. MATTHEE. 2005. A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). Molecular Biology and Evolution 22:1869–1886.

FENTON, M. B., S. BOUCHARD, M. J. VONHOFF, AND J. ZIGOURIS. 2001. Time expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. Journal of Mammalogy 82:721–727.

FENTON, M. B., M. D. SKOWRONSKI, L. P. MCGUIRE, AND P. A. FAURE. 2011. Variation in the use of harmonics in the calls of laryngeally echolocating bats. Acta Chiropterologica 13:169–178.

GERLACH, J. 2009a. Vocalisations of the Seychelles sheath-tailed bat *Coleura seychellensis*. Le Rhinolophe 18:17–24.

GERLACH, J. 2009b. Conservation of the Seychelles sheath-tailed bat *Coleura seychellensis* on Silhouette Island, Seychelles. Endangered Species Research 8:5–13.

GERLACH, J. 2011. Conservation of the Seychelles sheath-tailed bat *Coleura seychellensis* from 1997–2011 and future prospects. Phelsuma 19:54–68.

GOODMAN, S. M. 2011. Les chauves-souris de Madagascar. Association Vahatra, Antananarivo, Madagascar.

GOODMAN, S. M., ET AL. 2005. The distribution and conservation of bats in the dry regions of Madagascar. Animal Conservation 8:153–165.

GOODMAN, S. M., S. G. CARDIFF, J. RANIVO, A. L. RUSSELL, AND A. D. YODER. 2006. A new species of *Emballonura* (Chiroptera: Emballonuridae) from the dry regions of Madagascar. American Museum Novitates 3538:1–24.

GOODMAN, S. M., S. G. CARDIFF, AND F. H. RATRIMOMANARIVO. 2008. First record of *Coleura* (Chiroptera: Emballonuridae) on Madagascar and identification and diagnosis of members of the genus. Systematics and Biodiversity 6:283–292.

GOODMAN, S. M., B. RAMASINDRAZANA, C. P. MAMINIRINA, M. C. SCHOEMAN, AND B. APPLETON. 2011. Morphological, bioacoustical, and genetic variation in *Miniopterus* bats from eastern Madagascar, with the description of a new species. Zootaxa 2880:1–19.

GOODMAN, S. M., P. J. TAYLOR, F. RATRIMOMANARIVO, AND S. HOOFER. 2012. The genus *Neoromicia* (Family Vespertilionidae) in Madagascar, with the description of a new species. Zootaxa 3250:1–25.

HARRISON, D. L., AND P. J. J. BATES. 1991. The mammals of Arabia. 2nd ed. Harrison Zoological Museum, Sevenoaks, United Kingdom.

HUTCHEON, J. M. 1997. Tracking bats at Ankarana. Bats 15(1):14–15.

JONES, K. E., A. PURVIS, A. MACLARNON, O. R. P. BININDA-EMONDS, AND N. B. SIMMONS. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biological Reviews 77:223–259.

KOOPMAN, K. F. 1975. Bats of the Sudan. Bulletin of the American Museum of Natural History 154:355–443.

KOOPMAN, K. F. 1993. Order Chiroptera, Pp. 137–241 in Mammal species of the world: a taxonomic and geographical reference (D. E. Wilson and D. M. Reeder, eds.). 2nd ed. Smithsonian Institution Press, Washington, DC.

KOOPMAN, K. F. 1994. Chiroptera: systematics, Pp. 1–217 in Handbook of zoology (J. Niethammer, H. Schliemann, and D. Starck, eds.). Vol. 8. Walter de Gruyter, Berlin, Germany.

LIM, B. K. 2007. Divergence times and origin of Neotropical sheath-tailed bats (tribe Diclidurini) in South America. Molecular Phylogenetics and Evolution 45:777–791.

LIM, B. K., M. D. ENGSTROM, J. W. BICKHAM, AND J. C. PATTON. 2008. Molecular phylogeny of New World sheath-tailed bats (Emballonuridae: Diclidurini) based on loci from the four genetic transmission systems in mammals. Biological Journal of the Linnean Society 93:189–209.

MAYER, F., AND O. VON HELVERSEN. 2001. Cryptic diversity in European bats. Proceedings of the Royal Society of London, B. Biological Sciences 268:1825–1832.

