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A New Species of *Emballonura* (Chiroptera: Emballonuridae) from the Dry Regions of Madagascar

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ABSTRACT

We describe a new species of bat in the genus *Emballonura* (Chiroptera: Emballonuridae), *E. tiavato*, from the dry forest regions of Madagascar. This species is distinguished from the only other member of this genus found on the island, *E. atrata*, and extralimital species based on a variety of external and cranial characteristics. Details of the distribution, phylogeny, and natural history of the two species of Malagasy *Emballonura* are presented.

RÉSUMÉ

Une nouvelle espèce de chauve-souris du genre *Emballonura* (Emballonuridae: Chiroptera), *E. tiavato*, des régions de forêts sèches de Madagascar est décrite ici. *E. tiavato* se distingue de *E.*

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atrata, seul autre membre appartenant à ce genre sur l'île, et de toutes les autres espèces du même genre au point de vue des caractéristiques externes et crâniennes. La distribution, la phylogénie et l'histoire naturelle des deux espèces d'*Emballonura* malgaches sont présentées en détails dans ce manuscrit.

INTRODUCTION

The genus *Emballonura* (Family Emballonuridae) is broadly distributed from islands in the western Pacific Ocean, through mainland southeastern Asia and associated islands, to Madagascar. The latter island forms the western distributional limit of the genus. As currently configured, *Emballonura*, often referred to as a sheath-tailed bat, is composed of nine species (Simmons, 2005), of which eight are only found on islands and six are largely restricted to the Melanesian region. The majority of *Emballonura* spp. have relatively restricted geographical distributions.

Two species of Emballonuridae are mentioned in the literature as occurring on Madagascar—*Emballonura atrata* and *Taphozous mauritianus*—both known from specimen records across various portions of the island (Peterson et al., 1995; Goodman et al., 2005). A third species, *Coleura afra*, has been recently documented for the island (Goodman et al., in press). *E. atrata*, which is endemic to Madagascar, is previously recorded from very few sites and less than 30 specimens—nearly one-half of these are fluid preserved or dried mummies with unextracted skulls. Thus, to date, insufficient material has been available to examine patterns of geographic variation in this species.

Over the past decade we have conducted bat surveys on Madagascar, particularly in the dry western portion of the island. During the course of these inventories we have captured individuals of *Emballonura* at several sites, and, based on this new material, we are able to assess and quantify variation on a geographic level in members of this genus across much of the island. Contrary to early interpretations, *Emballonura* on Madagascar is widespread, rather than being restricted to the humid portions of the island (Honacki et al., 1982), and is not rare (Tate and Archbold, 1939), particularly in zones with exposed rock outcrops and caves.

MATERIALS AND METHODS

Morphological Analyses

We have consulted specimens of adult *Emballonura* spp. housed in several natural history museums. The acronyms of these institutions are: **AMNH** American Museum of Natural History, New York; **FMNH** Field Museum of Natural History, Chicago; **MNHN** Muséum national d'Histoire naturelle, Paris, France; **RMNH** Naturalis, Leiden, The Netherlands [formerly Rijksmuseum van Natuurlijke Histoire]; **ROM** Royal Ontario Museum, Toronto, Canada; **UADBA** Université d'Antananarivo, Département de Biologie Animale, Antananarivo, Madagascar; **USNM** National Museum of Natural History, Washington, D.C. [formerly United States National Museum]; **ZMAK** Zoologisches Museum Alexander Koenig, Bonn, Germany; and **ZMB** Museum für Naturkunde, Humboldt Universität, Berlin, Germany [formerly Zoologisches Museum, Berlin].

We recorded five external measurements in millimeters from captured individuals before preparation. These included: total length, tail length, hind foot length (not including claw), ear length, and forearm length. Further, we measured body mass in grams using a spring balance. For certain specimens, obtained by other collectors, measurement data were noted directly from labels or field catalogs held in various museums. There are considerable differences among field collectors in the techniques that they use to measure bats; most notable in this regard for emballonurids is rather inconsistent methods for total length, tail, and hind foot measurements. When tabulating descriptive statistics of external measurements, we have in some cases only used those of a single collector—although this reduces sample size, it also decreases the range and variance of external measurements. SMG also took four wing and two hind limb measurements in millimeters from liquid preserved specimens: total length of third digit (metacarpal), third digit (first phalanx), fourth

digit (metacarpal), fourth digit (first phalanx), tibia, and calcar.

SMG measured seven cranial and five dental characters using digital calipers, accurate to the nearest 0.1 mm. The measurements and their definitions are: **greatest skull length to canines**: from posteriormost part of occipital to anterior-buccal alveolar border of canines; **greatest zygomatic breadth**: width across zygomatic arches at widest point; **interorbital width**: dorsal width at most constricted part of skull; **mastoid width**: greatest width across skull at mastoid processes; **braincase height**: from basiosphenoid and basiooccipital bones to top of braincase (in Malagasy *Emballonura* the sagittal crest is present, but not well developed); **rostral width**: maximum width across rostrum dorsally at lacryimal protuberances; $\mathbf{C^1}$–$\mathbf{C^1}$: width across anterior-buccal alveolar border of canines; $\mathbf{M^1}$–$\mathbf{M^1}$: maximum width across palate at buccal alveolar borders of third molars; and $\mathbf{C^1}$–$\mathbf{M^3}$: crown length from the anterior-buccal alveolar border of the canine to the posterior buccal margin of the third molar.

As some species of *Emballonura* show sexual dimorphism in size, with males being smaller than females (Peterson et al., 1995; Bonaccorso, 1998), separate descriptive statistics were calculated for adults of each sex. To assist with the analysis of patterns of geographic variation in Malagasy *Emballonura*, particularly sites with small sample sizes, we have grouped specimens as operational taxonomic units (OTUs) based on general region of locality. These include the northern site of Ankarana (OTU 1), all eastern sites south of Maroantsetra (OTU 2), all western sites south of Nosy Be and Ambanja (OTU 3), and the northern sites of Daraina, Analamerana, and Andavakoera (OTU 4; fig. 1).

Genetic Analyses

Our intention with the genetic analyses was to assess whether they corroborated taxonomic conclusions drawn from the quantitative and qualitative analyses. Total genomic DNA was isolated using a DNeasy DNA isolation kit (Qiagen), and stored in the provided elution buffer. Approximately 250 bp of the mitochondrial D-loop was amplified in *E. atrata* using the primers F(mt) and Mt15996L (Wilkinson and Chapman, 1991; Campbell et al., 1995). The complete mitochondrial cytochrome *b* gene (cyt *b*) was amplified using the primer pairs L14724/H15506 and L15171/UMMZ04 in *E. atrata* (Irwin et al., 1991; Yoder et al., 1996; Jansa et al., 1999). PCRs were performed in 50-µl reaction volumes, containing 2.25 mM $MgCl_2$, 0.25 mM dNTPs, 2.5 U Taq DNA polymerase, 5 µl Promega 10× buffer, 5 µl genomic DNA, and 20 pmol of each primer. The amplification involved an initial denaturation at 94°C for 3 min, followed by 40 cycles of 94°C for 45 sec, 52°C for 45 sec, and 72°C for 1 min, with a final elongation step at 72°C for 4 min. The PCR product was then purified using either gel band excision (Gel Excision kit, Qiagen) or PCR purification (PCR Purification kit, Qiagen).

The purified fragment was sequenced from both directions using the BigDye terminator cycle sequencing kit v.3.1 (Applied Biosystems) in a 20-µl reaction containing 2 µl of the BigDye solution, 1.2 µl ABI 5× sequencing buffer, 5 pmol of primer, and 100–200 ng of purified PCR product. The temperature profile was conducted according to the manufacturer's instructions. The sequencing reactions were cleaned of unincorporated nucleotides using genCLEAN dye terminator removal plates (Genetix) and analyzed on an ABI3100 automated sequencer. Each individual was sequenced 4 to 15 times per locus from multiple PCR reactions to resolve any ambiguities present in single sequencing passes. We used Sequencher v.4.2 (Gene Codes Corp.) to assemble and edit consensus sequences for each individual, and aligned the data by eye using MacClade v.4.0 (Maddison and Maddison, 2000). All sequences were deposited with GenBank: cytochrome *b* (DQ178249–DQ178285) and D-loop (DQ178286–DQ178323).

We performed Bayesian and maximum parsimony phylogenetic analyses on the cyt *b* data using MrBayes v.3.0b4 (Huelsenbeck and Ronquist, 2001) and PAUP* v.4.0b10 (Swofford, 2002), respectively. Sequences of *Saccopteryx bilineata* (Juste et al., 1999) and *E. alecto* (Hulva and Horáček, 2002) were used as the outgroups. Maximum parsimony analyses were performed using heuristic

