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MITOGENOME REPORT

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Complete mitochondrial DNA sequences of *Eliurus webbi* and *Eliurus minor*, endemic tufted-tailed rats in Madagascar

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ABSTRACT
The Webb's tufted-tailed rat (*Eliurus webbi*) and the lesser tufted-tailed rat (*Eliurus minor*) are nocturnal and primarily arboreal rodents native to Madagascar, classified in the subfamily Nesomyinae. After species confirmation using *cytochrome b*, we assembled the first complete mitogenomes of *E. webbi* ($n = 7$) and *E. minor* ($n = 3$) from southeastern Madagascar. These mitochondrial genomes range from 16,310 to 16,313 nt for *E. webbi* and 16,296 to 16,302 nt for *E. minor*. These are the first assemblies of mitogenomes from Nesomyinae. This report enhances the evolutionary study and identification of Malagasy endemic rodents, and will support biodiversity research and wildlife conservation efforts.

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Eliurus; mitogenome; Nesomyinae; southeastern Madagascar

Introduction

Madagascar, one of the largest islands and located off Africa's eastern coast, is recognized as one of the world's top biodiversity hotspots, harboring incredible plant and animal endemism alongside intense anthropogenic change (Myers et al. 2000). The rodent subfamily Nesomyinae is composed of nine genera (*Brachytarsomys, Brachyuromys, Eliurus, Gymnuromys, Hypogeomys, Macrotarsomys, Monticolomys, Nesomys*, and *Voalavo*), all of which are exclusively found in Madagascar. Often referred to as the tufted-tailed rats, *Eliurus* is the most speciose genus within Nesomyinae, including 13 described species, all with characteristically tufted tails (Jansa et al. 2019). This study focuses on the lowland rainforest of the Manombo Special Reserve in southeastern Madagascar, home to, among other endemic rodents, *Eliurus webbi* Ellerman 1949 (Webb's tufted-tailed rat) and *Eliurus minor* Major 1896 (lesser tufted-tailed rat) (Figure 1). The geographic ranges of *E. webbi* and *E. minor* extend throughout northern and eastern forests of Madagascar, with *E. minor* additionally occurring in the western central highlands (Kennerley 2016a, 2016b). Tufted-tailed rat taxonomy has been largely driven by morphological and biogeographical characteristics, underscoring the need for more comprehensive genetic resources across the genus to confirm species relationships (Carleton and Goodman 2007; Goodman et al. 2009; Jansa et al. 2019). Tufted-tailed rats have limited genetic resources, although progress has been made in characterizing mitochondrial *cytochrome b* (*cytb*) gene sequences and four nuclear loci (Everson et al. 2020; Ilarde et al. 2026). However, complete mitochondrial genomes provide higher phylogenetic resolution than *cytb* sequences do, capturing variation across coding and noncoding regions. Here, we contribute the first complete mitochondrial genomes from *E. webbi* and *E. minor* using oral swab samples.

Materials and methods

The Manombo Special Reserve (MSR) in southeastern Madagascar is composed of lowland rainforest (more inland with a taller, denser canopy) and littoral forest (coastal, sandy with a shorter canopy) parcels. Samples were collected from tufted-tailed rats that were captured and chemically immobilized (Zoletil, 10 mg/kg) by a certified veterinarian in the lowland rainforest of the MSR. Despite extensive trapping efforts, no tufted-tailed rats were captured in the littoral forest parcel. Oral swabs were collected with sterile flocked swabs

