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M Alejandra Camacho, Pablo Menéndez-Guerrero, Balázs Horváth, Dániel Cadar, Jérôme Murienne. A polytypic species revisited: phylogenetic and morphological variation, taxonomic status, and geographical distribution of *Trachops* (Chiroptera: Phyllostomidae). *Journal of Mammalogy*, 2024, 105 (5), pp.1001-1021. 10.1093/jmammal/gya067 . hal-04909503

HAL Id: hal-04909503

<https://hal.science/hal-04909503v1>

Submitted on 24 Jan 2025

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A polytypic species revisited: Phylogenetic and morphological variation, taxonomic status, and geographical distribution of *Trachops* (Chiroptera: Phyllostomidae)

Journal:	<i>Journal of Mammalogy</i>
Manuscript ID	Draft
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Camacho, M. Alejandra; Pontificia Universidad Católica del Ecuador, Museo de Zoología Menéndez-Guerrero, Pablo; Pontificia Universidad Católica del Ecuador, 3Laboratorio de Macroecología y Cambio Global, Facultad de Ciencias Exactas y Naturales Horváth, Balázs; Bernhard Nocht Institute of Tropical Medicine, WHO Collaborating Centre for Arbovirus and Haemorrhagic Fever Reference and Research Cadar, Dániel; Bernhard Nocht Institute of Tropical Medicine, WHO Collaborating Centre for Arbovirus and Haemorrhagic Fever Reference and Research Murienne, Jérôme ; Université Toulouse III-Paul Sabatier, Centre de Recherche sur la Biodiversité et l'Environnement (CRBE)
Keywords:	Fringed-Lipped Bat, Mitochondrial DNA analysis, Neotropical Phyllostomids, Taxonomic evaluation, <i>T. cirrhosus</i> , <i>T. ehrhardtii</i> , <i>Trachops</i> diversity

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A polytypic species revisited: Phylogenetic and morphological variation, taxonomic status, and geographical distribution of *Trachops* (Chiroptera: Phyllostomidae)

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20 **Short running title:** Phylogenetic and morphological characterization of *Trachops*

22 Abstract

24 The taxonomic status of the neotropical bat genus *Trachops* has been reevaluated through an
25 integrated study that incorporates morphological, morphometric, and molecular data across its
26 extensive geographic range. Our research, which included previously unexamined regions,
27 revealed substantial insights into the diversity within *Trachops*. The results support the elevation

28 of *T. cirrhosus ehrhardti* to species status, due to genetic and morphological differences in
29 southeastern Brazil specimens. Conversely, our comprehensive analysis found insufficient
30 evidence to maintain the subspecific distinction of *T. c. coffini*, which lacks diagnosable
31 morphological characters and is not genetically distinct from *T. c. cirrhosus* across its distribution
32 range. Additionally, our findings challenge the previous belief of a latitudinal differentiation in
33 body size for *Trachops cirrhosus*, as specimens from western South America and northeastern
34 South America exhibit similar sizes to those from Central America. These results underscore the
35 importance of revising the taxonomic framework for this bat genus, contributing to a more precise
36 understanding of its evolutionary relationships, and further enhancing conservation efforts,
37 considering the potential threats to the newly recognized *T. ehrhardti* in the imperiled Atlantic
38 Forest of Brazil.

39

40 **Keywords:** Fringed-Lipped Bat, Mitochondrial DNA analysis, Neotropical Phyllostomids,
41 Taxonomic evaluation, *T. cirrhosus*, *T. ehrhardti*, *Trachops* diversity.

42

43 **Resumen**

44

45 El estatus taxonómico de los murciélagos neotropicales del género *Trachops* ha sido reevaluado
46 mediante un estudio integrado que incorpora datos morfológicos, morfométrico y moleculares a
47 través de su extensa distribución geográfica. Nuestra investigación, que incluyó regiones
48 previamente no examinadas, reveló perspectivas sustanciales sobre la diversidad dentro del
49 género *Trachops*. Los resultados respaldan la elevación de *T. cirrhosus ehrhardti* al estatus de
50 especie debido a las diferencias genéticas y morfológicas en especímenes en el sudeste de Brasil.
51 Por otro lado, nuestro análisis no encontró suficiente evidencia para mantener la distinción
52 subespecífica de *T. c. coffini*, que carece de caracteres morfológicos diagnosticables, y no difiere
53 genéticamente de *T. c. cirrhosus* en su rango de distribución. Adicionalmente, nuestros hallazgos
54 confrontan las creencias previas de una diferenciación latitudinal en el tamaño corporal de

55 *Trachops cirrhosus*, ya que especímenes del oeste y noreste de Sudamérica exhiben tamaños
56 similares a los encontrados en individuos de Centroamérica. Estos resultados subrayan la
57 importancia de examinar el marco taxonómico para este género de murciélagos, contribuyendo a
58 una comprensión más precisa de sus relaciones evolutivas, para aumentar los esfuerzos de
59 conservación a futuro, considerando los riesgos potenciales a la recientemente reconocida especie
60 *T. ehrhardti* en los Bosques Atlánticos amenazados de Brasil.

61

62 **Palabras clave:** Análisis DNA mitocondrial, diversidad *Trachops*, Evaluación taxonómica,
63 Filostómidos Neotropicales, Murciélagos de labio verrugoso, *T. cirrhosus*, *T. ehrhardti*

64

65 Introduction

66

67 The Frog-Eating bat, *Trachops cirrhosus* ([Spix 1823](#)), is a member of the family Phyllostomidae
68 ([Gray 1825](#)), and the only member of its genus ([Solari et al. 2019](#)). This species has a wide
69 distribution in the Americas, ranging from southern Mexico to Brazil, and occurring at mid to high
70 elevations at both sides of the Andes Cordillera, across the Amazon, and in the Atlantic Forest
71 ([Jones and Carter 1976](#); [Cramer et al. 2001](#); [Williams and Genoways 2008](#); [Solari et al. 2019](#)). The
72 species occurs in humid tropical and subtropical forests, and its distribution encompasses
73 primary, secondary, disturbed and gallery forests, at woodland edge and near cultivated areas
74 ([Fenton et al. 1992](#); [Ditchfield 1996](#); [Tirira 2017](#); [Solari et al. 2019](#)).