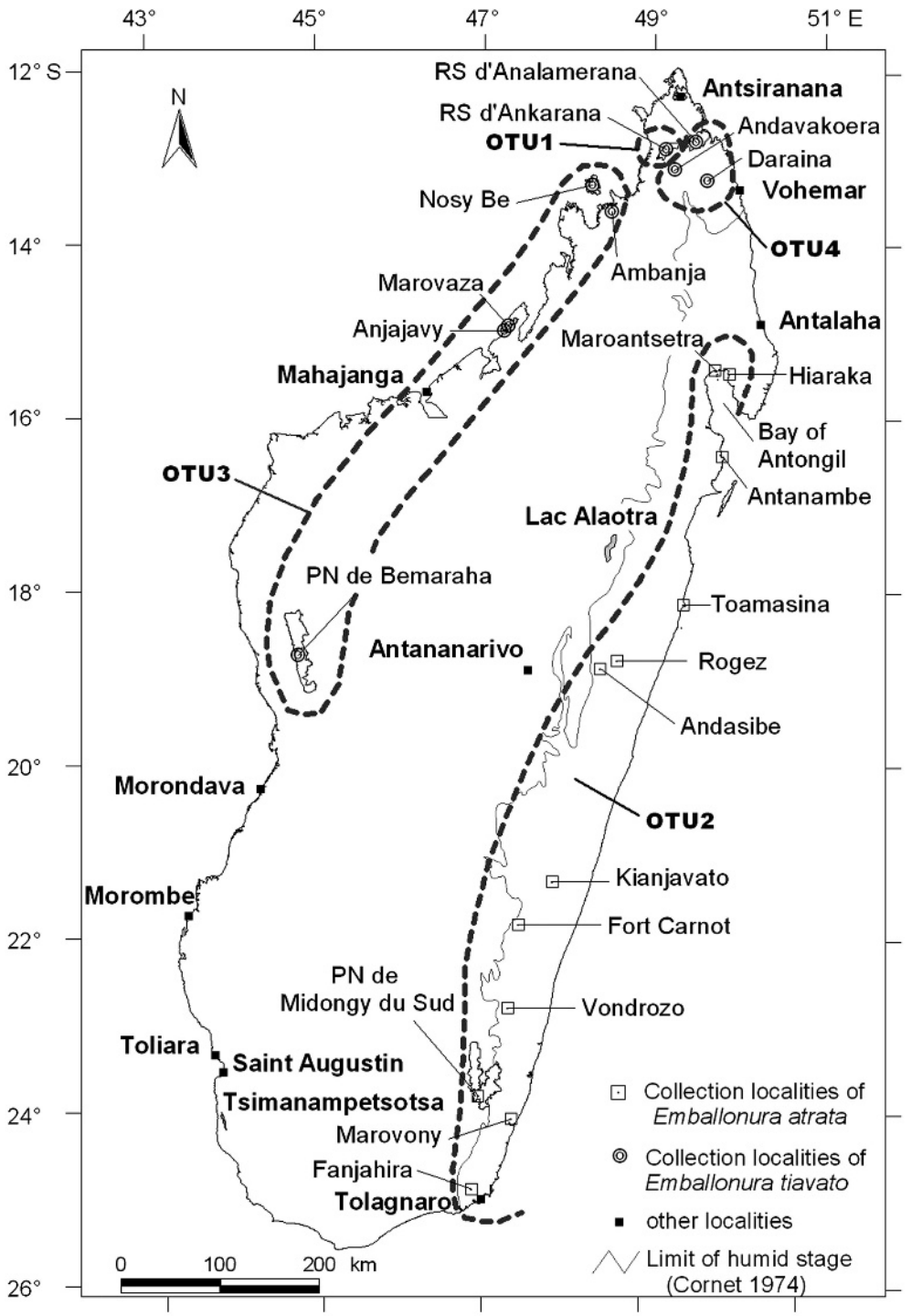

Fig. 1. Map of collection localities of *Emballonura* spp. on Madagascar and other sites mentioned in the text. To the east of the north–south meandering line is Cornet's (1974) "étage humide" or humid stage based on his bioclimatic classification of the island.

searches with tree bisection–reconnection (TBR) branch swapping, and setting the maximum number of saved trees to 1000. Parsimony bootstrap analyses were performed using heuristic searches, TBR branch swapping, and 100 replicates of the random addition search option. Bayesian analyses were performed with flat priors, running four chains of 10 million generations each, with sampling every 500 generations. The chains were heated using the temperature scaling factor $T = 0.2$. We specified an HKY + Γ model with four rate categories for the gamma distribution, the model having been specified using ModelTest v.3.06 (Posada and Crandall, 1998). After examining the likelihood profile using Tracer v.1.1 (http://evolve.zoo.ox.ac.uk/software.html?id=tracer), we discarded the first 4000 trees as a burn-in and constructed a 50% majority consensus tree from the remaining 16,000 trees in PAUP* (Swofford, 2002).

For each species and for each locus, we used ModelTest v.3.06 to determine the best-fitting model of evolution. Using the prescribed model and parameter values, we used Arlequin v.2.001 (Schneider et al., 2001) to test for genetic structure among geographic regions and sampling sites. We also used DnaSP v.4.0 (Rozas et al., 2003) to calculate descriptive measures such as haplotype diversity (h) and nucleotide diversity (π). Parsimony networks were constructed for each species and for each locus using TCS v.1.18 (Clement et al., 2000).

Emballonura atrata Peters, 1874

This taxon was described based on a single specimen collected "aus dem Innern von Madagascar" (Peters, 1874: 694), or in the interior of Madagascar. The holotype, which has been examined in the Museum für Naturkunde, Humboldt Universität, Berlin, is cataloged as number 4692. The cadaver is in alcohol and the pelage faded in coloration. The extracted skull is in relatively good shape, although the premaxillaries and associated incisors are not attached, the zygomatic processes are not intact, the occipital and palatine bones are partially broken, and considerable soft tissue still remains in the alisphenoid and basisphenoid region and partially obscures these structures. A label glued to the bottle containing the specimen has written upon it "4692 ♀, *Emballonura atrata* Ptrs. Madagaskar Crossly" and no date is associated with the specimen. The collector is undoubtedly Alfred Crossley, a British natural historian who visited Madagascar on several occasions, and obtained specimens particularly in the eastern portion of the island that are deposited in numerous European collections (Tattersall, 1986; Dorr, 1997). There is no evidence that he traveled to drier western portions of the island, particularly areas of deciduous forest. It has been previously suggested that J. M. Hildebrandt collected the *E. atrata* holotype (Peterson et al., 1995, footnote, p. 56), which is not correct.

Further evidence that the holotype specimen of *E. atrata* comes from the eastern humid forests is that, within the same accession at the Berlin Museum as specimen 4692, there are a variety of other mammal specimens, such as the lipotyphlan *Hemicentetes* and the primates *Propithecus diadema* and *Lichanotus mitratus* [=*Indri indri*] that represent taxa of this biome. Crossley collected the holotype of *L. mitratus* in the northern portion of Madagascar in the region of "Nossi Vola und Saralalan" (Peters, 1871). This site has been interpreted by Schwarz (1931) as probably from the Lalo River, east of the Bay of Antongil. If this is indeed the case, the site is close to the modern city of Maroantsetra. Another possibility is that the site of "Nossi Vola" is Nosivola (17°43′S, 48°39′E), which is located to the east of Lac Alaotra and on the road between Ambatondrazaka and Manakambahiny-Est. What is almost certain is this material would have been collected on his late 1869 expedition to Madagascar, when Crossley disembarked at Vohemar and collected in various portions of the eastern humid forest and the region of Lac Alaotra (Grandidier, 1872; Tattersall, 1986). Using the above-presented information, we restrict the type locality to the "lowland regions of the northern portion of eastern Madagascar."

On the basis of details presented below, we have examined specimens of a large and dark form of *Emballonura* that are assigned to *E. atrata* from the region of Maroantsetra south

to Tolagnaro and covering much of the eastern portion of the island (fig. 1; appendix 1). All of these specimens come from lowland sites or the lower end of the montane zones (less than 900 m) and we are unaware of any evidence of this species in the Central Highlands. After comparison of our recently collected specimens of Malagasy *Emballonura* from several different sites, as well as older museum material, to the holotype of *E. atrata*, it is evident that an undescribed species exists in the drier northern and western portions of the island. This conclusion is corroborated by genetic analyses of the mitochondrial cyt *b* gene and D-loop region.

Emballonura tiavato, new species

Figures 2, 3, 4, 5, Table 1, Appendices 2, 3

HOLOTYPE: Field Museum of Natural History number 169705, adult male prepared as skin, skull, and partial postcranial skeleton (original number 11923a), collected January 22, 2001, by S. M. Goodman.

The study skin is in a good state of preservation, with both wings folded under the body and the tail membrane spread. The skull is intact with the delicate premaxillaries still attached and the rami of the mandible separated. Portions of the postcranial skeleton were also saved. The habitat noted on the specimen label is "In dry deciduous forest at base of *tsingy*"; this latter word from the Malagasy refers to a particular type of eroded limestone formation. The individual was captured in a harp trap placed along a trail in the forest and within 40 m of the north entrance of Andrafiabe Cave. The collection site is a limestone karst area with an extensive underground cave system (Cardiff and Befourouack, 2003).

External measurements noted on the specimen label are: total length—64 mm, tail length—15 mm, hind foot length (not including claw)—5 mm, tragus length—5 mm, ear length—14 mm, and forearm length—36 mm. The fresh body mass of the specimen was 3.7 g. The testes were abdominal, measured 2 $\times$ 1 mm, and the epididymes not convoluted.

TYPE LOCALITY: Madagascar: Province d'Antsiranana, Réserve Spéciale d'Ankarana, 2.6 km E of Andrafiabe, in forest near Andrafiabe Cave, 12°55.9′S, 49°03.4′E, ± 50 m.

ETYMOLOGY: The name *tiavato* is derived from the Malagasy and means "likes rocks". This refers to the propensity of this species to occur in areas with exposed rock outcrops and caves.

DIAGNOSIS: A diminutive species of *Emballonura* (forearm length = 36–41 mm in males and 35–42 mm in females) with notably long rounded ears (11–15 mm in males and 12–15 mm in females). The dorsum pelage coloration is uniform pale to medium grayish-brown and the ventrum is paler buff-brown (fig. 2, left). Inner portion of tragus convex with distinct hatchet-shaped anterior projection. Calcar slightly shorter in length than tibia. Nasal bone hourglass shaped and with distinct central sulcus. Relatively narrow diastema between PM^1 and PM^2. Basisphenoid pits distinctly rounded and of medium depth and separated by median septum.

REFERRED SPECIMENS: See appendix 1.

DISTRIBUTION: Known from the drier portions of Madagascar, from the Daraina region inland from Vohemar north to Ankarana and then south along the western side of the island to at least Bemaraha (fig. 1). We have not examined a specimen of *Emballonura* reported from "Tuléar" [=Toliara] (Peterson et al., 1995), but we presume it to be referable to this species. Fieldwork in the Mikea Forest between Toliara and Morombe and to the south near Saint Augustin and Tsimanampetsotsa has not provided any evidence of the presence of this genus (Goodman and Razakarivony, 2004; Goodman et al., 2005).

DESCRIPTION: Dorsum cover fur notably long and slightly shaggy, with slightly silky texture, and uniform pale to medium grayish-brown color: basal one-quarter notably lighter and approaching medium-gray in color. The ventrum is paler buff-brown, with a slightly grayish-brown cast: basal one-third distinctly lighter and medium-gray in color. Little anterior–posterior variation in dorsum or ventrum coloration. Pelage in *E. atrata* notably darker, approaching brownish-black on dorsum and ventrum (fig. 2, right).