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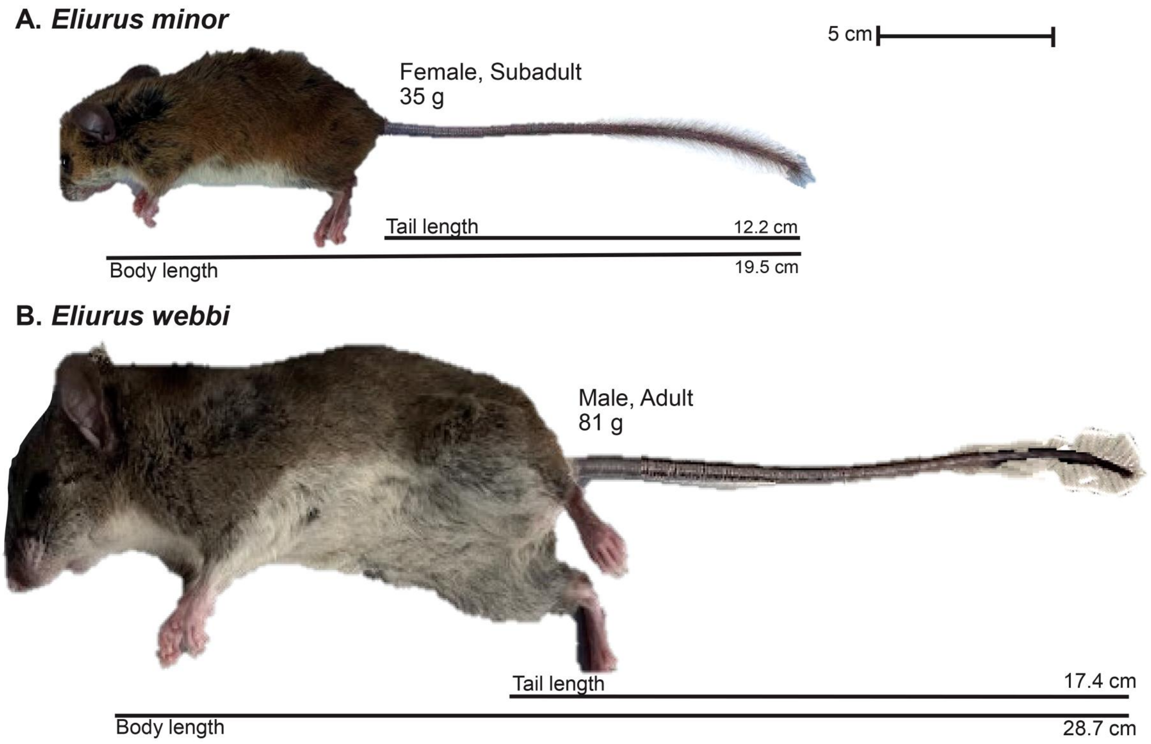

Figure 1. (A) *Eliurus minor* female subadult (Biosample SAMN49916530) and (B) *Eliurus webbi* male adult (Biosample SAMN49916647) sampled in the lowland rainforest of the Manombo Special Reserve in southeastern Madagascar. Body length was measured from the crown of the head to the tip of the tail. Tail length was measured from the tail base to the tip of the tail. Images are depicted at the same scale. Photos were taken by author E.N.P.

from tufted-tailed rats in October 2022 and July 2023 as part of a larger multi-species One Health study (Paietta et al. 2025), stored in Universal Transport Medium (UTM) in a 1.8 ml cryotube, and kept on ice until being flash-frozen in liquid nitrogen within 12 h. Tufted-tailed rats were released at the point of capture, on the same day of capture, once mobile and alert. Samples were maintained in liquid nitrogen during sample transport to Duke University (Durham, NC, USA) and stored in a −80 °C freezer until nucleic acid extraction. Metadata for each individual sampled including geographic coordinates, age, weight, and accession information is included in Supplementary material, Data 1.

After thawing and vortexing, DNA was extracted from 200 µl of each sample using the Roche HighPure Viral Nucleic Acid Kit and amplified using the Illustra Templiphi rolling circle amplification kit targeting circular sequences. Libraries were prepared with the Illumina DNA Prep (M) Tagmentation Kit and sequenced on the NovaSeq X Plus with Psomagen Inc. Paired-end reads were trimmed using Trimmomatic-0.39 (Bolger et al. 2014) and *de novo* assembled with MEGAHITv.1.2.9 (Li et al. 2015). Circular contigs were identified based on terminal redundancy. Contigs were analyzed for mitochondrial-like sequences using Diamond (Buchfink et al. 2015) BLASTx against a mitochondrial RefSeq database (release 223). Publicly available *cytb* sequences across *Eliurus* species (Jansa et al. 1999; Shi et al. 2013; Rakotoarisoa et al. 2013a; Steppan and Schenk 2017; Everson et al. 2020) along with morphometrics were used to confirm species identifications as *E. webbi* or *E. minor* (>99.5% *cytb* identity to respective database sequences). Mitochondrial sequences were annotated using available rodent mitogenomes and manual curation. Pairwise identities between whole mitogenomes or between *cytb* nucleotide sequences were computed with SDTv1.3 (Muhire et al. 2014).