75

76 *Trachops* is monophyletic genus ([Ditchfield 1996](#); [Baker et al. 2003](#); [Camacho et al. 2022](#) and can
77 be easily distinguished from other bats by its finger-like dermal projections on the chin and lips
78 (Figure 1). Historically, *Trachops* taxonomy has undergone numerous changes ([Spix 1823](#); [Gray
79 1825](#), [Gray,1847](#); [Felten 1956a](#); [Schinz 2012](#)) until the late 1950s, when its current taxonomy was
80 established with three recognized subspecies: *Trachops cirrhosus cirrhosus* ([Spix 1823](#)), occurring
81 from Costa Rica to northeastern Brazil; *Trachops cirrhosus coffini* ([Goldman 1925](#)), distributed

82 from Mexico to Nicaragua; and *Trachops cirrhosus ehrhardti* ([Felten, 1956b](#)), which is found only
83 in southeastern Brazil (Figure 2) ([Jones and Carter 1976](#); [Solari et al. 2019](#)).

84
85 The descriptions of the subspecies of *Trachops cirrhosus* are brief and lack comparisons with
86 specimens from Central and South America locations, leading to unclear geographic ranges and
87 diagnostic characters. Moreover, only a few recent studies have addressed the systematics of
88 *Trachops* itself. [Ditchfield \(1996\)](#) used partial sequences of the mitochondrial Cytochrome b gene
89 and identified 5 distinct haplotypes with an average sequence divergence ranging from 5.5% to
90 11%, demonstrating strong geographic structuring and limited sharing of haplotypes among
91 distant localities. Later, and despite the high genetic divergences yielded by the mitochondrial
92 marker COI, [Clare et al. \(2007\)](#) and [Clare \(2011\)](#) could not find congruence with the topology
93 yielded by the nuclear marker Dby. However, they observed many intraspecific groups occupying
94 sympatric distributions, strongly suggesting ongoing or past speciation events. Most recently,
95 [Fonseca \(2019\)](#) proposed elevating *T. c. ehrhardti* to the species level, based on integrative
96 evidence in morphology, ecology, and genetics, while maintaining *T. c. cirrhosus* and *T. c. coffini* as
97 subspecies of *T. cirrhosus*. But these taxonomic changes, initially proposed by [Fonseca \(2019\)](#),
98 have not yet been formalized in a peer-reviewed publication, and the morphological guidelines
99 for characterization of *Trachops cirrhosus* subspecies remain unclear.

100
101 In the present study, we revise the taxonomic composition and phylogenetic structure of the
102 *Trachops* genus based on molecular, morphological, morphometric, and geographic data that
103 includes a significant sample from the West South American region. We aim to address this issue
104 by answering the following questions: (1) Do the current subspecies of *Trachops cirrhosus* have
105 valid phylogenetic and morphological justifications? (2) What are the distinct and diagnosable
106 characters of each subspecies? (3) Can biodiversity of cryptic species be inferred in *Trachops*
107 through molecular and morphological analysis? We seek to clarify, correctly diagnose, and
108 geographically limit *T. cirrhosus* subspecies. We used a phylogenomic dataset based on complete

109 mitochondrial genome which has provided meaningful information in Phylostomids ([Camacho et](#)
110 [al. 2022](#)). In addition, we performed an extended taxon sampling, ensuring comprehensive spatial
111 coverage. This diverse geographic sampling encompasses a wide range of habitats and ecological
112 zones where *Trachops cirrhosus* subspecies are found.

113

114 **Methods**

115

116 **Specimens, tissue samples, and biorepositories:** For the morphometric analyses, we measured
117 238 specimens of *Trachops cirrhosus*. Only adults were included, following the consideration from
118 [Kunz et al. \(1996\)](#) for sex, age, and reproductive conditions of mammals. We included
119 representatives from all named subspecies and from their complete distribution areas in Central
120 and South America. The samples comprised fluid-preserved specimens, study skins, and skulls
121 deposited in the following institutions: **AMNH**, American Museum of Natural History, New York,
122 NY, USA; **IAvH**, Colección de Mamíferos del Instituto de Investigación de Recursos Biológicos
123 Alexander von Humboldt, Villa de Leyva, Colombia; **MEPN**, Museo de Historia Natural Gustavo
124 Orcés, Escuela Politécnica Nacional, Quito, Ecuador; **QCAZ**, Museo de Zoología, División de
125 Mastozoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; **SMF**, Senckenberg
126 Naturmuseum Frankfurt, Frankfurt, Germany; **USNM**, National Museum of Natural History,
127 Smithsonian Institution, Washington, DC, USA; and **UV**, Colección del Mamíferos de la Universidad
128 del Valle, Cali, Colombia. The measurements of the specimens of *Trachops cirrhosus ehrhardti* from
129 the SMF ($n = 3$) were shared by the curator of this collection. We obtained tissue samples from the
130 following collections: **AMNH**; **FMNH**, Field Museum of Natural History, Chicago, IL, USA; **MSB**,
131 Museum of Southwestern Biology, Albuquerque, NM, USA; **QCAZ**; **ROM**, Royal Ontario Museum,
132 Toronto, Canada; and **SMF** (Supplementary Table 1).

133

134 **Genomic DNA isolation, amplification, and sequencing:** We gathered a dataset comprising 78
135 tissue samples, some of them dating back to 1910. The tissue samples encompassed heart, liver,

136 claws, and wing snippets. Mitochondrial DNA sequencing was achieved using a genome skimming
137 procedure following [Camacho et al. \(2022\)](#). Laboratory procedures were carried out at the NGS
138 Core Facility of the Bernhard Nocht Institute for Tropical Medicine in Hamburg. The extraction
139 and amplification of archival DNA were performed in a dedicated clean room facility, which was
140 separate from the area where current samples and post-PCR products were handled. Stringent
141 contamination prevention protocols and negative controls were also implemented.

142

143 The DNA extraction process for various sample types (dried skin, ethanol, or formaldehyde-
144 preserved tissues) involved proteinase K digestion at 55°C using 20 µl of proteinase K and 220 µl
145 of ATL lysis buffer (MinElute Reaction Cleanup kit, Qiagen). Prior digestion, the samples were
146 thoroughly washed with nuclease-free water (Qiagen). The incubation time for proteinase K
147 digestion varied depending on the tissue type and sample preservation, ranging from 5 to 24
148 hours. Following digestion, DNA was extracted and purified using the Qiagen MinElute kit, with
149 each sample eluted to a final volume of 60 µl. DNA concentration was measured using Qubit and
150 Bioanalyzer instruments. For library preparation, the QIAseq FX DNA Library Kit (Qiagen) was
151 used, with double index barcode labelling according to the manufacturer's instructions. DNA
152 fragmentation was often avoided due to the high degradation of nucleic acid material and low
153 concentration. The HiFi PCR Master Mix from the QIAseq FX kit was utilized to amplify DNA
154 regions with varying GC contents, minimizing sequencing bias caused by PCR, such as nucleotide
155 misincorporations from cytosine deamination. Subsequently, the libraries underwent quality
156 control to determine fragment size using the Agilent 2100 Bioanalyzer, and concentration was
157 assessed using a Qubit 2.0 Fluorometer. After normalization, the samples and negative controls
158 were pooled and subjected to sequencing on the NextSeq 2000 platform (2 × 100 cycles) (Illumina,
159 San Diego, CA, USA).