Ears long (11–15 mm in males and 12–15 mm in females), terminating with slightly pointed tip, but notably more acutely pointed

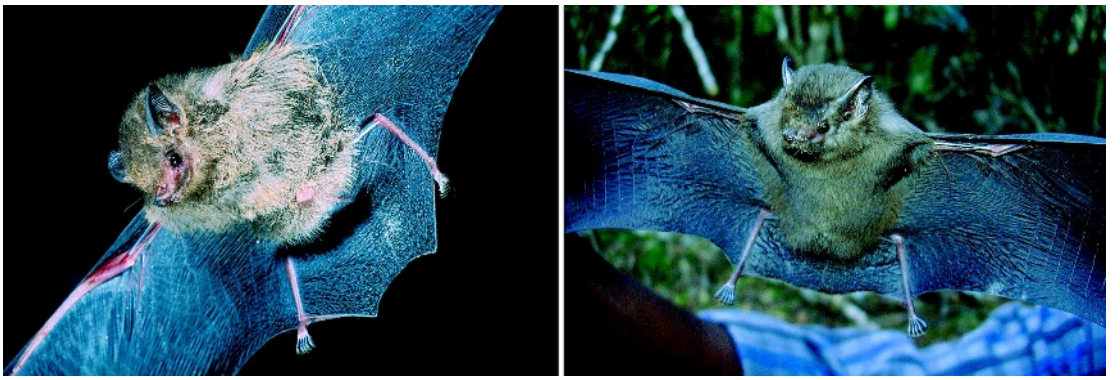

Fig. 2. Color photographs of the two species of *Emballonura* known from Madagascar. **Left**, holotype of *E. tiavato* (FMNH 169705) obtained near the Andrafiabe Cave in the Réserve Spéciale d'Ankarana (photograph courtesy of Harald Schütz); **right**, specimen of *E. atrata* (FMNH 178595) captured in the central humid forest in the vicinity of Midongy du Sud (photograph by Steven M. Goodman). Note difference in pelage coloration between the two species.

in *E. atrata* (fig. 3). In *E. tiavato*, the inner portion of tragus convex with distinct hatchet-shaped sharp anterior projection, and in *E. atrata*, this structure is distinctly less developed and more rounded (fig. 3). In *E. tiavato*, there is a distinct swelling at base of outer portion of tragus that is not present in *E. atrata*. On average calcar shorter than tibia in *E. tiavato*, while in *E. atrata* these two structures are approximately the same length.

Cranium notably small, distinct rostral expansion across the nasal and maxilla, and postorbital processes greatly reduced in size (fig. 4). Rostral width narrower with respect to *E. atrata*. In *E. tiavato* and *E. atrata*, postorbital crest not confluent with sagittal crest. Occipital portion of skull less inflated than in *E. atrata*. In *E. tiavato*, nasal bones are distinctly hourglass shaped and with well-defined, deep, and relatively broad nasal

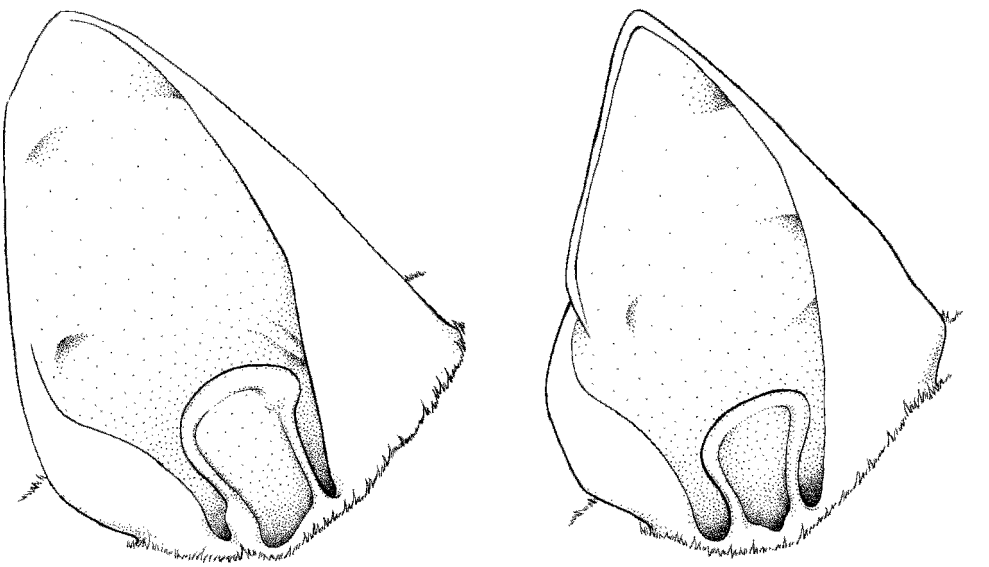

Fig. 3. Comparison of ear and tragus structures in Malagasy *Emballonura* spp. **Left**, *E. tiavato* (FMNH 179357) taken at Andavakoera; **right**, *E. atrata* (FMNH 178595) obtained near Midongy du Sud.

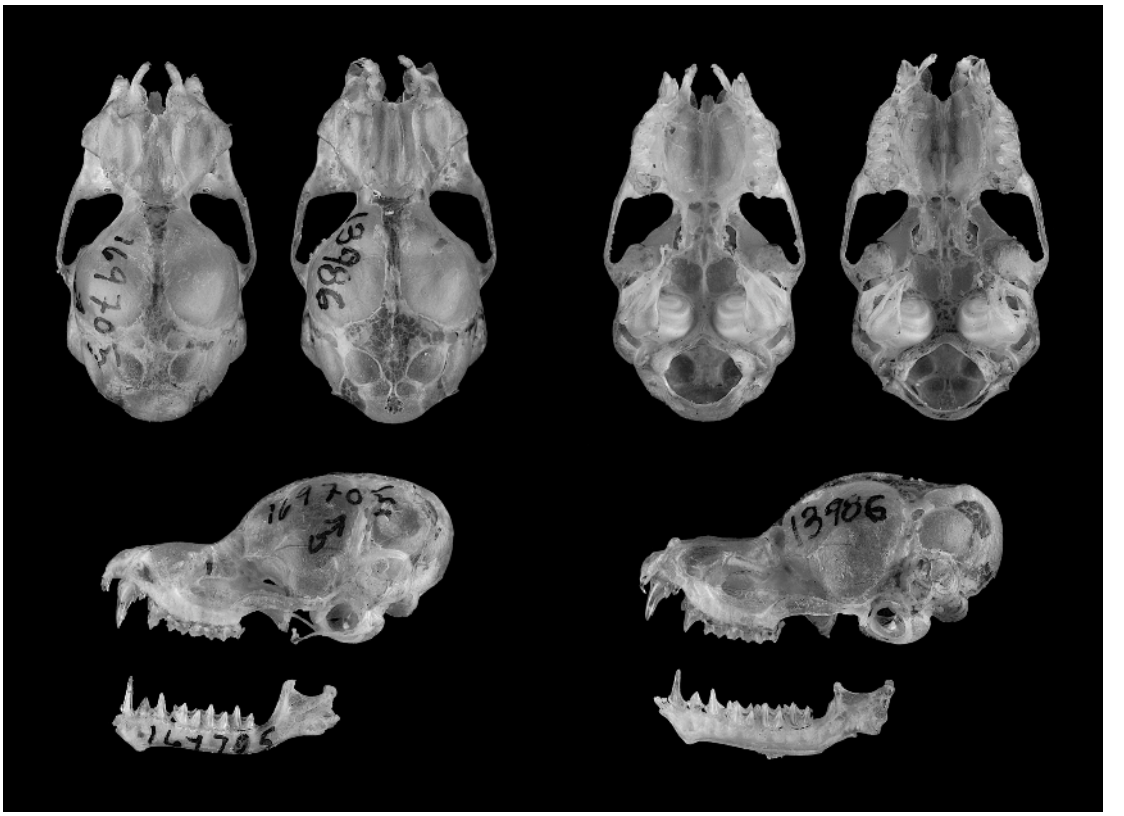

Fig. 4. Dorsal, ventral, and lateral views of adult crania and mandibles of Malagasy *Emballonura* spp. **Left**, holotype of *E. tiavato* (FMNH 169705; greatest skull length to canines = 13.0 mm) from near Andrafiabe Cave, Réserve Spéciale d'Ankarana, from the dry deciduous forests of northern Madagascar; **right**, *E. atrata* (FMNH 178595) from near Midongy du Sud, from the eastern humid forests of southeastern Madagascar.

sulcus that terminates well before the anterior margin of the nasal (fig. 5). This is in contrast to *E. atrata*, in which the lateral edges of the nasal bones are largely in parallel, the nasal sulcus is less broad, and the anterior margin of the sulcus nearly reaches the superior edge of the nasal. *E. tiavato* has a relatively narrow diastema between PM^1 and PM^2, which is distinctly wider in *E. atrata* (fig. 4). Basisphenoid pits in *E. tiavato* of medium depth and separated by median septum as in *E. atrata*. The distal limit of the pit is rounded and in *E. atrata* more oblong in shape and extends distally toward the auditory bullae.

COMPARISONS: Other than *Mosia*, *Emballonura* is the only genus of Emballonuridae with the dental formula of 2/3-1/1–2/2-3/3. All adult specimens of *Emballonura* that we have examined from Madagascar possess this dental formula. *Mosia*, which is often placed as a subgenus of *Emballonura*, is notably different from *Emballonura* based on structural differences in the hyoid apparatus, tragus, and penis (Griffiths and Smith, 1991; Griffiths et al., 1991).

Excluding *E. atrata*, of the eight species recognized in this genus (sensu Simmons, 2005), the following six have forearm lengths notably greater than that of the Malagasy species and are not included in the morphological comparisons below: *E. furax* Thomas, 1911; *E. dianae* Hill, 1956; *E. alecto* (Eydoux and Gervais, 1836); *E. monticola* Temminck, 1838; *E. semicaudata* (Peale, 1848), and *E. serii* Flannery, 1994 (Taylor, 1934; Flannery, 1994, 1995a, 1995b; Bonaccorso, 1998; Ingle and

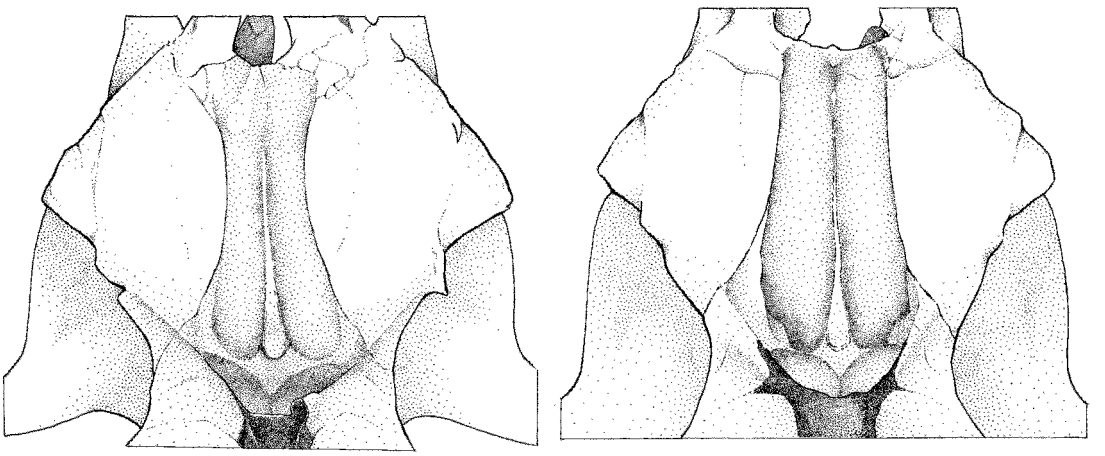

Fig. 5. Dorsal view of rostral portion of Malagasy *Emballonura* spp. **Left**, holotype of *E. tiavato* (FMNH 169705) from near Andrafiabe Cave, Réserve Spéciale d'Ankarana; **right**, *E. atrata* (FMNH 178595) from near Midongy du Sud. Note the difference in the shape of the nasal bones between the two species.