Whole mitogenomes from Nesomyidae rodents were downloaded from GenBank and pulled from our dataset, then aligned with MAFFT (alignment length: 16,649 nt) (Katoh et al. 2002). A complete mitogenome maximum likelihood phylogenetic tree was built using IQ-Tree 2 (Minh et al. 2020) with the model finder option and aLRT branch support (1000 replicates). The best-fit model was TIM2 + F + I + G4 and the tree was rooted with Muridae mitogenomes (PV670005, PP503064 (Wang et al. 2024)). Additionally, because only *cytb* sequences were available for *Eliurus* species, *cytb* nucleotide sequences were pulled from publicly available datasets downloaded from GenBank and from our dataset, then aligned with MAFFT (alignment length: 1146 nt) (Katoh et al. 2002). Further highlighting historical focus on *cytb*, there were no complete mitochondrial genomes from any Nesomyinae rodents available on GenBank. A *cytb* maximum likelihood phylogenetic tree was built using IQ-Tree 2 (Minh et al. 2020) with the model finder option and aLRT branch support (1000 replicates). The best-fit model was TPM2 + F + R4. The tree was rooted with representative *cytb* sequences from *Gymnuromys*.

Results

Mitogenomes were assembled successfully with high sequencing coverage (Supplementary material, Figure 1). Mean coverage ranged from 30.1 to 478.3, and the number of paired reads generated for each sample ranged from 27,449,272 to 94,622,596 (Supplementary material, Data 1).

The seven complete *E. webbi* mitochondrial genomes (PX582274, PX582275, PX582278, PX582279, PX582282, PX582283, PX582284) characterized in this study ranged from 16,310 to 16,313 nt in length, whereas the three complete *E. minor* mitochondrial genomes (PX582196, PX582208, PX582280) ranged from 16,296 to 16,302 nt (Supplementary material, Data 1). The mitochondrial genomes have 13 protein-coding genes (PCGs), 2 ribosomal RNA (rRNA) genes, and 22 transfer RNA (tRNA) genes (Figure 2). *E. minor* mitogenome GC content ranged from 36.7% to 36.9%, whereas *E. webbi* mitogenome GC content ranged from 35.7-35.8%. For both *E. webbi* and *E.* minor, the PCGs primarily start with ATG with the exception of ND2, ND3, and ND5, which initiate with ATT, for which there is precedent in rodents (Tomasco and Lessa 2014).

A mitogenome-wide phylogeny was used to assess the relationship of *Eliurus* sequences to other Nesomyidae sequences. The complete *Eliurus* mitogenomes (subfamily Nesomyinae) were phylogenetically distant from other Nesomyidae rodents. However, only three sequences were available, one sequence for each of three subfamilies within Nesomyidae: Delanymyinae, Cricetomyinae, Dendromurinae (Figure 3A). For *E. minor*, mitogenomes shared 99.2%–99.3% nucleotide identity. For *E. webbi*, mitogenomes shared 99.3%–100% nucleotide identity. Comparing *E. webbi* and *E. minor* mitogenomes, *E. webbi* and *E. minor* share 88.9%–89.3% mitogenome-wide nucleotide identity with one another. In comparison with publicly available sequences (mitogenomes from Nesomyidae and closely related genomes from an initial BLASTn search), *E. webbi* and *E. minor* mitogenomes interestingly shared the highest nucleotide identity, 80.4%–80.9%, with a mitogenome (MN807610) of *Thamnomys kempi* (Kemp's thicket rat), a rodent of central Africa in the family Muridae. *E. webbi* and *E. minor* shared 77.1%–80.2% mitogenome-wide nucleotide identity with the sequences from Nesomyidae (PP726909, PP726911, and PQ310123) (Mulualem et al. 2024; Denys et al. 2025).

Because no mitochondrial genomes were yet publicly available for the Nesomyinae subfamily, a *cytb* phylogeny was used to assess the phylogenetic position of the sequences identified in this study. *Cytb* was also used to assess the diversity within the *Eliurus* genus, as sequences were available for the majority of *Eliurus* species currently characterized. The *cytb* sequences characterized in this study for *E. webbi* or *E. minor* phylogenetically cluster with available sequences for *E. webbi* or *E. minor* respectively, confirming the species identifications used for the complete mitogenomes (Figure 3B). *E. webbi* sequences, including 45 publicly available sequences and 7 sequences identified in this study, demonstrated a range of 86.6%–100% *cytb* nucleotide identity with one another. Given lack of aLRT branch support, *E. webbi*'s phylogenetic placement remains relatively uncertain, although a recent study suggests a closer relationship of *E. webbi* to *E. myoxinus* and *E. tanala* species complexes (Ilarde et al. 2026). *E. minor* sequences, including 73 publicly available sequences and 3 sequences identified in this study, demonstrated a range of 91.8%–100% *cytb* nucleotide identity with one another and shared the closest phylogenetic relationship, as has been seen previously (Jansa et al. 1999; 2019; Ilarde et al. 2026), with sequences from *Eliurus myoxinus* and an unclassified sequence, *Eliurus* sp. (OR392533).