160

161 **Mitogenomes assembly and annotations:** Raw reads were first subjected to a qualitative
162 assessment, followed by the removal of adaptor sequences and the filtration of polyclonal and

163 low-quality reads (<55 bases long) using CLC Workbench (Qiagen). Overlapping paired-end (PE)
164 reads were merged to improve quality, while non-overlapping pairs and orphan reads were left
165 unchanged. Deduplication was performed with an assumed 100% identity using BBTools
166 ([Bushnell 2014](#)), expanding the length of contigs produced during de novo assembly. Custom
167 assembly was conducted using Megahit ([Li et al. 2016](#)) and Spades ([Prjibelski et al. 2020](#))
168 applications. A specialized Chiroptera mitochondrial database and BLASTN were employed to
169 identify potential bat mitochondrial genomes in the resulting contigs. This process was followed
170 by remapping and visual validation of circularization using CLC Genomics Workbench 22. Finally,
171 the GeSeq online tool ([Tillich et al. 2017](#)) was used to annotate genomic features. All the
172 assembled mitochondrial genomes were annotated using the MITOS2 metazoan pipeline ([Bernt](#)
173 [et al. 2013](#); [Al Arab et al. 2017](#)), followed by manual adjustment in Geneious v.9.0.5
174 (<https://www.geneious.com>). The mitochondrial DNA sequences obtained in this study have
175 been deposited in GenBank (Appendix 1).

176 **Phylogenetic analysis:** Ribosomal RNA (rRNA) and transfer RNA (tRNA) loci were aligned using
177 MUSCLE ([Edgar 2004](#)), while protein-coding genes sequences were aligned using TranslatorX
178 ([Abascal et al. 2010](#)). As outgroups, we selected sequences from *Phyllostomus hastatus*,
179 *Macrophyllum macrophyllum*, and *Phylloderma stenops*, shown as closely related in previous
180 phylogenetic studies ([Botero-Castro et al. 2018](#); [Camacho et al. 2022](#)). We used the optimal
181 partitioning scheme of 38 partitions (2 independent partitions for rRNAs and 36 partitions for
182 tRNAs, one partition for each codon for each gene) and a Generalized Time Reversible (GTR)
183 model of substitution rates along with a gamma (G) distribution and a fraction of invariable (I)
184 sites (GTR+G+I).

185
186 We performed a Maximum Likelihood (ML) analysis using RAxML-NG ([Kozlov et al. 2019](#)),
187 starting from 10 parsimony trees and 10 random trees. Bootstrap support values were obtained
188 using the classical Felsenstein metric ([Felsenstein 1985](#)) and transfer bootstrap expectation
189 ([Lemoine et al. 2018](#)). Bayesian inference (BI) analyses were performed using MrBayes v.3.2.7

190 ([Ronquist et al. 2012](#)). We partitioned the sequences in 38 sets corresponding to 2 independent
191 partitions for rRNAs and for tRNAs plus 36 partitions, one partition for each codon for each gene,
192 and used the best analytical scheme as evaluated by the AIC. We ran 8 Markov chain Monte Carlo
193 (MCMC) chains for 10 million generations, with default heating values. The sampling frequency
194 was set every 1000 generations, and the first 25 000 samples were discarded as burn-in. A
195 consensus tree was built under the majority rule consensus of all trees obtained in the 8 runs after
196 the burn-in period. We used the ‘sumt’ command to produce summary statistics for trees sampled
197 during a Bayesian MCMC analysis. Posterior probabilities of nodes were regarded as estimators
198 of confidence. Trees were visualized and edited in FigTree v.1.4.4
199 (<http://tree.bio.ed.ac.uk/software/figtree/>). We adopted the nodal support criteria established
200 by [Moratelli et al. \(2017\)](#): in the ML analysis, robust support is considered when bootstrap values
201 exceed or equal to 75%, while support is deemed moderate when values range from 50% to 75%.
202 Values equal to or below 50% are indicative of negligible support in our analyses. We calculated
203 uncorrected pairwise (*p*) distances within and among samples of *Trachops cirrhosus* using MEGA
204 11 ([Stecher et al. 2020](#); [Tamura et al. 2021](#)).

205
206 **Morphological and morphometric analyses:** A total of 27 measurements were taken. Among
207 these, 9 cranial measurements and 4 external measurements were selected for statistical analyses,
208 as indicated by asterisks (*) below; the remaining measurements were employed for descriptive
209 purposes:

210
211 *Calcar length (CL):* From the joint with the ankle to the calcar tip.
212 *Ear length (E):* Intertragic notch of the ear to the outer tip
213 **Forearm length (FA):* Distance from the elbow (tip of the olecranon process) to the wrist
214 (including the carpal). This measurement is taken with partially folded wings.
215 *Hindfoot length (HF):* Distance from the ankle to the tip of the claw.

- 216 **Metacarpal III (MET-III)*: Distance from the joint of the wrist (carpal bones) with the 3rd
217 metacarpal to the metacarpophalangeal joint of 3rd digit.
- 218 **Metacarpal IV (MET-IV)*: Distance from the joint of the wrist (carpal bones) with the 4th
219 metacarpal to the metacarpophalangeal joint of 4th digit.
- 220 **Metacarpal V (MET-V)*: Distance from the joint of the wrist (carpal bones) with the 5th metacarpal
221 to the metacarpophalangeal joint of 5th digit.
- 222 *Tail length (T)*: Distance from dorsal flexure at base of the tail to the tip of the last caudal vertebra.
- 223 *Tibia length (TiL)*: Length from the proximal end of the tibia to the distal base of the calcar.
- 224 *Total length (TL)*: Head and body length excluding tail.
- 225 *Weight (W)*: Mass in grams.
- 226 *Braincase height (BCH)*: Height of the braincase, posterior to the auditory bullae from the
227 basioccipital to the sagittal crest.
- 228 **Breadth across upper molars (M2-M2)*: Greatest width of palate across labial margins of the alveoli
229 of M2s.
- 230 **Breadth of brain case (BB)*: Greatest breadth of the globular part of the braincase, excluding
231 mastoid and paraoccipital processes.
- 232 *Condylarcanine length (CCL)*: Distance from the occipital condyles to the anterior border of the of
233 the upper canines.
- 234 **Condyloincisor length (CIL)*: Distance between a line connecting the posteriormost margins of
235 the occipital condyles and the anteriormost point on the upper incisors.
- 236 *Coronoid height (COH)*: Perpendicular height from the ventral margin of mandible to the tip of
237 coronoid process.
- 238 *Dentary length (DENL)*: Distance from midpoint of condyle to the anteriormost point of the
239 dentary.
- 240 **Greatest length of skull (GLS)*: Greatest distance from the occiput to the anteriormost point on the
241 premaxilla (including the incisors).