Heaney, 1992). The other two non-Malagasy *Emballonura* species can be distinguished from the species described herein, *E. tiavato*, by their multicolored dorsal pelage with distinctly white under fur (*E. raffrayana* Dobson, 1879), notable differences in tail and hind foot length (*E. beccarii* Peters and Doria, 1881, *E. raffrayana*; appendix 2), distinct rostral swelling (*E. beccarii*, *E. raffrayana*), and anterolateral extension of basisphenoid pits and absence of median septum between the pits (*E. beccarii*, *E. raffrayana*).

The differentiation of *E. tiavato* and *E. atrata* is based on a suite of different characters. The primary distinguishing characters are pelage, ear tip shape, tragus shape, shape of nasals, PM^1 and PM^2 diastema width, and shape of basisphenoid pits (see Description section above). For immediate recognition of an individual in the hand, pelage and a few external characters can be used to separate these species. The dorsum pelage coloration of *E. atrata* is a distinctly monocolored blackish-brown to black, with a slightly lighter ventrum (fig. 2). In contrast, the dorsum of *E. tiavato* is a notably lighter uniform pale to medium grayish-brown and the ventrum is paler buffy-brown (fig. 2). In *E. tiavato*, the anterior lateral portion of the tragus has a distinct hatchet shape, as compared to the blunter tragus tip in *E. atrata* (fig. 3). Further, there is no overlap in adult body weight between *E. tiavato* (mean = 3.6 g, range 2.7–4.5 g, $N = 37$) and *E. atrata* (mean = 5.3 g, range 5.0–7.1 g, $N = 6$; $t = 2.02$, $df = 41$, $P = 1.54^{-7}$)—these comparisons exclude pregnant females with moderate to large embryos.

To better evaluate differences in external measurements of these two taxa, we restricted our comparisons to specimens measured by the same field collector (SMG)—for *E. tiavato* these include specimens obtained at Ankarana (OTU 1) and for *E. atrata* those from Midongy du Sud (subset of OTU 2). With the exception of hind foot length, all of the mean external measurements made in the field of animals from these two populations were significantly different (table 1; appendix 2). For a suite of other variables, including other external (wing metacarpals and phalanges, tibia, and calcar), cranial, and dental measurements, we compared all of the adult individuals of OTUs 1, 3, and 4 (= *E. tiavato*) against those of OTU 2 (*E. atrata*). In these cases, significant differences were found between *E. tiavato* and *E. atrata* in body weight, all wing bone measurements, tibia, calcar, and all of the cranial-dental measurements, with the exception of C^1–C^1 (table 1; appendix 3).

Given the ambiguity associated with the exact locality where the holotype of *E. atrata*

TABLE 1
Selected Measurements of Combined Adult Male and Female *Emballonura tiavato* and *E. atrata*[a]

	E. tiavato	*E. atrata*
Total length	59.2 ± 3.34 55–64, $N = 13$	65.0 ± 3.46 63–69, $N = 3$
Tail length	16.0 ± 1.28 15–18, $N = 12$	18.7 ± 1.15 18–20, $N = 3$
Hind foot length	5.6 ± 0.51 5–6, $N = 13$	6.0 ± 0.00 6–6, $N = 3$
Ear length	12.5 ± 0.88 11–14, $N = 13$	16.3 ± 2.31 15–19, $N = 3$
Forearm length	37.2 ± 1.69 35–41, $N = 13$	40.3 ± 0.58 40–41, $N = 3$
Body mass	3.3 ± 0.40 2.7–3.8, $N = 13$	5.9 ± 1.10 5.0–7.1, $N = 3$
3rd digit–metacarpal	31.9 ± 1.15 29.8–34.0, $N = 37$	32.7 ± 1.26 29.0–35.3, $N = 26$
3rd digit–1st phalanx	14.3 ± 0.53 12.9–15.3, $N = 37$	14.8 ± 0.59 13.6–16.1, $N = 26$
4th digit–metacarpal	24.5 ± 1.11 22.7–26.3, $N = 37$	25.2 ± 0.96 22.7–27.1, $N = 25$
4th digit–1st phalanx	8.9 ± 0.42 8.1–9.8, $N = 37$	9.2 ± 0.36 8.7–10.0, $N = 24$
Tibia	15.4 ± 0.77 13.1–16.7, $N = 39$	15.8 ± 0.72 14.8–17.5, $N = 24$
Calcar	14.2 ± 0.84 12.3–16.4, $N = 39$	15.7 ± 0.63 14.8–16.9, $N = 21$
Greatest skull length to canines	13.0 ± 0.36 12.2–13.6, $N = 40$	13.3 ± 0.29 12.8–13.8, $N = 13$
Greatest zygomatic breadth	7.5 ± 0.17 7.0–7.8, $N = 38$	7.8 ± 0.27 7.4–8.4, $N = 15$
Interorbital width	2.5 ± 0.14 2.3–2.8, $N = 41$	2.7 ± 0.13 2.4–2.9, $N = 20$
Mastoid width	6.8 ± 0.17 6.4–7.2, $N = 41$	7.2 ± 0.17 6.7–7.4, $N = 18$
Braincase height	6.2 ± 0.19 5.8–6.5, $N = 37$	6.4 ± 0.19 6.1–6.8, $N = 14$
Rostral width	5.5 ± 0.14 5.1–5.7, $N = 40$	5.8 ± 0.23 5.3–6.2, $N = 16$
C^1–C^1	3.3 ± 0.11 3.1–3.5, $N = 40$	3.3 ± 0.23 3.0–3.7, $N = 17$
M^1–M^1	5.6 ± 0.13 5.4–5.9, $N = 40$	5.7 ± 0.21 5.4–6.0, $N = 19$
C^1–M^3	4.9 ± 0.13 4.7–5.2, $N = 41$	5.1 ± 0.10 4.9–5.3, $N = 20$

[a] External measurements are limited to a single field collector. For certain variables these two species exhibit sexual dimorphism or subtle geographic differences that are presented in greater detail in appendices 2 and 3.

was obtained, it was critical to associate this species name with one of the two distinct species of this genus occurring on Madagascar. On the basis of numerous external, cranial, and dental characters, the name *atrata* is applicable to the larger and darker eastern species. The holotype of *E. atrata* (ZMB 4692) is distinctly faded in coloration, which is not unexpected after well over 130 years in alcohol. However, in his description of *E. atrata*, Peters (1874) noted dark pelage coloration, matching that of eastern members of this genus. Further, Dorst (1947), in a key to the bats of Madagascar, noted that the pelage of *E. atrata* was uniformly blackish.

A principal component analysis was conducted on a series of cranial measurements available for the holotype of *E. atrata*, and these were compared to individuals from the four different OTUs. The first two factors of the analysis explained 83.5% of the variance, and greatest zygomatic breadth, mastoid width, and rostral width had heavy loadings (table 2). When the scores of these two factors are plotted against one another (fig. 6), there is a clear separation between populations occurring in the humid forest formations (OTU 2) and dry forest formations (OTUs 1, 3, and 4). Further, the holotype of *E. atrata* (ZMB 4692) falls within the scatter of points associated with the humid forest formations, providing further evidence that this population is referable to this species.

TAXONOMIC NOTE: To our knowledge, the only name previously used for a species of *Emballonura* on Madagascar is *E. atrata* Peters, 1874. The exception is the mention of *E. madagascariensis* by Sclater (1864), which we consider a nomen dubium.

TABLE 2
Factor Loadings of Principal Component Analysis for Selected Cranial Measurements Available from the Slightly Damaged Holotype of *Emballonura atrata* and Compared to Specimens from All Four OTUs[a]

Variable	Factor 1	Factor 2
Mastoid width	0.855	−0.329
Rostral width	0.853	0.128
Greatest zygomatic breadth	0.834	−0.356
Interorbital width	0.662	0.708
Eigenvalue	2.58	0.752
% total variance	64.7	18.8

[a] The number of variables used is reduced because of the state of the holotype.

CORROBORATING GENETIC RESULTS

Phylogenetic and network analyses show that regional sampling sites are well differentiated. The three samples of *Emballonura* from Midongy du Sud, in southeastern Madagascar, have identical haplotypes at both the cyt *b* and D-loop loci. Alternatively, network analyses of both loci reveal that the southeastern haplotype is the most divergent among all sampled Malagasy *Emballonura*, being at least six mutations removed at the D-loop (fig. 7) and at least 20 mutations removed at the cyt *b* locus (fig. 8).

Analyses of molecular variance confirm the patterns of regional genetic structure observed in the network analyses. Malagasy *Emballonura* samples are significantly structured between northern and western (= *E. tiavato*) and southeastern (*E. atrata*) regions, with 68.83% of the variance at the cyt *b* locus found between the two regions ($\phi_{ST} = 0.688$; $P < 0.001$) and 69.08% of the variance at the D-loop found between the two regions ($\phi_{ST} = 0.690$; $P < 0.001$).

An intriguing variant is seen in FMNH 173002, a specimen of *E. tiavato* from the Réserve Spéciale d'Ankarana. This individual is morphologically indistinguishable from its conspecifics, yet is genetically more similar to *E. atrata* at both mitochondrial loci examined here. We consider this to be a result of incomplete lineage sorting acting on the nonrecombining mitochondrial genome, and may indicate a relatively recent time since the divergence of these two species.