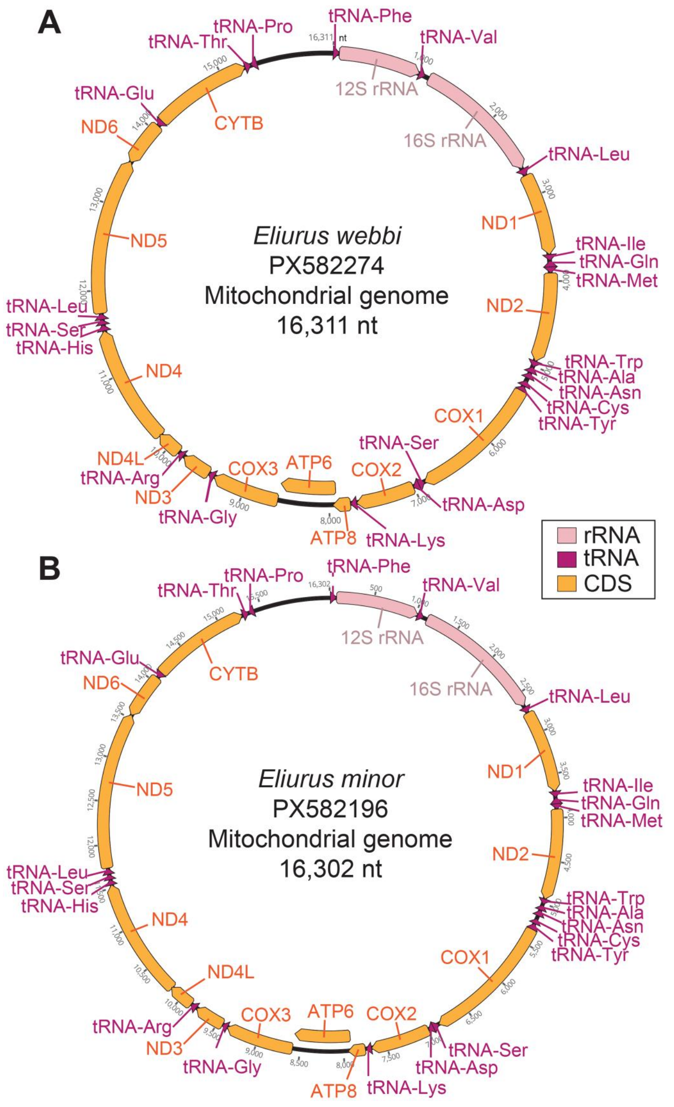

Figure 2. Metagenome-assembled mitochondrial genome organizations of (A) *Eliurus webbi* (accession number PX582274) and (B) *Eliurus minor* (accession number PX582196) from oral swab samples.

Ear biopsy specimens for these individuals are available through the Arizona State University Vertebrate Natural History Collections: Vertebrate Tissue Collection (https://www.biokic.asu.edu/collections/mammalogy-collection) under voucher numbers ASUVTC004015, ASUVTC004016, ASUVTC004017, ASUVTC004018, ASUVTC004019, ASUVTC004020, and ASUVTC004021 for *E. webbi* and ASUVTC004022, ASUVTC004023, and ASUVTC004024 for *E. minor*.

Discussion and conclusion

The mitogenomes presented here are the first complete mitochondrial genomes not only from the *Eliurus* genus, but also from the Nesomyinae subfamily. Given unresolved questions in *Eliurus* taxonomy, and more broadly Nesomyinae taxonomy, these mitogenomes provide an important step for characterizing mitochondrial genetic diversity in rodents.