242 *Mandibular toothrow length (MANDL)*: Distance from the anteriormost surface of the lower canine
243 to the posteriormost surface of m3.

244 **Mastoid (process) breadth (MPW)*: Greatest breadth across skull, including mastoid processes.

245 *Maxillary toothrow (MTRL)*: Distance from the anteriormost surface of the upper canine to the
246 posteriormost surface of the crown of M3.

247 **Molariform toothrow (MLTRL)*: Distance from the anteriormost surface of P3 to the
248 posteriormost surface of the crown of M3.

249 **Palatal width at canines (C-C)*: Distance between the outermost extremities of the cinguli of upper
250 canines.

251 *Palatal length (PL)*: Distance from the posterior palatal notch to the anteriormost border of the
252 incisive alveoli.

253 **Post orbital constriction breadth (PB)*: Least breadth at the postorbital constriction.

254 **Zygomatic breadth (ZB)*: Greatest breadth across the zygomatic arches.

255

256 External and osteological characteristics were based on, but not limited to the guidelines
257 proposed by [Velazco \(2005\)](#), [Tavares et al. \(2014\)](#), [Molinari et al. \(2017\)](#), and [Garbino et al. \(2020\)](#).

258 Dental nomenclature follows [Miller \(1907\)](#), [Freeman \(1998\)](#), [Garbino and Tavares \(2018\)](#), and
259 [Garbino et al. \(2020\)](#). Skull, dentition, and external characters were measured with digital calipers

260 (to the nearest 0.01 mm). Total length, tail, hindfoot, ear, and body mass were recorded from skin
261 labels and were only used for descriptive assessments (mean, range, and standard deviation).

262

263 We log-transformed the variables and ensuring normality via Kolmogorov-Smirnov tests ([Sokal
264 and Rohlf 1995](#)); then we performed two Analyses of Variances (ANOVAs) with the 13
265 morphological variables to determine sex-based differences within subspecies. With no
266 significant differences found (all $p < 0.05$), we combined data from males and females for further
267 analysis. We used Principal Component Analysis (PCA) as a unified statistical approach to
268 investigate morphological variation in *Trachops cirrhosus*, applying it in two distinct contexts:

269

270 (1) Morphological Variation Among Subspecies: To assess the morphometric divergence among
271 recognized *Trachops* subspecies, we first applied the PCA focusing on taxonomic identification
272 and current distribution ranges. This involved summarizing key characteristics of the dataset to
273 interpret complex relationships and trends in morphological traits ([Sokal and Rohlf 1995](#)).
274 Subsequently, PCA scores were subjected to a multivariate analysis of variance (MANOVA) and
275 Post-hoc multiple comparisons (Holm-Bonferroni correction) to detect significant morphometric
276 differences among subspecies ([Rice 1989](#); [Irschick and Shaffer 1997](#)).

277

278 (2) Geographic Variation Analysis: The second application of PCA was directed towards
279 understanding geographic variation patterns. Here, the same PCA was employed, but with the
280 variable being a more specific geographic distribution area, rather than country boundaries.
281 Geographic areas were established as follows, based on [Molinari et al \(2023\)](#):

282

- 283 • **CAm - Central America**, from Mexico to Panama, delimited by the Atrato-San Juan
284 Depression to the south, in Colombia.
- 285 • **WSAm - West South America**, defined as the western slopes of the northern Andes,
286 including the Colombian Western Cordillera, the Central Colombian Cordillera, and the
287 Pacific coasts of Colombia, Ecuador, and Peru, to the Central Andes, delimited by the
288 Atrato-San Juan Depression to the north and the Southern Andes to the south.
- 289 • **ESAm - East South America**, demarcated as the upper forested slopes on the eastern side
290 of the Andes and the low Amazon of Colombia, Ecuador, Peru, and Bolivia; the entire
291 Amazon drainage of Brazil, including northeastern Bolivia, and the Orinoco drainages of
292 Colombia and Venezuela.
- 293 • **NEC/NWV**, NE Colombia and NW Venezuela, comprising the Orinoco llanos and Andean
294 piedmont plus the Venezuelan Coast range, including the Guajira peninsula and the
295 Maracaibo depression ([Ferrer-Pérez et al. 2009](#)).

- 296 • **GS - the Guyana Shield**, including the Venezuelan states of Bolívar and Amazonas, and a
297 portion of Delta Amacuro, the entire territories of Guyana, Surinam, and French Guyana,
298 and parts of northern Brazil.
299 • **AF - Atlantic Forest**, confined to the southernmost eastern region of Brazil, including the
300 Mata Atlántica ecosystem.

301

302 **Results**

303

304 **Specimens, tissue samples, and biorepositories:** Altogether, we measured 238 specimens of
305 *Trachops cirrhosus* from all named subspecies (i.e., 202 *T. c. cirrhosus*, 31 *T. c. coffini*, and 5 *T. c.*
306 *ehrhardti*), sourced from 7 scientific collections (Supplementary Table 1). Additionally, out of the
307 78 tissue samples, we successfully sequenced a total of 54 complete mitochondrial genomes (i.e.,
308 47 *T. c. cirrhosus*; 5 *T. c. coffini*; 2 *T. c. ehrhardti*; Supplementary Table 1, Appendix 1). The
309 remaining 24 individuals that could not be sequenced corresponded, mostly, to samples of ancient
310 tissues preserved in formalin. 22 specimens were both measured and sequenced. To analyze
311 geographic data, we used 173 unique collection locations, duly documented (Figure 2).

312

313 **Phylogenetic analysis:** Monophyly of *Trachops* was recovered with strong support from both the
314 ML analysis (bootstrap support [BS] = 100%), and from the Bayesian analysis (Bayesian posterior
315 probability [BPP] = 1). There is broad agreement between analysis methods (ML and BI) for this
316 dataset. We found two well-supported and genetically distant clades: one containing the
317 subspecies *T. c. coffini*, nested within *T. c. cirrhosus* (Clade 1; Figure 3) while the other contained
318 the subspecies *T. c. ehrhardti* (Clade 2, Figure 3).