MCHALE, M. 1987. Bats. Cave Science, Transactions of the British Cave Research Association 14:107–119.

MCKENNA, M. C., AND S. K. BELL. 1997. Classification of mammals above the species level. Columbia University Press, New York.

MCWILLIAM, A. N. 1987. The reproduction and social biology of *Coleura afra* in a seasonal environment, Pp. 324–350 in Recent advances in the study of bats (M. B. Fenton, P. Racey, and J. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

MILLER, G. S., JR. 1907. The families and genera of bats. Bulletin of the United States National Museum 57:1–282.

MILLER, S. A., D. D. DYKES, AND H. F. POLESKY. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. Nucleic Acids Research 16:1215.

MONADJEM, A., P. J. TAYLOR, F. P. D. COTTERILL, AND M. C. SCHOEMAN. 2010. Bats of southern Africa: a biogeographic and taxonomic synthesis. Wits University Press, Johannesburg, South Africa.

NICOLL, M. E., AND J. M. SUTTIE. 1982. The sheath-tailed bat, *Coleura seychellensis* (Chiroptera: Emballonuridae) in the Seychelles Islands. Journal of Zoology (London) 197:421–426.

O'BRIEN, J., ET AL. 2009. Multiple colonisations of the western Indian Ocean by *Pteropus* fruit bats (Megachiroptera: Pteropodidae): the furthest islands were colonised first. Molecular Phylogenetics and Evolution 51:294–303.

PETERS, W. C. H. 1852. Naturwissenschaftliche Reise nach Mossambique, auf Befehl seiner Majestät des Königs Friedrich Wilhelm IV. in den Jahren 1842 bis 1848 ausgeführt. Säugethiere, 51.

PETERS, W. C. H. 1868. Über die zu den *Glossophagae* gehörigen Flederthiere und über eine neue Art der Gattung *Coleura*. Monatsbericht der Königlich Preussischen Akademie der Wissenschaftlichen zu Berlin 1868:469–481.

PETERSON, R. L., J. L. EGER, AND L. MITCHELL. 1995. Chiroptères. Vol. 84. Faune de Madagascar. Muséum national d'Histoire naturelle, Paris, France.

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024

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

Puechmaille, S. J., G. Mathy, and E. J. Petit. 2007. Good DNA from bat droppings. Acta Chiropterologica 9:269–276.

Puechmaille, S. J., and E. J. Petit. 2007. Empirical evaluation of non-invasive capture-mark-recapture estimates of population size based on a single sampling session. Journal of Applied Ecology 44:843–852.

Puechmaille, S. J., et al. 2011. The evolution of sensory divergence in the context of limited gene flow in the bumblebee bat. Nature Communications 2:573.

Rambaut, A., and A. Drummond. 2007. Tracer v1.4 MCMC Trace Analysis Package. Institute of Evolutionary Biology University of Edinburgh (Scotland) & Department of Computer Science University of Auckland (New Zealand) (2003–2007), http://beast.bio.ed.ac.uk/Tracer.

Ruedi, M., N. Friedli-Weyeneth, E. C. Teeling, S. J. Puechmaille, and S. M. Goodman. 2012. Biogeography of Old World emballonurine bats (Chiroptera: Emballonuridae) inferred with mitochondrial and nuclear DNA. Molecular Phylogenetics and Evolution 64:204–211.

Russell, A. L., S. M. Goodman, and M. P. Cox. 2008. Coalescent analyses support multiple mainland-to-island dispersals in the evolution of Malagasy *Triaenops* bats (Chiroptera: Hipposideridae). Journal of Biogeography 35:995–1003.

Schoeman, M. C., and D. S. Jacobs. 2008. The relative influence of competition and prey defences on the phenotypic structure of animalivorous bat ensembles in southern Africa. PLoS ONE 3(11):e3715.

Shimodaira, H., and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16:1114–1116.

Sikes, R. S., W. L. Gannon and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammal species of the world: a taxonomic and geographical reference (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland. Vol. 1.

Smith, M. F., and J. L. Patton. 1991. Variation in mitochondrial cytochrome *b* sequences in natural populations of South America akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution 8:85–103.