Overall, we find evidence of two distinctive groups of *Emballonura* on Madagascar. The observed genetic patterns are consistent with the presence of multiple demes, but due to the low sampling size and the lack of geographically intermediate sampling sites, we cannot exclude simple isolation by distance as a viable hypothesis based solely on genetic data. However, the totality of the evidence, considering these genetic patterns in light of the morphological and distributional data, strongly support the existence of a previously

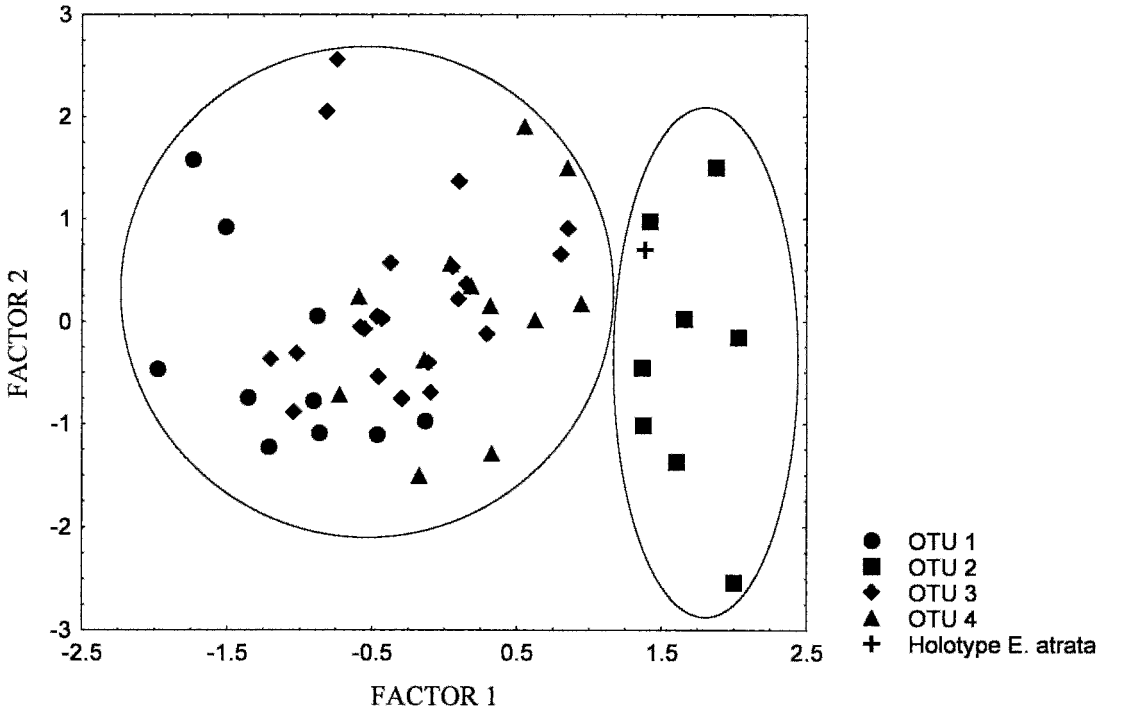

Fig. 6. Projection of factor 1 and factor 2 in principal component analysis of select cranial measurements of the holotype of *Emballonura atrata* and specimens from the four OTUs. The oval to the right is associated with specimens we allocate to *E. atrata* and includes the holotype of that species and specimens from the eastern humid forest (OTU 2). The circle to the left encompasses the specimens allocated to *E. tiavato* from the drier regions of the island (OTUs 1, 3, and 4). Loading contributions of variables to each axis are shown in table 2.

undescribed species in the dry areas of northern and western Madagascar.

DISCUSSION

Notes on Natural History

Emballonura tiavato is a delicately flying bat that is among the first species to become airborne at dusk. They have been captured at Ankarana and other sites in the dry north on several occasions actively foraging in the forest understory when the last fading rays of daylight still remain. The stomach contents of one individual of *E. tiavato* collected in the Daraina area in November 2001 contained the wing scale remains of a Lepidoptera (Razakarivony et al., 2005).

All of the individuals of *Emballonura* we have captured on Madagascar were obtained at the entrance of caves and rock overhangs or in areas with rock outcrops, and on the basis of this field experience, this genus is not synanthropic. However, Peterson et al. (1995) reported that near the eastern humid forest site of Périnet [= Andasibe], a local inhabitant brought to them a specimen that had been obtained in a house. We assume that this individual was actively feeding and simply sought shelter between foraging bouts rather than using the house as a day-roost. A large number of dwellings and buildings in villages within the eastern humid forest zone have been surveyed for synanthropic-living species of bats and no sign of *Emballonura* has been found (F. H. Ratrimomanarivo, personal commun.). In May 2005 at Marovaza, up to five individuals of *E. tiavato* were found after dusk roosting on the ceiling of a house without windows and within 5 m of an exposed limestone *tsingy* rock face. These animals did not use the house as a day-roost,

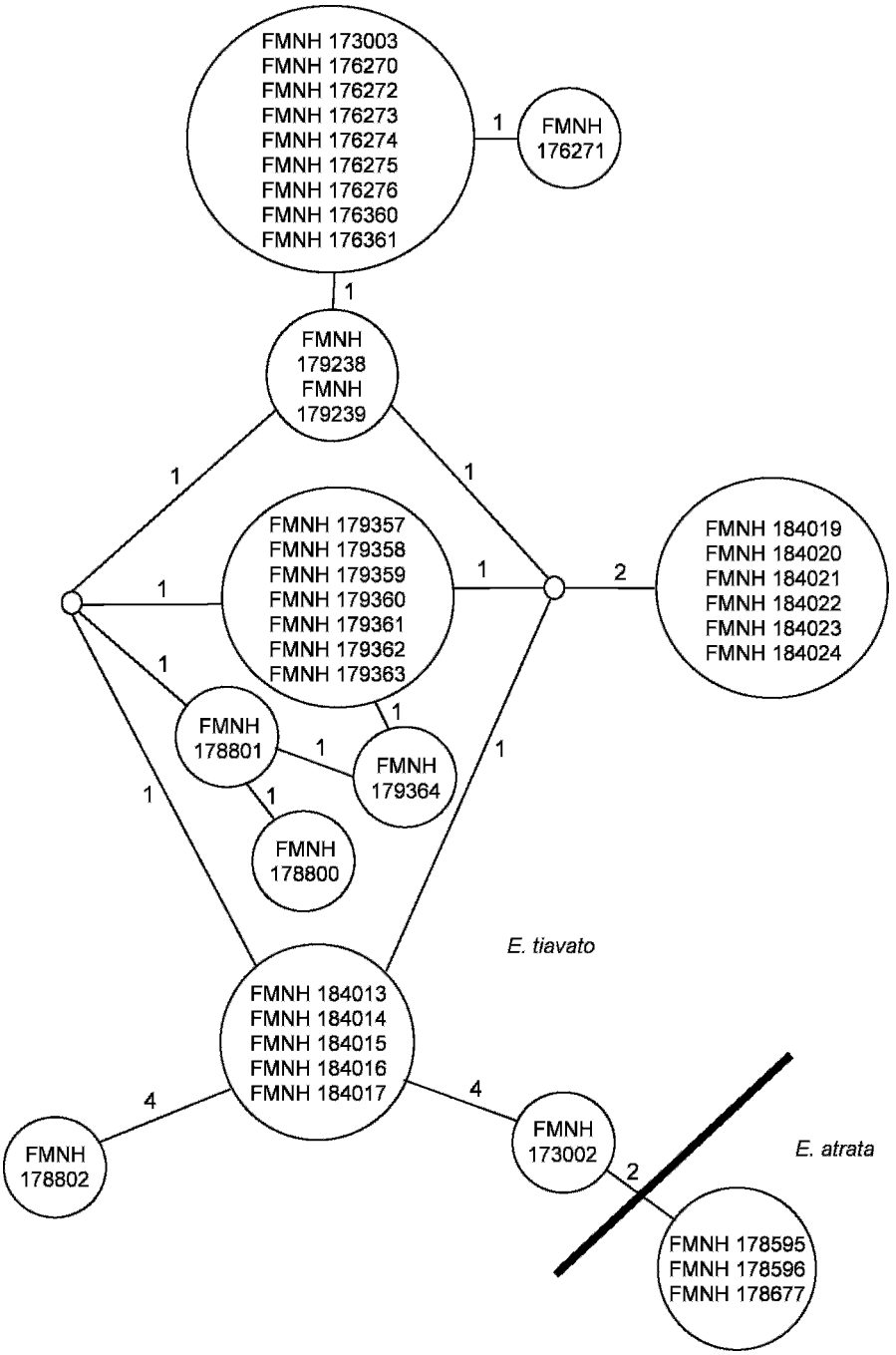

Fig. 7. Unrooted network analysis of Malagasy *Emballonura* spp. D-loop sequences. Each labeled circle represents a unique haplotype; unlabeled circles represent missing inferred haplotypes. Numbers by the lines connecting haplotypes indicate the number of mutational steps at each connection. The thick line indicates the division between species.