319

320 In Clade 1 we recovered 2 clear phylogroups: Phylogroup A comprising samples from Mexico,
321 Guatemala, Honduras, Panama, western and northeastern Colombia, and northwestern
322 Venezuela, and western Ecuador. According to the geographical groups analyzed in the

323 morphometric analyzes (see Methodology and following section of Results), all these sequences
324 correspond to the geographic groups CAm (Central America), WSAm (West South America) and
325 NEC/NWV (NE Colombia and NW Venezuela), except for one sequence from Bolivia (FMNH
326 114877), which in the ML topology appears nested with individuals from western Ecuador. Within
327 this phylogroup, there is a sequence from the province of El Petén, Guatemala, which is located 93
328 km away from the type locality of *T. c. coffini* (Guyo, Petén, Guatemala). The subspecies do not
329 align with geographically distinct monophyletic groups, and furthermore, they do not match the
330 geographical distributions historically associated with *T. c. cirrhosus* and *T. c. coffini* subspecies.
331 Mean pairwise uncorrected sequence distances between what has been named as *T. c. cirrhosus*
332 and *T. c. coffini* is 5.6% (Table 1), which is not different from the computed intraspecific
333 divergence values of 5.5% in *T. cirrhosus* (Table 2).

334

335 We have identified a sister clade to Phylogroup A that we named as B (Figure 3), comprising
336 individuals from Eastern Ecuador and Eastern Venezuela (Orinoco Basin), corresponding to the
337 geographical group ESAm (East South America), as identified in our morphometric analyses.
338 Besides these two strongly supported phylogroups, no further distinct phylogenetic relationships
339 were found within Clade 1, although there is a noticeable clustering of samples from the
340 northeastern region of South America, corresponding to the Guyana Shield.

341

342 According to the concordant phylogenies of ML and BI analyses, Clade 2 forms a monophyletic
343 clade containing specimens from the southeastern region of São Paulo, in Brazil, which is
344 geographically close to the state of Santa Catarina (type locality of *T. c. ehrhardti*). According to
345 the geographical groups analyzed in the morphometric analyses (see Methodology and the
346 following Results section), these sequences correspond to the geographic group AF (Atlantic
347 Forest; Figure 3).

348

349 **Morphologic and morphometric variation**

350 Our examination of the *Trachops* subspecies highlights the morphological congruence,
351 particularly in qualitative traits, between *T. c. cirrhosus* and *T. c. coffini*, contrasting with the
352 distinct morphology of *T. c. ehrhardti*. Our scrutiny failed to discern marked morphological
353 divergences between *T. c. cirrhosus* and *T. c. coffini*, challenging their current classification as
354 distinct entities. The attributes previously considered distinctive, such as skull shape, rostrum
355 morphology, dimensions of premolars and molars, and mandible features, displayed uniformity
356 across these two subspecies in our geographical sampling (Figure 4). Table 3, illustrating variable
357 ranges among the *Trachops* subspecies, suggests a considerable overlap, rendering these
358 variables ineffective as discrete discriminators among the 3 subspecies.

359

360 In the Principal Component Analysis (PCA), two principal components cumulatively accounted for
361 73% of the total variance in our log-transformed dataset (Table 4). The PCA plot (Figure 5) reveals
362 substantial overlap in the 2D morpho-space among the subspecies, attributed to their size and
363 shape congruities. Notably, *T. c. cirrhosus* is positioned towards the right on PC1, indicating its
364 relatively larger size compared to *T. c. coffini*, which is leaned towards the left. However, this
365 positioning does not demarcate distinct groupings. PC1 predominantly shows size variations,
366 influenced by skull length metrics such as Condyle-Incisor Length (CIL), Greatest Length of Skull
367 (GLS), Maxillary Palatal Width (MPW), and Maxillary Toothrow Length (MTRL), each with factor
368 loadings exceeding 0.8. Conversely, PC2 appears to reflect shape variations, primarily influenced
369 by Palatal Breadth (PB).

370

371 Despite the apparent overlap in morpho-space depicted in Figure 5, our multivariate analysis of
372 variance (MANOVA), employing Pillai's Trace test, identified statistically significant differences
373 among the subspecies on both PC1 and PC2 ($F = 16.373, p < 0.01$). Further post-hoc multiple
374 comparison analyses delineated a statistical distinction between *T. c. cirrhosus* and *T. c. coffini* in
375 terms of size on PC1 ($p < 0.01$), but not between *T. c. cirrhosus* and *T. c. ehrhardti* ($p > 0.05$).
376 Moreover, no statistical differences were noted between *T. c. coffini* and *T. c. ehrhardti* ($p > 0.05$).

377 These statistical disparities might be influenced by the limited sample size for *T. c. ehrhardti*,
378 which does not sufficiently echo in morphological differentiation. The observed statistical
379 differences, particularly between *T. c. cirrhosus* and *T. c. coffini*, are evident in the context of size,
380 as indicated by PC1. However, the overarching morphological congruence, especially considering
381 the overlap in the PCA plot, suggests that these subspecies, despite some statistical variance, share
382 a degree of morphological commonality.

383

384 **Geographic variation**

385 There is a noteworthy overlap in the 2D morpho-space between the geographic-based groups
386 (Figure 6). The multivariate analysis of variance suggested there are differences between the
387 geographic groups on PC1 and PC2, as suggested by Pillai's Trace test ($F = 17.629, P < 0.01$). Post-
388 hoc multiple comparison analyses unveiled variation in size (PC1) among the samples.
389 Specifically, there was a size difference between the samples from Central America (CAm)
390 compared to those from East South America (ESAm), the Guyana Shield (GS), and North South
391 America (NEC/NWV), but not when compared to the West South American (WSAm) samples. The
392 plot illustrates that both CAm and WSAm samples cluster to the left along PC1, denoting their
393 smaller size, but they do not end up forming a separate cluster. Conversely, the Atlantic Forest
394 (AF) specimens were notably smaller in size compared to Guyana Shield (GS) samples, though not
395 significantly different from the rest of the regions. In fact, the GS sample exhibited the largest size
396 relative to all other groupings. Notably, NEC/NWV specimens did not display a clear grouping
397 pattern. Regarding the PC2, AF specimens exhibited notable differences, particularly in variables
398 such as palate width, in comparison to ESAm specimens. Additionally, a highly significant
399 difference was observed between CAm and ESAm specimens.

400

401 Both qualitative and quantitative assessments reveal a noticeable degree of morphological and
402 genetic similarity between the traditionally recognized subspecies *T. c. cirrhosus* and *T. c. coffini*.
403 Moreover, our geographical analysis reveals that the distribution of morphological variation

404 among different regions does not align with the historical classification of subspecies. These
405 findings strongly support their consideration as part of the same taxonomic group. Additionally,
406 our investigation provides definitive evidence for elevating *T. c. ehrhardti* to the status of a distinct
407 species, due to significant genetic and morphological disparities observed in specimens from the
408 southeastern region of Brazil.