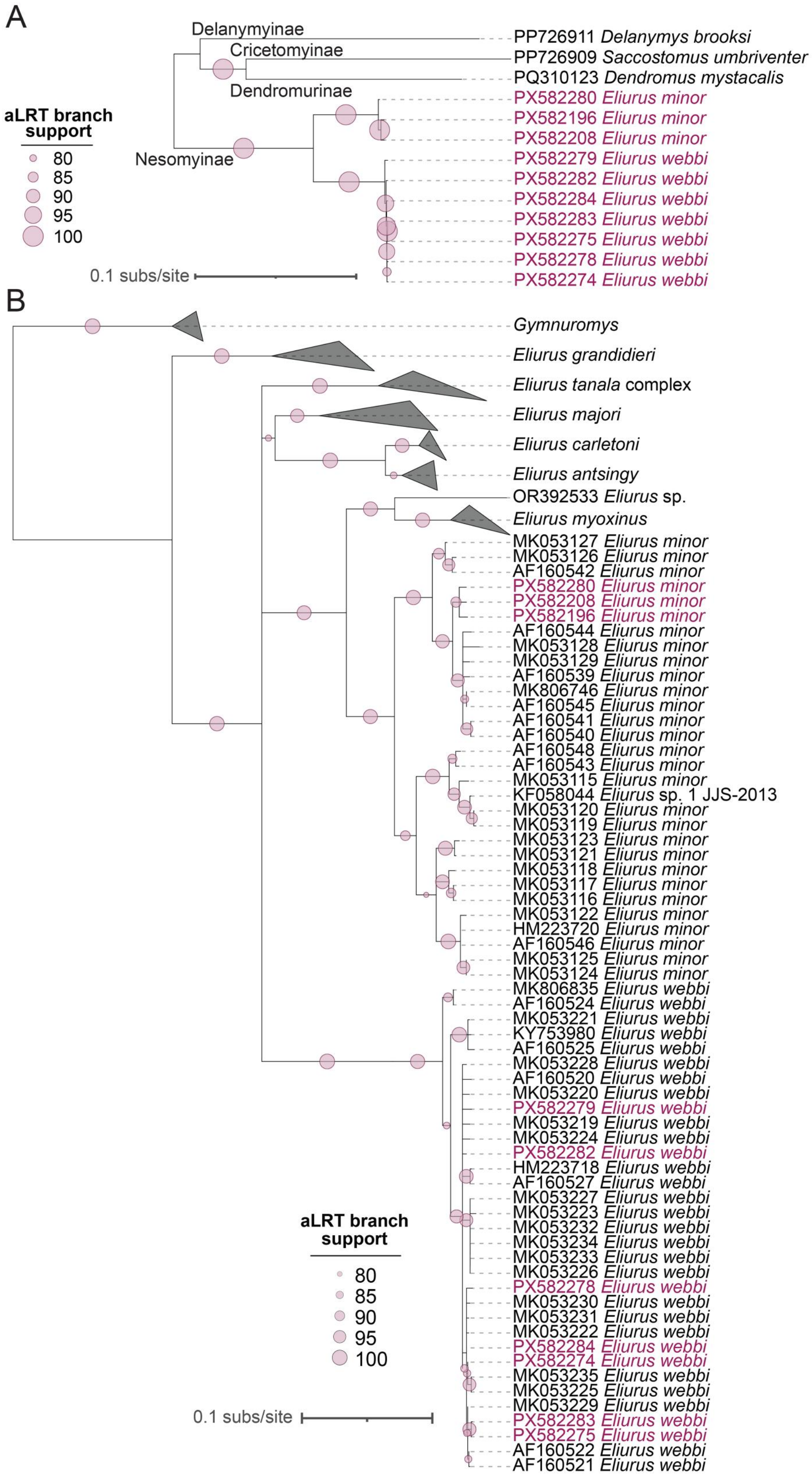

Figure 3. (A) Maximum likelihood phylogenetic tree of complete mitogenomes of available mitochondrial genomes for rodents in the Nesomyidae family (PP726909 and PP726911 (Denys et al. 2025), PQ310123 (Mulualem et al. 2024)) rooted with sequences from Muridae. (B) Maximum likelihood phylogenetic tree of *cytb* nucleotide sequences from *Eliurus* species, rooted with sequences from *Gymnuromys*. Only *cytb* sequences were publicly available for rodents in Nesomyinae. *Eliurus* sequences identified in this study are depicted in pink font. The following sequences were used: AF160520-AF160573 and AF160577 (Jansa et al. 1999), GQ420655-GQ420668 (Goodman et al. 2009), HM223602-HM223722 and KC433971-KC434031 (Rakotoarisoa et al. 2013a), JQ866514-JQ866617 (Rakotoarisoa et al. 2013b), KF058044-KF058171 and KF170838-KF170843 (Shi et al. 2013), KY753977-KY753980 (Steppan and Schenk 2017), MK052996-MK053235 (Everson et al. 2020), MK806697-MK806850 (Jansa et al. 2019), OR392529-OR392533 and OR392540-OR392545 (Sgarlata et al. 2024). For both trees, branches with <80% aLRT support were collapsed with TreeGraph2 (Stöver and Müller 2010).