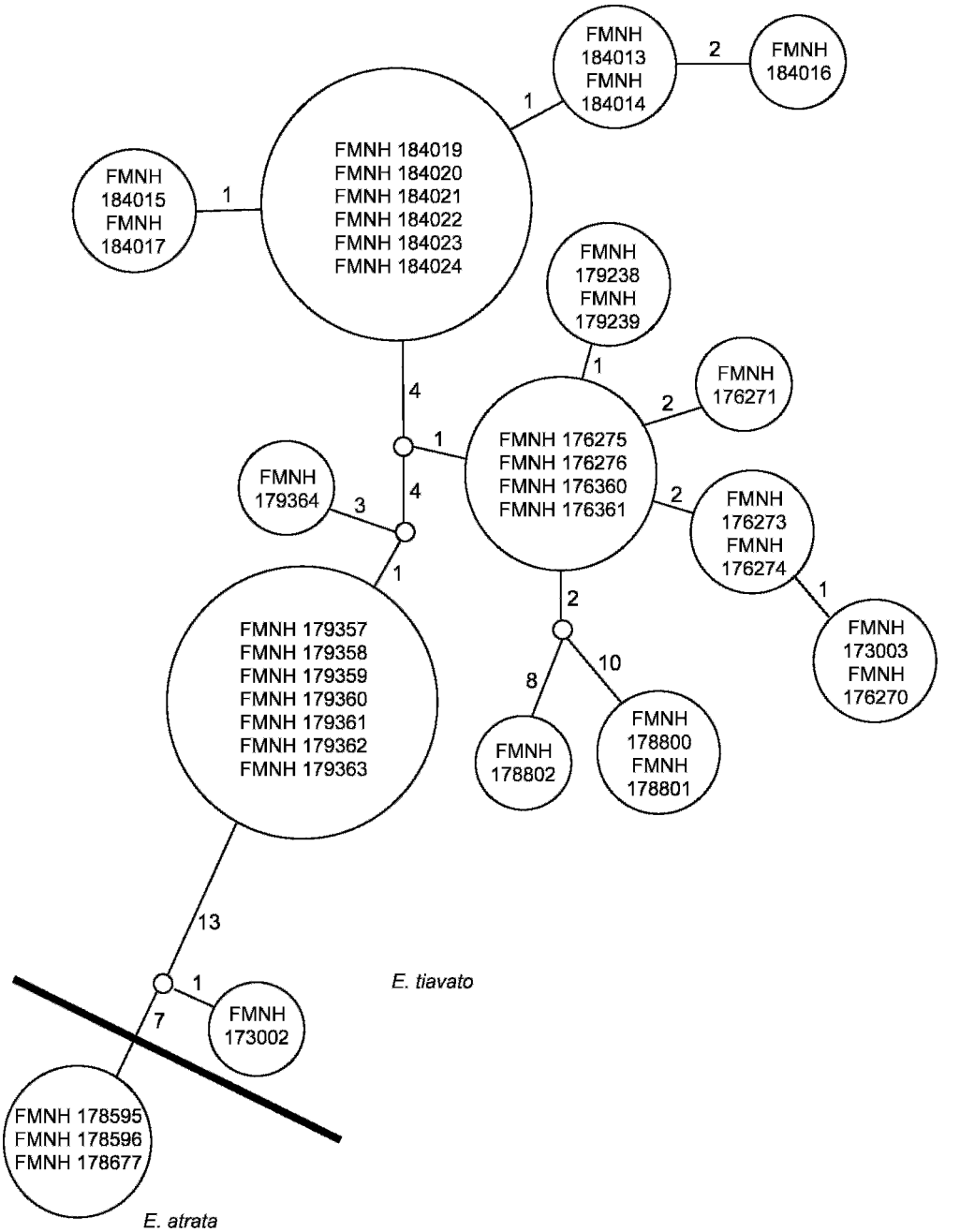

Fig. 8. Unrooted network analysis of Malagasy *Emballonura* spp. cyt *b* sequences. Each labeled circle represents a unique haplotype; unlabeled circles represent missing inferred haplotypes. Numbers by the lines connecting haplotypes indicate the number of mutational steps at each connection. The thick line indicates the division between species.

but rather as a resting site during night foraging bouts.

On the basis of specimens we have examined, we can offer the following insights about the seasonality of reproduction in *E. tiavato*. On February 4, 2004, at Andavakoera, a female was collected with a single embryo (crown-rump length of 16 mm), three other females were obtained in full lactation, each with a single placental scar, and two were subadults. Over the course of four days in mid-December 2004 in the region of Marovaza and Anjajavy, a number of females were captured that were pregnant and all with single embryos and large mammae. These included two individuals in a sea cave with embryo crown-rump lengths of 18 and 21 mm. Of six individuals captured at a slightly inland cave, all were female, and five were carrying embryos (12–18 mm crown-rump length). The sixth individual, an adult female, did not show any signs of reproductive activity. Given that not a single male was captured at this latter cave, it may have been the site of a nursery colony. The only other pregnant female *E. tiavato* that we captured is an individual on November 5, 2001, in the Daraina area that had a single embryo measuring 9 mm in crown-rump length. Females with enlarged mammae have been obtained in mid-April to early May in Ankarana. We have not handled a male that was clearly in reproductive condition, although one at Anjajavy on December 7, 2004, had testes measuring 3 × 2 mm and slightly convoluted epididymis, another at Andavakoera on February 4, 2002, had 3 × 1 mm testes and slightly convoluted epididymis, and a third individual at Ankarana on May 19 had 4 × 2 mm testes and slightly convoluted epididymes. Thus, on the basis of this information, we conclude that the litter size is one and it would appear that there is notable variation between populations in northern and northwestern Madagascar as to the time of parturition. Evaluating whether this difference is associated with latitudinal variation in seasonality or fluctuating from year to year based on local rainfall patterns requires further field studies.

Much less information is available on the reproductive season of *E. atrata*. On November 15, 2004, three females were obtained near Midongy du Sud: One was adult and showed no sign of sexual activity and the other two had enlarged mammae and single embryos (crown-rump length 15 mm and 18 mm). Russ and Bennett (1999) reported seeing a pair mating on a cave ceiling during the month of March 1999 (J. Russ, personal commun.). Of three females collected in late May 2005 near Kianjavato, two had large mammae, no embryos, and one placental scar each. The third individual was an adult with no recent sign of breeding activity.

Taxonomy, Biogeography, and Conservation

Tate and Archbold (1939) identified a number of cranial characters that they used to separate species groups and species in the genus *Emballonura*. They concluded that *E. atrata* had "simple" features assumed to be ancestral character states for this genus (p. 5). Griffiths et al. (1991) reexamined and scored the character states identified by Tate and Archbold (1939) as apomorphic or plesiomorphic and used them in a cladistic analysis. Their results reflect those of Tate and Archbold (1939), indicating that *E. atrata* is the least derived of any living *Emballonura* and that it lacks a number of characters found in other members of this genus. The character states scored by Griffiths et al. (1991) for *E. atrata* are identical to those found in *E. tiavato*. These include the presence of a nasal sulcus and absence of lateral rostral swelling, confluent basal pits, anterolateral extension of the basal (basisphenoid) pits, and posterior recession of basisphenoid pits. On the basis of these characters, *E. atrata* and *E. tiavato* form a species group and are each other's closest relatives, which implies a single colonization of the island by this genus and subsequent speciation.

Multiple species of *Emballonura* have been found to co-occur on several tropical islands. The highest species richness for any island occurs on New Guinea. Five species, including *Mosia* (often recognized as a subgenus of *Emballonura*; Griffiths et al., 1991), occur in the same general portion of the island and in many cases in sympatry, and a sixth species occurs on nearby islands (Flannery, 1995b; Bonaccorso, 1998). Thus, the presence of two

species of *Emballonura* on Madagascar is not exceptional, and current information indicates that they are allopatric in their distributions.

What is intriguing in a biogeographic sense is the complete absence of any species of *Emballonura* on any other island in the Indian Ocean. The westernmost non-Malagasy species is *E. monticola*, found in southern Myanmar, the Malay Peninsula, and the islands of Sumatra, Java, and Borneo (Simmons, 2005). There is a water expanse of about 5600 km between this species and Madagascar that crosses the islands or archipelagos of Andamar, Sri Lanka, Maldives, Seychelles, Mascarenes, and the Comoros. Island size probably does not explain the absence of *Emballonura* from these different sites, as members of this genus are known from some very small western Pacific islands (Flannery, 1995b). Further, many of these islands have caves and rock outcrops, the day-roost sites typically occupied by members of this genus. Finally, given the presumed ability of *Emballonura* to reach Madagascar across a considerable expanse of water, its absence from the African continent is inexplicable.

Cornet (1974) devised a very useful system to explain biotic variation on Madagascar in the form of bioclimatic zones, very similar to the life zone ecology of Holdridge (1964). Cornet's system was based on data from a series of weather stations across the island and calculated from the parameters of water deficit (annual rainfall minus potential evapotranspiration), mean minimum temperature in the coldest month of the year, and length of the dry season. Five different stages were delimited in this system, and the wettest portion of the island fell under the "étage humide" or moist stage. The line separating this stage from the four drier stages closely matches the distributional limit of *E. atrata* (fig. 1). Further, the southern limit of *E. tiavato*, based on our survey data, along the western lowland portion of the island coincides with the division of "étage sec" or dry stage and "étage subaride" or subarid stage. There is a specimen record of *Emballonura* from Toliara (Peterson et al., 1995: 57), but we have not captured a member of this genus during several bat inventories in the region.

Emballonura tiavato occurs across the drier portions of Madagascar, including the northern and western lowland portions of the island. This species seems to be broadly distributed in karstic limestone areas of the lowland central west, particularly in the region north of Mahajanga. It is known to occur in several protected areas including the Réserve Spéciale d'Ankarana, Réserve Spéciale d'Analamerana, and Parc National de Bemaraha (Goodman et al., 2005), as well as from numerous sites outside of the existing reserve system.

Fewer precise details are available on the distribution of *E. atrata* in the east, as compared to *E. tiavato* in the west. In the MNHN there is a series of close to 25 specimens of *E. atrata* collected in the Maroantsetra area over the course of 2 weeks in the mid-1930s. A label in one jar with 19 specimens (1947-289a to 1947-289t) reads, "Brought in by natives who said that they had removed them from small caves or crevices in rocks in forest." On the Masoala Peninsula, not far from Maroantsetra, a cave colony was found with at least 100 bats, a portion of which were *E. atrata*, and in this same region up to three individuals have been found together in hollow standing and downed tree trunks (Russ and Bennett, 1999). During a mid-November 2003 survey of the Parc National de Midongy du Sud and surrounding region a group of about 10 individuals was located in an underground rock shelter with a small hole opening to the surface (S. M. Goodman, unpubl.). This species appears to be broadly distributed across lowland areas of the complete length of the eastern humid forest, a region nearly 1500 km in length, but has not been reported from many protected areas. However, few eastern lowland reserves have been surveyed for bats.

Emballonura spp. on Madagascar are not collected as wild meat, presumably because of their small size and because they are not known to form large colonies. Members of this genus tend to live in day-roosts associated with forest habitat and they may be among the few bat species on the island that are forest dependent (Goodman et al., 2005). In our experience, it is highly unusual to capture

Emballonura out of forest settings. Thus, the maintenance of natural habitat may be important for their long-term survival. Further, a variety of different types of human use of caves might disturb day-roosting individuals and pose another potential threat to the *Emballonura*.