409

410 **Discussion**

411

412 Our investigation of *Trachops*, which integrates data from morphology, morphometrics, and
413 molecular analysis encompassing almost the totality of its distribution range, has provided
414 clarification into the taxonomic status of the species. Our main findings include the recognition of
415 specific status of *T. ehrhardti*, and *T. c. coffini* as a junior synonym of *T. cirrhosus*. Incorporating *T.*
416 *cirrhosus* specimens from Colombia, Ecuador, and Peru was crucial to our classification, as it
417 represented the first taxonomic exploration of the species in the West South American region. We
418 not only expanded the geographical scope of the analysis, but also shed light on previously
419 unexplored genetic and morphological variations within *T. cirrhosus* populations.

420

421 ***Trachops* in phylogenetic context**

422

423 The mitochondrial DNA (mtDNA) diversity in *Trachops cirrhosus* is significant, as evidenced by
424 three previous studies. Using 10 partial sequences of the mitochondrial gene Cytb from localities
425 such as Guatemala, Panama, French Guyana, and Brazil, [Ditchfield \(1996\)](#) identified 5 clades.
426 These findings suggested that current subspecies classifications may underestimate haplotypic
427 diversity, indicating that *Trachops* should be considered a complex. In this topology, *T. c. coffini* is
428 not monophyletic as opposed to *T. c. cirrhosus*, and the author attributed this haplotypic diversity
429 to reduced mobility or increased philopatry in *Trachops* across its geographic range, though these
430 hypotheses remain unconfirmed ([Ditchfield 1996](#)).

431

432 Later, [Claire \(2011\)](#) investigated pattern congruence between two independently evolving genetic
433 regions (mitochondrial genome and Y chromosome), finding significant mitochondrial haplotypic
434 divergence, but not in the Dby 7th intron region. Despite using more samples than [Ditchfield](#)
435 ([1996](#)), the author did not include specimens from West South America. In this topology, *T. c.*
436 *coffini* was once again not a monophyletic clade distinct from *T. c. cirrhosus*, lacking geographical
437 congruence to support its separation as a subspecies.

438

439 Finally, [Fonseca \(2019\)](#) proposed a more integrative approach with a greater number of
440 sequences using a dataset composed of 2341 bp of Cyt-b, COI, D-loop and STAT5A from 129
441 tissues. Samples from western South America, particularly Colombia, Ecuador, and Peru, were not
442 included in this study. In consistency with [Clare et al. \(2011\)](#), the ML phylogeny did not render *T.*
443 *c. coffini* as an independent clade of *T. c. cirrhosus*, with little genetic differentiation ([Fonseca](#)
444 ([2019](#))). The author proposed that *Trachops* should be divided into two lineages recognized at the
445 species level: *Trachops ehrhardti*, monotypic, and *T. cirrhosus*, with two subspecies (*T. c. cirrhosus*
446 and *T. c. coffini*). However, the phylogenetic justification for maintaining *coffini* as a subspecies
447 and its distribution was unclear.

448

449 In this study, we included an extensive taxon sampling with new localities from Colombia,
450 Ecuador, and Peru, as well as information from complete mitochondrial genomes. Our findings
451 revealed two reciprocally monophyletic clades, each exhibiting significant genetic divergence. The
452 first clade, *T. cirrhosus*, notably includes sequences from northern Central America (*T. c. coffini*).
453 This challenges the classical notion of *T. c. coffini* as a distinct subspecies, suggesting instead a
454 more cohesive genetic identity within the *T. cirrhosus* clade. The second clade, *T. ehrhardti*, stands
455 as a monophyletic group, sister to *T. cirrhosus*. These results prompt a reconsideration of
456 *Trachops'* taxonomic structure, particularly the delineation of *T. ehrhardti* and *T. cirrhosus*, and
457 the subspecies status of *T. c. coffini* within this framework.

458

459 **Trachops in the morphometric context**

460

461 When *T. coffini* was described as a separate species by [Goldman \(1925\)](#), he reported larger
462 measurements for *T. cirrhosus*. The author revised 18 specimens from the type locality of *T. coffini*
463 with others from Venezuela, Colombia, and Panama, assuming that they represented typical *T.*
464 *cirrhosus*, without specifying quantity or localities. However, his analysis, based on a limited
465 geographical range and a small sample size, raised questions about the robustness of these early
466 findings. [Felten \(1956a\)](#) and [Felten \(1956b\)](#) revisited this classification, incorporating a broader
467 geographic range, including Central America. His work, which suggested classifying the Central
468 American forms as *T. c. coffini* subspecies, highlighted the potential intraspecific variation within
469 the species. However, Felten's conclusions, particularly regarding the dental morphology and size
470 differences, were largely inferential, lacking quantitative rigor. The author proposed maintaining
471 the two subspecies and added *T. c. ehrhardti* as a subspecies, based on 3 specimens from
472 southeastern Brazil, with no apparent difference other than the smaller size, in relation to samples
473 from Colombia, recorded by [Hershkovitz \(1949\)](#), but similar in size to the samples from El
474 Salvador ([Felten 1956a](#)).

475

476 No other significant morphological study of *Trachops* was published until six decades later, when
477 [Fonseca \(2019\)](#) revised specimens mostly from localities in Brazil. The quantitative analysis
478 revealed a substantial overlap in the morphometric space across the three subspecies studied,
479 notably between *T. c. cirrhosus* and *T. c. coffini*, challenging the notion of distinct morphometric
480 differentiation between these subspecies. This finding was an indicative of a morphometric
481 continuum rather than discrete categories. Qualitatively, she observed that *T. c. coffini*, exhibited
482 a pronounced angle between the rostrum and the braincase in lateral view, a characteristic less
483 evident in *T. c. cirrhosus*. In dental morphology, [Fonseca \(2019\)](#) noted that the first lower
484 premolar (p1) in *T. c. coffini* possesses a unique shape, distinct to this subspecies, although the

485 specifics of this form were not delineated. Additionally, she reported that the m1 tooth in *T. c.*
486 *coffini* demonstrates a more developed paraconid, compared to *T. c. cirrhosus*. The potential
487 displacement of p3 to the labial surface in *T. c. coffini*, as opposed to the lingual surface in *T. c.*
488 *cirrhosus*, suggests further morphological variability. Notably, [Fonseca \(2019\)](#) noted that the
489 specimens from Costa Rica displayed morphological traits and cranial sizes more akin to *T. c.*
490 *coffini*, diverging from the expected distribution patterns. Furthermore, the individuals from
491 Panama exhibited traits from both *T. c. coffini* and *T. c. cirrhosus* in equal frequencies. This
492 observation led Fonseca to propose a clinal variation in size across the species' range, with smaller
493 individuals observed in Central America and larger ones in South America, positioning Panama as
494 a zone of intergradation.