However, the identification of mitochondrial genomes in other *Eliurus* (or Nesomyinae) species and across the geographic ranges of *E. webbi* and *E. minor* is needed in order to expand upon the substantial genetic variation observed in *cytb* alone and confirm rodent taxonomies built using morphology and biogeography. Although *E. webbi* and *E. minor* are classified as least concern (Kennerley 2016a, 2016b), the most recent assessment was nearly a decade ago (2016), and we suspect likely population decline in the MSR, particularly considering that no endemic rodents were sampled in the coastal littoral forest despite intensive sampling efforts, and nonnative black rats (*Rattus rattus*) were abundant throughout all forest and non-forested areas. Endemic rodents in Madagascar are facing both extensive habitat decline and competition with nonnative rodents (i.e. black and brown rats) across the island (Lehtonen et al. 2001; Miljutin and Lehtonen 2008; Tollenaere et al. 2010; Brouat et al. 2014). Thus, as the IUCN noted that population trends for both *E. webbi* and *E. minor* are unknown, the contribution of complete mitochondrial genomes may allow clearer identification of Madagascar's cryptic endemic rodents. We additionally highlight the utility of oral swabs for obtaining mitogenomes. Further, we hope that the characterization of the first complete mitochondrial genome sequences for the subfamily Nesomyinae may open doors for increasing mitogenomic resources across the nine genera of endemic rodents in this biogeographically-unique subfamily.

Acknowledgments

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Ethical approvals

The described sample collection was approved by the Duke University Institutional Animal Care and Use Committee under Protocol Registry Number A075-23-03 and the Zoo New England Institutional Animal Care and Use Committee under Protocol Number 2022-56. Further, the described procedures were approved by the Madagascar Ministry of the Environment and Sustainable Development under permits n° 215/22/MEDD/SG/DGGE/DAPRNE/SCBE.Re and n° 215/23/MEDD/SG/DGGE/DAPRNE/SCBE.Re. This research adhered to all the laws and regulations of Madagascar.

Author contributions

CRediT: **Elise N. Paietta**: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing; **Santatriniaina F. Randrianarisoa**: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing; **Tahina T. Razanamahenina**: Investigation, Methodology, Writing – review & editing; **Antsa Ramboninarimalala**: Investigation, Methodology, Writing – review & editing; **Toussaint G. Raherinirina**: Methodology, Writing – review & editing; **Laurent Raveloson**: Methodology, Project administration, Writing – review & editing; **Nina L. Finley**: Project administration, Writing – review & editing; **Anne D. Yoder**: Conceptualization, Funding acquisition, Investigation, Supervision, Writing – review & editing; **Eric Baitchman**: Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing; **Arvind Varsani**: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing; **Rachel A. Johnston**: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing – review & editing.

Disclosure of interest

No potential conflict of interest was reported by the authors.

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Data availability statement

The sequences described in this study are deposited in GenBank under accession numbers PX582274, PX582275, PX582278, PX582279, PX582282, PX582283, PX582284 for *E. webbi* and PX582196, PX582208, PX582280 for *E. minor*. The raw reads for *E. webbi* samples are deposited in SRA under BioProject number PRJNA1290322; Biosample numbers SAMN49916530, SAMN49916553, SAMN49916647, SAMN49916648, SAMN49916652, SAMN49916653, SAMN49916654; SRA accession numbers SRR34496600, SRR34496639, SRR34496646, SRR34496650, SRR34496652, SRR34496653, SRR34496654. The raw reads for *E. minor* samples are deposited in SRA under BioProject number PRJNA1290322; Biosample numbers SAMN49916656, SAMN49916659, SAMN49916666; SRA accession numbers SRR34496658, SRR34496659, SRR34496693. Metadata associated with each sample is included in Supplementary material, Data 1 (weight, sex, age class, latitude, longitude, collection date, accessions).

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