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APPENDIX 1

SPECIMENS OF *EMBALLONURA* SPP. FROM MADAGASCAR USED IN THIS STUDY

Abbreviations used: PN = Parc National, RS = Réserve Spéciale

Emballonura tiavato—**Province d'Antsiranana**: Ambanja, lower Sambirano River (MCZ 45087–88); Andavaka Matsaborimadio, at edge of Matsaborimadio, 10.5 km NE Ambondromifehy, 12°48.625′S, 49°15.252′E, 290 m (FMNH 179239); Andavadrano, 5.5 km SE Ambery, 12°50.632′S, 49°20.897′E, 330 m (FMNH 179238); Forêt d'Andavakoera, Grotte d'Andakaty, 2.9 km N Betsiaka, 13°07.778′S, 49°14.039′E, 210 m (FMNH 179357–364); Forêt de Binara, 7.5 km SW Daraina, 13°15′18″S, 49°36′59″E (FMNH 172680); Nosy Be, Pointe à la Fièvre (MNHN 1985.410); RS d'Analamerana, Grotte de Bazaribe, 3.6 km SE de Menagisy, 12°42.728′S, 49°28.411′E, 90 m (FMNH 178800–802); RS d'Ankarana, 2.6 km E Andrafiabe, near Andrafiabe Cave, 12°55.9′S, 49°03.4′E, 50 m (FMNH 169705, 176275–276, 176360–361); RS d'Ankarana, Antsironandoha Cave (west), 10 km NW Mahamasina, 12°53′20″S, 49°5′51″E, 100 m (FMNH 173002); RS d'Ankarana, Ambahibe Cave, 2 km W Mahamasina, 12°58′03″S, 49°7′13″, 100 m (FMNH 173003); RS d'Ankarana, Grotte d'Ambahibe, 3.0 km NW Mahamasina, 12°58′5″S, 49°07′09″E, 80 m (FMNH 176270–274). **Province de Mahajanga**. Marovaza, 14°56′48.0″S, 47°16′28.6″E, 5 m (FMNH 184025-026); 4.0 km NE Anjajavy, 14°59.713′S, 47°13.916′E, 10 m (FMNH 184080); 3.0 km NE Anjajavy, 15°0.471′S, 47°14.331′E, 10 m (FMNH 184018–024); 18.5 km S. Anjajavy, 15°11.426′S, 47°12.175′E, 50 m (FMNH 184016–017); 26.5 km SW Anjajavy, 15°11.871′S, 47°02.534′E, sea level (FMNH 184013-015); PN de Bemaraha, Anjohitantely, 19°08.460′S, 44°48.783′E, 64 m (UADBA uncataloged RBJ 157, 158, 162).

Emballonura atrata—**Province de Fianarantsoa**. Fort Carnot [= Ikongo] (MCZ 45649); grotte au N de Vondrozo (MCZ 45089); Kianjavato, 21°22.442′S, 47°51.604′E, 150 m (FMNH 185224–226); W slope of Mt. Ambatobe, 1.2 km ENE Ampatramary, 9.5 km NE Midongy su Sud, 23°30.6′S, 47°03.1′E, 650 m (FMNH 178677, 178595–596). **Province de Toamasina**: Hiaraka, Baie d'Antongil, Masoala (MNHN 1985.948); Maroantsetra (MNHN 1985.411); 20 km SW Maroantsetra (FMNH 74198–74203; MNHN 1947.288 [7 specimens], 1947.289 A à T [19 specimens], 1996.358–360); 40 km NW Maroantsetra (MNHN 1947.288 [7 specimens]); Périnet [= Andasibe] (MNHN 1985.418, ROM 42056); région d'Antanambe, Mananara (MNHN 1997–2133); Rogez (MNHN 1984.757–758); Tamatave [= Toamasina] (MCZ 16401–402). **Province de Toliara**. Evondro [= Isaka-Ivondro?], valley of high Fanjahira (MCZ 45081–086); Marovony Forest, 24°08′S, 47°22′E, 30 m (USNM 577062–063). **Uncertain localities**. Aus dem Innern von Madagaskar (holotype, ZMB 4692); Grande forêt de l'Est (MCZ 45091); probably côte est (MCZ 57538); Tanala (MCZ 45647).

APPENDIX 2

External Measurements (in mm) and Body Mass (in g) of *Emballonura tiavato* and *E. atrata*

Descriptive statistics presented as mean ± standard deviation (minimum – maximum, *N*). Samples measured by a single field collector are in bold. Separate *t*-test statistical comparisons of measurements of *E. tiavato* and *E. atrata* were conducted to examine differences between the sexes: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Descriptive statistics of external measurements presented in bold were made by the same field collector (SMG). To examine differences in external measurements made in the field, including forearm, between these two species of *Emballonura*, we used the Ankarana (OTU 1) and Midongy du Sud (subset of OTU 2) samples, which were measured by the same field collector and *t*-test statistical comparisons of measurements (sexes combined for each species), while those of weight, different wing bones, tibia, and calcar we used combined OTUs 1, 3, and 4 compared to OTU 2—in both cases sexes combined: $^{+}P < 0.05$, $^{++}P < 0.01$, $^{+++}P < 0.001$, $^{++++}P < 0.0001$.

	Total length	Tail length	Hind foot length	Ear length	Forearm length	Body mass
Emballonura tiavato						
Ankarana (OTU 1)						
♂	**57.5 ± 3.16***	**15.7 ± 1.11**	**5.5 ± 0.53**	**12.4 ± 0.92**	**36.6 ± 0.74**	**3.1 ± 0.35***
	55–64, *N* = 8	**15–18, *N* = 7**	**5–6, *N* = 5**	**11–14, *N* = 8**	**36–38, *N* = 8**	**2.7–3.7, *N* = 8**
♀	**61.8 ± 1.30**	**16.4 ± 1.52**	**5.8 ± 0.45**	**12.8 ± 0.84**	**38.2 ± 2.39**	**3.6 ± 0.16**
	60–63, *N* = 5	**15–18, *N* = 5**	**5–6, *N* = 5**	**12–14, *N* = 5**	**35–41, *N* = 5**	**3.4–3.8, *N* = 5**
sexes combined	**59.2 ± 3.34**	**16.0 ± 1.28**	**5.6 ± 0.51**	**12.5 ± 0.88**	**37.2 ± 1.69**	**3.3 ± 0.40**
	55–64, *N* = 13	**15–18, *N* = 12**	**5–6, *N* = 13**	**11–14, *N* = 13**	**35–41, *N* = 13**	**2.7–3.8, *N* = 13**
dry region sites (OTUs 1, 3, 4)						
♂	59.5 ± 4.25***	16.2 ± 1.26	5.8 ± 0.68	13.1 ± 1.04	37.6 ± 1.31**	3.5 ± 0.52**
	55–70, *N* = 19	15–18, *N* = 15	5–7, *N* = 16	11–15, *N* = 20	36–41, *N* = 20	2.7–4.3, *N* = 20
♀	63.2 ± 4.02	17.2 ± 3.14	6.0 ± 0.50	13.2 ± 1.11	39.0 ± 1.56	4.1 ± 0.70
	57–70, *N* = 20	13–24, *N* = 20	5–7, *N* = 17	12–15, *N* = 20	35–42, *N* = 21	3.0–6.0, *N* = 20
sexes combined	61.4 ± 4.48	16.8 ± 2.50	5.9 ± 0.60	13.2 ± 1.15	38.3 ± 1.60	3.6 ± 0.54^{+++}
	55–70, *N* = 39	13–24, *N* = 36	5–7, *N* = 33	11–16, *N* = 41	35–42, *N* = 42	2.7–4.5, *N* = 37[a]
Emballonura atrata						
holotype (ZMB 4692)	—	—	5.8	—	39.4	—
Midongy du Sud						
♀	**65.0 ± 3.46^{+}**	**18.7 ± 1.15^{++}**	**6.0 ± 0.00**	**16.3 ± 2.31^{+++}**	**40.3 ± 0.58^{++}**	**5.9 ± 1.10**
	63–69, *N* = 3	**18–20, *N* = 3**	**6–6, *N* = 3**	**15–19, *N* = 3**	**40–41, *N* = 3**	**5.0–7.1, *N* = 3**
east coast (OTU 2)						
♀	63.2 ± 3.71	18.4 ± 1.77	6.0 ± 0.48	14.9 ± 1.89	39.6 ± 1.25	5.3 ± 0.93^{++++}
	58–69, *N* = 4	16–21, *N* = 8	5–7, *N* = 10	13–19, *N* = 8	37–42, *N* = 13	5.0–7.1, *N* = 6

APPENDIX 2
(*Continued*)

	Total length	Tail length	Hind foot length	Ear length	Forearm length	Body mass
sexes combined	62.3 ± 4.11 57–67, $N = 7$	17.8 ± 2.09 14–21, $N = 11$	6.5 ± 0.92 5–8, $N = 15$	14.6 ± 1.62 13–19, $N = 12$	38.8 ± 1.36 37–42, $N = 50$	5.3 ± 0.93 5.0–7.1, $N = 6$
E. beccarri	60.7 ± 2.00 58–63, $N = 7$	12.0 ± 1.15 10–13, $N = 7$	8.0 ± 0.00 8–8, $N = 7$	15.9 ± 1.07 14–17, $N = 7$	37.5–42.0, $N = 541$[b]	3.5–5.0, $N = 37$[b]
E. raffrayana						
♂[b]	—	10.5–12.7, $N = 10$	—	11.0–13.1, $N = 10$	37.5–41.8, $N = 14$	5.0–6.0, $N = 14$
♀[b]	—	11.7–14.0, $N = 4$	7.0–8.5, $N = 4$	11.5–15.2, $N = 4$	38.7–41.6, $N = 7$	4.2–6.0, $N = 3$

	3rd digit metacarpal	3rd digit 1st phalanx	4th digit metacarpal	4th digit 1st phalanx	tibia	calcar
Emballonura tiavato						
Ankarana						
♂	31.0 ± 1.12 30.1–32.5, $N = 4$	14.2 ± 0.57 13.7–15.0, $N = 4$	23.5 ± 0.90 22.7–24.7, $N = 4$	8.9 ± 0.31 8.4–9.1, $N = 4$	14.6 ± 1.17 13.1–16.1, $N = 6$	14.5 ± 1.06 13.6–16.4, $N = 6$
♀	31.0 ± 1.04 29.9–32.7, $N = 5$	13.9 ± 0.55 13.5–14.9, $N = 5$	24.0 ± 1.09 22.8–25.3, $N = 5$	9.0 ± 0.52 8.4–9.6, $N = 5$	15.3 ± 0.25 14.9–15.5, $N = 5$	15.0 ± 0.41 14.5–15.6, $N = 5$
sexes combined	31.0 ± 1.01 29.9–32.7, $N = 9$	14.0 ± 0.54 13.5–15.0, $N = 9$	23.8 ± 1.00 22.7–25.3, $N = 9$	8.9 ± 0.42 8.4–9.6, $N = 9$	14.9 ± 0.92 13.1–16.2, $N = 11$	14.7 ± 0.85 13.6–16.4, $N = 11$
dry region sites						
♂	31.5 ± 1.11 29.8–33.1, $N = 16$	14.3 ± 0.60 12.9–15.0, $N = 16$	24.1 ± 1.12* 22.7–26.0, $N = 16$	8.7 ± 0.30* 8.1–9.3, $N = 16$	15.2 ± 0.86 13.1 –16.2, $N = 18$	14.0 ± 0.87* 12.9–16.4, $N = 18$
♀	32.2 ± 1.10 29.9–34.0, $N = 20$	14.4 ± 0.50 13.7–15.3, $N = 20$	24.8 ± 1.00 22.8–26.3, $N = 20$	9.0 ± 0.45 8.2–9.8, $N = 20$	15.5 ± 0.66 13.9–16.7, $N = 20$	14.4 ± 0.68 13.3–15.6, $N = 20$