495

496 In our study, encompassing specimens from the western region of the Andes and northern South
497 America, we did not observe the diagnostic characters reported by [Fonseca \(2019\)](#). Specifically,
498 our samples from Central America did not exhibit the morphological differences between the
499 northern and southern regions as previously proposed. This discrepancy, particularly regarding
500 the distinct cranial angles in *T. c. coffini* and the unique shape of p1, suggests a less complex
501 morphological variability within the *Trachops* genus. Even though the Principal Component
502 Analysis (PCA) revealed a size variation on PC1, predominantly influenced by skull length metrics,
503 the PCA plot depicted considerable overlap in morpho-space, indicating a high degree of
504 morphological congruence. This overlap challenges the current subspecies classification based on
505 size and shape traits. Contrary to the proposed latitudinal cline in size, our data indicate that the
506 specimens from the western South America (WSAm), encompassing the Pacific regions of
507 Colombia and Ecuador, and NEC/NWV are similar in size to those from Central America. This
508 finding is consistent with zoogeographical studies that have identified a closer affinity between
509 the bat fauna of the western Andes and Central America [Koopman \(1976\); \(1978\); \(1982\)](#);
510 [Hoffmann and Baker \(2003\); Clare \(2011\)](#). Such patterns suggest the influence of historical
511 events, ecological processes, and landscape heterogeneity ([Manel et al. 2003](#)) in shaping the

512 distribution and morphology of bat species, including *Trachops*. The role of heterogeneity of
513 habitats and environmental conditions as causes of morphological and genetic divergence
514 ([Turmelle et al. 2011](#); [Lindsey and Ammerman 2016](#)) is also evident in our findings.

515

516 **On the subspecific status of *Trachops cirrhosus coffini***

517

518 Despite previous assertions, notably by [Fonseca \(2019\)](#), our findings indicate that *T. c. cirrhosus*
519 and *T. c. coffini* lack distinct morphological synapomorphies and do not exhibit reciprocal
520 monophyly, as required for subspecies designation. This observation aligns with the criteria
521 outlined by [Patten \(2015\)](#), who mentions that a subspecies should be morphologically distinct
522 and geographically circumscribed, yet not necessarily forming a distinct genetic clade. According
523 to [Molinari \(2023\)](#), subspecies designation is appropriate for populations with significant and
524 heritable morphological differences, even if genetic differentiation is insufficient for species-level
525 recognition. Our analyses, however, reveal that the morphological distinctions traditionally used
526 to separate *T. c. coffini* and *T. c. cirrhosus* do not meet these standards. The lack of clear
527 geographical circumscription, combined with our findings that these groups are not
528 morphologically diagnosable nor genetically distinct, challenges the validity of their current
529 subspecific status.

530

531 The reliance on size-only differences is contentious. [Molinari \(2023\)](#) underscores that diagnostic
532 morphological characters should not be attributed to phenotypic plasticity. Considering studies
533 indicating size variation as a source of morphological plasticity in bats ([McLellan 1984](#); [Jarrín-V](#)
534 [et al. 2010](#); [Jarrín-V. & Menéndez-Guerrero 2011](#); [López-Aguirre et al. 2015](#)), the use of body size
535 as a sole criterion for taxonomic decisions becomes problematic. Geographic variation in body
536 size, influenced by a multitude of factors, including genetic adaptations and environmental
537 conditions affecting growth rates, further complicates its reliability as a distinguishing feature
538 ([McLellan 1984](#); [Berry et al. 1987](#); [Ebenhard 1990](#); [Jarrín-V et al. 2010](#); [Jarrín-V. & Menéndez-](#)

539 [Guerrero 2011](#); [López-Aguirre et al. 2015](#)). Additionally, methodological inconsistencies,
540 including instrumental and human errors, can lead to data discrepancies ([Fox et al. 2020](#)), casting
541 doubt on the robustness of size-based differentiation. Our study, therefore, suggests that the
542 current classification of *T. c. coffini* as a subspecies of *Trachops cirrhosus* lacks support, both
543 morphologically and genetically.

544

545 **On the specific status of *T. ehrhardti***

546

547 *Trachops ehrhardti* should be elevated to the species status based on the presence of clear
548 diagnosable morphological characters, geographically circumscription in the Atlantic forests of
549 South Brazil (Mata Atlântica), and substantial molecular divergence. Broader cranial
550 measurements (BB, MPW, ZB) allow *T. cirrhosus* to be separated from *T. ehrhardti* and both
551 species form reciprocally monophyletic clades separated by a genetic divergence of over 8%. It is
552 its geographic isolation that would primarily imply loss of ecological exchangeability, and possibly
553 mating impediments with *Trachops cirrhosus*. Originally proposed by [Haffer \(1969\)](#), the Refuge
554 Theory for the Neotropics suggests that the Pleistocene glaciation cycles created contraction and
555 subsequent expansion of forested areas that, in turn, would create allopatry between populations
556 of the same forest-dwelling species, leading to intraspecific differentiation and consequently
557 speciation. Paleopalynological research indicates the high dynamism of Neotropical forested
558 regions: the Atlantic Forest and the Amazon were connected in the past ([Vivo 1997](#)), separating
559 themselves as increasing aridity in the Tertiary triggered the formation of the belt of xeromorphic
560 formations between them ([Martins et al. 2009](#)). There seemed to be a predominantly arboreal
561 vegetation during most of the Pleistocene, with typical Amazonia and Atlantic Forest tree species
562 found in what it is now the dry diagonal that separates these two biomes. The extent to which
563 these climatic fluctuations and associated vegetation changes affected the patterns of distribution
564 and diversification of the fauna remains a central question in understanding the evolution of
565 forest-associated taxa.