Stadelmann, B., D. S. Jacobs, C. Schoeman, and M. Ruedi. 2004. Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome *b* sequences. Acta Chiropterlogica 6:177–192.

Surlykke, A., and E. K. V. Kalko. 2008. Echolocating bats cry out loud to detect their prey. PLoS ONE 3(4):e2036.

Swofford, D. L. 2003. PAUP*. Phylogenetic analysis using parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Systat. 2004. Systat. Version 11. Systat Software, Inc., Chicago, Illinois.

Taylor, P. J., C. Geiselman, P. Kabochi, B. Agwanda, and S. Turner. 2005. Intraspecific variation in the calls of some African bats (Order Chiroptera). Durban Museum Novitates 30:24–37.

Teeling, E. C., M. S. Springer, O. Madsen, P. Bates, S. J. O'Brien, and M. J. Murphy. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584.

Thomas, O. 1915. Notes on the bats of the genus *Coleura*. Annals and Magazine of Natural History, series 8, 15:576–579.

Trujillo, R. G., J. C. Patton, D. A. Schlitter, and J. W. Bickham. 2009. Molecular phylogenetics of the bat genus *Scotophilus* (Chiroptera: Vespertilionidae): perspectives from paternally and maternally inherited genomes. Journal of Mammalogy 90:548–560.

Weyeneth, N., S. M. Goodman, W. T. Stanley, and M. Ruedi. 2008. The biogeography of *Miniopterus* bats (Chiroptera: Miniopteridae) from the Comoro Archipelago inferred from mitochondrial DNA. Molecular Ecology 17:5205–5219.

Wilson, J. 1987. The crocodile caves of Ankarana: expedition to northern Madagascar, 1986. Cave Science 14:107–119.

Submitted 27 July 2011. Accepted 18 May 2012.

Associate Editor was Burton K. Lim.

Appendix I

Specimens examined.—List of the specimens examined for the morphological comparisons within *Coleura*. Museum acronyms are described in the Materials and Methods.

***Coleura afra*.–Djibouti:** March 1999, MNHN 2000.552; **Kenya:** Diani, coast, 1 September 1963, NMK 2 uncatalogued specimens; 9 km south of Mombasa, Ngombeni, 19 August 1969, BMNH 74.881; Limale District, Ndiani, coast, 23 November 1970, BMNH 73.532; Lindi, 29 November 1912, ZMB 67426; Moto Cave, Diani, 15 August 1963, BMNH 75.2427; Ngombeni, near Mombasa, 3 October 1962, NMK 6708, 6710; Port Dawnford, 4 January 1913, NMK 1339–1349; **Mozambique:** Tete, BMNH 7.1.1.703, 58.6.18.12 (Peters co-types of *afra*); **Somaliland:** nr. Berbera, 30 December 1953, BMNH 54.994; Zeyla, 25–29 October 1910, BMNH 11.8.2.1, 11.8.2.3–11.8.2.6; **Sudan:** 5 km from mouth of Bahr el Zaraf, BMNH 15.3.6.76 (holotype of *gallarum nilosa*); Bahr el Zaraf, BMNH 15.3.6.75, 15.3.6.86; Gebel Geraf, Bahr el Zeraf, 10 March 1913, BMNH 33.10.14.2; **Tanzania:** Amboni Cave, 5 July 1966, NMK 7397–7402; Amboni Caves, Tanga, BMNH 39.242; Tanga Region, Tanga District, Amboni Caves, 10 August 2007, 05.0727°S, 39.04848°E, FMNH 197987–198000, 198020–198032.

***C. seychellensis*.–Seychelles:** Praslin, BMNH 48.263–48.265, 2 uncatalogued specimens; Amirante BMNH 28.1.24.3; Silhouette BMNH 6.3.18.2–6.3.18.8, 76.10.10.1, 2 uncatalogued specimens; Grande Anse, Praslin, BMNH 1939.1368–1939.1369, 1939.1371–1939.1379, 1 uncatalogued specimen; Mariane, MNHN 1876.549; La Digue, BMNH 73.524; unspecified island, BMNH 69.2.19.2, 83.8.6.1; MNHN 1985.1053–1985.1054, 1985.265; ZMB 3470.2.

Downloaded from https://academic.oup.com/jmammal/article/93/6/1440/910878 by guest on 25 April 2024