APPENDIX 2
(*Continued*)

	Total length	Tail length	Hind foot length	Ear length	Forearm length	Body mass
sexes combined	31.9 ± 1.15[+] 29.8–34.0, $N = 37$	14.3 ± 0.53[++] 12.9–15.3, $N = 37$	24.5 ± 1.11 22.7–26.3, $N = 37$	8.9 ± 0.42[++] 8.1–9.8, $N = 37$	15.4 ± 0.77 13.1–16.7, $N = 39$	14.2 ± 0.84[+++] 12.3–16.4, $N = 39$
Emballonura atrata holotype (ZMB 4692)	34.2	—	15.3	—	26.6	—
Midongy du Sud						
♀	33.6–34.0, $N = 2$	15.1–15.5, $N = 2$[+]	25.5–26.9, $N = 2$	9.0–10.0, $N = 2$	15.8–16.3, $N = 2$	15.1–15.7, $N = 2$
east coast (OTU 2)						
♂	33.0 ± 1.26 31.8–34.3, $N = 3$	14.4 ± 0.87 13.9–15.4, $N = 3$	25.2 ± 1.18 24.5–26.6, $N = 3$	 8.7–9.3, $N = 2$	15.0 ± 0.17** 14.9–15.2, $N = 3$	 15.3, $N = 1$
♀	32.7 ± 1.51 29.0–35.3, $N = 15$	15.0 ± 0.58 13.6–16.1, $N = 15$	25.3 ± 1.14 22.7–27.1, $N = 15$	9.3 ± 0.39 8.8–10.1, $N = 15$	16.1 ± 0.65 15.4–17.5, $N = 13$	15.9 ± 0.60 14.8–16.9, $N = 13$
sexes combined	32.7 ± 1.26 29.0–35.3, $N = 26$	14.8 ± 0.59 13.6–16.1, $N = 26$	25.2 ± 0.96 22.7–27.1, $N = 25$	9.2 ± 0.36 8.7–10.1, $N = 24$	15.8 ± 0.72 14.8–17.5, $N = 24$	15.7 ± 0.63 14.8–16.9, $N = 21$

[a] Does not include pregnant females with moderate to large embryos.
[b] Based on measurements presented in Bonaccorso (1998) and hind foot includes the claw.

APPENDIX 3
CRANIAL AND DENTAL MEASUREMENTS (in mm) OF *EMBALLONURA TIAVATO* AND *E. ATRATA*

Descriptive statistics presented as mean ± standard deviation (minimum − maximum, *N*). Separate *t*-test statistical comparisons of measurements of *E. tiavato* and *E. atrata* were conducted to examine differences between the sexes: $^{*}P < 0.05$. To examine differences in cranial and dental measurements between these two species of *Emballonura*, we used OTUs 1, 3, and 4 compared to OTU 2 and *t*-test statistical comparisons of measurements (sexes combined for each species): $^{+}P < 0.05$, $^{++}P < 0.01$, $^{+++}P < 0.001$, $^{++++}P < 0.0001$.

	Greatest skull length to canines	Greatest zygomatic breadth	Interorbital width	Mastoid width	Braincase height	Rostral width
Emballonura tiavato						
Ankarana (OTU 1)						
♂	12.7 ± 0.31	7.4 ± 0.10	2.4 ± 0.11	6.7 ± 0.24	6.1 ± 0.15	5.3 ± 0.20
	12.2–13.0, *N* = 7	7.2–7.5, *N* = 7	2.3–2.6, *N* = 7	6.4–7.0, *N* = 7	5.9–6.3, *N* = 6	5.1–5.6, *N* = 7
♀	12.8 ± 0.25	7.5 ± 0.13	2.4 ± 0.05	6.8 ± 0.10	6.1 ± 0.13	5.4 ± 0.06
	12.5–13.1, *N* = 4	7.3–7.6, *N* = 4	2.3–2.4, *N* = 5	6.7–6.9, *N* = 5	6.0–6.3, *N* = 5	5.3–5.4, *N* = 4
sexes combined	12.7 ± 0.28	7.4 ± 0.12	2.4 ± 0.09	6.7 ± 0.20	6.1 ± 0.14	5.3 ± 0.16
	12.2–13.1, *N* = 11	7.2–7.6, *N* = 11	2.3–2.6, *N* = 12	6.4–7.0, *N* = 12	5.9–6.3, *N* = 11	5.1–5.6, *N* = 11
dry region sites (OTUs 1, 3, 4)						
♂	13.0 ± 0.40	7.4 ± 0.18*	2.6 ± 0.15	6.8 ± 0.18	6.2 ± 0.18	5.5 ± 0.18
	12.2–13.6, *N* = 19	7.0–7.7, *N* = 18	2.3–2.8, *N* = 19	6.4–7.0, *N* = 19	5.8–6.4, *N* = 17	5.1–5.7, *N* = 19
♀	13.0 ± 0.32	7.6 ± 0.15	2.5 ± 0.11	6.9 ± 0.14	6.1 ± 0.20	5.5 ± 0.10
	12.5–13.5, *N* = 20	7.3–7.8, *N* = 19	2.3–2.7, *N* = 21	6.7–7.2, *N* = 21	5.9–6.5, *N* = 19	5.3–5.7, *N* = 20
sexes combined	13.0 ± 0.36^{++}	7.5 ± 0.17^{+++}	2.5 ± 0.14^{+++}	6.8 ± 0.17^{++++}	6.2 ± 0.19^{+++}	5.5 ± 0.14^{++++}
	12.2–13.6, *N* = 40	7.0–7.8, *N* = 38	2.3–2.8, *N* = 41	6.4–7.2, *N* = 41	5.8–6.5, *N* = 37	5.1–5.7, *N* = 40
Emballonura atrata						
holotype (ZMB 4692)	13.2	7.8	2.7	7.0	6.5	6.0
Midongy du Sud						
♀	7.8 ± 0.10	2.7 ± 0.20	7.2 ± 0.17	6.4 ± 0.26	6.0 ± 0.15	
	13.4–13.5, *N* = 2	7.7–7.9, *N* = 3	2.5–2.9, *N* = 3	7.1–7.4, *N* = 3	6.1–6.6, *N* = 3	5.9–6.2, *N* = 3
east coast (OTU 2)						
♂	13.4 ± 0.12	7.8 ± 0.36	2.7 ± 0.07	7.1 ± 0.10	6.5 ± 0.35	5.7 ± 0.08
	13.3–13.5, *N* = 3	7.5–8.2, *N* = 3	2.6–2.8, *N* = 5	7.0–7.2, *N* = 3	6.1–6.8, *N* = 3	5.6–5.8, *N* = 4
♀	13.3 ± 0.34	7.8 ± 0.27	2.6 ± 0.15	7.1 ± 0.20	6.4 ± 0.15	5.8 ± 0.28
	12.8–13.8, *N* = 8	7.4–8.4, *N* = 12	2.4–2.9, *N* = 12	6.7–7.4, *N* = 12	6.1–6.6, *N* = 11	5.3–6.2, *N* = 11

APPENDIX 3 (*Continued*)

	Greatest skull length to canines	Greatest zygomatic breadth	Interorbital width	Mastoid width	Braincase height	Rostral width
sexes combined	13.3 ± 0.29 12.8–13.8, $N = 13$	7.8 ± 0.27 7.4–8.4, $N = 15$	2.7 ± 0.13 2.4–2.9, $N = 20$	7.2 ± 0.17 6.7–7.4, $N = 18$	6.4 ± 0.19 6.1–6.8, $N = 14$	5.8 ± 0.23 5.3–6.2, $N = 16$
	C^1–C^1	M^3–M^3	C^1–M^3			
Emballonura tiavato						
Ankarana						
♂	3.3 ± 0.15 3.1–3.5, $N = 7$	5.5 ± 0.14 5.4–5.7, $N = 7$	4.8 ± 0.10 4.7–5.0, $N = 7$			
♀	3.3 ± 0.06 3.2–3.3, $N = 4$	5.5 ± 0.08 5.4–5.6, $N = 4$	4.8 ± 0.09 4.7–4.9, $N = 5$			
sexes combined	3.3 ± 0.12 3.1–3.5, $N = 11$	5.5 ± 0.11 5.4–5.7, $N = 11$	4.8 ± 0.09 4.7–5.0, $N = 12$			
Dry region sites						
♂	3.3 ± 0.13 3.1–3.5, $N = 19$	5.5 ± 0.14 5.3–5.8, $N = 19$	4.9 ± 0.13 4.7–5.2, $N = 19$			
♀	3.3 ± 0.09 3.2–3.5, $N = 20$	5.6 ± 0.13 5.4–5.9, $N = 20$	5.0 ± 0.12 4.7–5.2, $N = 21$			
sexes combined	3.3 ± 0.11 3.1–3.5, $N = 40$	5.6 ± 0.13^{++} 5.3–5.9, $N = 40$	4.9 ± 0.13^{++++} 4.7–5.2, $N = 41$			
Emballonura atrata						
Holotype (ZMB 4692)	3.5	5.7	5.2			
Midongy du Sud						
♀	3.3–3.5, $N = 2$	5.7–6.0, $N = 2$	5.1–5.2, $N = 2$			
east coast						
♂	3.4 ± 0.20 3.2–3.6, $N = 3$	5.8 ± 0.32 5.4–6.0, $N = 3$	5.2 ± 0.13 5.0–5.3, $N = 4$			
♀	3.3 ± 0.26 3.0–3.7, $N = 11$	5.8 ± 0.21 5.4–6.0, $N = 12$	5.1 ± 0.10 4.9–5.2, $N = 12$			
sexes combined	3.3 ± 0.23 3.0–3.7, $N = 17$	5.7 ± 0.21 5.4–6.0, $N = 19$	5.1 ± 0.10 4.9–5.3, $N = 20$			