566

567 **Implications to conservation**

568

569 Recognized bat diversity has increased due to new species descriptions and taxa raised from
570 subspecific level or synonymy ([Burgin et al. 2018](#)), but also as a result of clarification of cryptic
571 species within several genera (e.g. *Platyrrhinus* ([Velazco et al. 2023](#)); *Glossophaga* ([Calahorra-](#)
572 [Oliart et al. 2021](#)) or *Sturnira* ([Yáñez-Fernández et al. 2023](#)). These changes in taxonomy may have
573 an impact on the conservation of species. The genus *Trachops* is composed of two monotypic
574 species: *Trachops cirrhosus* maintains its “Least Concern” conservation status at the global level,
575 with no major threats known throughout its range ([Miller et al. 2015](#)). However, it is important to
576 revise the status of *Trachops ehrhardti*. The current range of *T. ehrhardti* is restricted to
577 southeastern Brazil. The Atlantic Forest is one of the world's leading biodiversity 'hotspots'; these
578 areas possess the highest concentrations of species endemism, and simultaneously, are the most
579 severely threatened by habitat loss ([Baptista & Rudel 2006](#)). In this biome, the persistent land
580 cover is made up of 476 000 Km², which comprises 9% of the Brazil's land area ([Souza et al. 2020](#)),
581 but is highly fragmented by roads and urban centers, and immersed in a large agriculture matrix,
582 resulting in less than 12% of old secondary forest cover (i.e., >30 years) ([de Rezende et al. 2015](#);
583 [Souza et al. 2020](#)). If this scenario remains unchanged, then elevating *Trachops ehrhardti* to a
584 species should trigger immediate protection efforts in conservation.

585

586 We present a revised description of the genus *Trachops* and the subspecies *Trachops cirrhosus* and
587 *Trachops ehrhardti* below.

588

589 **Taxonomy**

590 The genus *Trachops* can be easily recognized by their highly specialized warty outgrowths or
591 protuberances on the lips and chin. The margin of the nose leaf is finely serrated on the edge,
592 anteriorly connected to the upper lip ([Spix 1823](#)). Ears are large and anteriorly covered with hairs

593 projecting beyond anterior margins ([Goldman 1925](#)); folds inside the pinnae are well marked. The
594 tail is short and appears on the upper side of a broad interfemoral membrane ([Goodwin and](#)
595 [Greenhall 1961](#)). The ventral fur is characterized by a pale brown coloration ([Spix 1823](#)). Dorsal
596 fur is cinnamon-brown, varying to darker shades in some specimens ([Goodwin and Greenhall](#)
597 [1961](#)). The base of the hairs is always white, and the tips are ashy. Underparts are dull brownish
598 tinged with grayish brown ([Goodwin and Greenhall 1961](#)).

599

600 ***Trachops cirrhosus* Gray, 1847**

601 *Vampyrus cirrhosus* Spix, 1823:64. No type locality is stated in Spix's description, but on
602 page 53 Spix said the bats were collected in Brazil. Type locality restricted to Para, Brazil,
603 by Husson (1962: 115).

604 *Phylllostoma]. cirrhosum*: Fischer, 1829:126. Name combination.

605 *Vampyris cirrhosum*: Gray, 1847:481. Emendation of *Vampyrus cirrhosus* Spix

606 *Trachops fuliginosus*: Gray, 1865:14. Type locality "Pernambuco," Brazil (= *Vampyrus*
607 *cirrhosus* Spix).

608 *Phyllostoma angusticeps* Gervais, 1856: 47. Type locality "province de Bahia, au Brasil."

609 *Tylostoma mexicana* Saussure, 1860 :484. Type locality "les régions chaudes du Mexique."

610 *Trachyops cirrhosus*: Dobson, 1878:481. First use of name combination and incorrect
611 subsequent spelling of *Trachops* Gray, 1847.

612 *Trachops coffini* Goldman, 1925:23. Type locality "Guyo, Petén, Guatemala." Type locality
613 restricted to "El Gallo, 8 mi. west Yaxhá, on the Remate-El Cayo trail, Petén, Guatemala" by
614 de la Torre (1956:189).

615 *Trachops cirrhosus coffini*: Felten, 1956a:189. Type locality restricted to Para, Brazil, by
616 Husson (1962: 115).

617

618 This species is monotypic.

619 **Amended distribution and habitat:** This species is widely distributed in eastern and southern
620 Mexico, extending from Veracruz, in the southeast, southeastward through Central America, into
621 South America, including Colombia, Venezuela, the Guyanas, Ecuador, northern and central Peru,
622 Bolivia, Trinidad, as well as northern, southern, and central Brazil (Figure 7). This species occurs
623 at elevations from sea level (e.g., Belem, Para, Brazil) up to 1800 m (Las Tolas, Pichincha, Ecuador;
624 [Arcos et al. 2007](#)). Records of *Trachops cirrhosus* are predominantly associated with habitats in
625 humid tropical forests, as well as sub-montane and montane forests.

626

627 **Emended diagnosis and comparison:** *Trachops cirrhosus* is a relatively robust ([Spix 1823](#)),
628 medium-size bat (FA: 49.57–64.70 mm; GLS 24.70–31.24 mm). Overall size is larger than *Trachops*
629 *ehrhardti* (Table 5). The skull is large and elongated. The elevated braincase above the rostrum
630 was previously believed to be a distinguishing characteristic, potentially separating the
631 subspecies *cirrhosus* and *coffini*. The latter was described as having a smaller and slenderer shape
632 compared to *T. c. cirrhosus*, although similar to *T. c. ehrhardti*. This characteristic is not diagnostic;
633 rather, it displays variability across the entire species distribution. The sagittal crest may or may
634 not be developed in males and females, contrary to the well-developed sagittal crest character
635 mentioned by [Goodwin and Greenhall \(1961\)](#). Poorly developed sagittal crest is common in most
636 specimens reviewed for the entire area of distribution. However, the faint notch in the cutting
637 edge of the upper incisors ([Goldman 1925](#)), is variable. Inferior premolar 1 (p1) is taller compared
638 to the same tooth in *T. c. ehrhardti* which is wider overall. The first lower premolar is three-fourths
639 the height of the third premolar but wider in cross-section ([Dobson 1878](#)). The mandible of *T.*
640 *cirrhosus* is broad and robust; upper and lower premolars are relatively narrower than in *T.*
641 *ehrhardti*. The dentary is tall and has a contracted premolar toothrow, and an expanded molar
642 toothrow, with the last molar being closer to the fulcrum, a high coronoid process, and an
643 expanded angular process (Figure 4).

644

645 **Remarks:** The character of m1 with a less developed paraconid in *T. c. cirrhosus* than in *T. coffini*
646 mentioned by [Dobson \(1878\)](#) was not evident as a diagnostic character.

647

648 **Natural history:** *Trachops cirrhosus* is a large-eared gleaning bat that hunts by listening for prey-
649 generated sounds ([Obrist et al. 1993](#)). It roosts in caves, hollow trees, road culverts, sewer
650 systems, and buildings, in groups of up to 50 individuals ([Hall and Dalquest 1963](#); [Fleming et al.](#)
651 [1972](#); [Alvarez-Castañeda and Álvarez 1991](#); [Kalko et al. 1999](#); [Halczok et al. 2018](#)). The relatively
652 sedentary foraging behavior of these gleaners is reflected in their wing morphology, a
653 characteristic that influences their use of small foraging areas and short commuting distances.
654 They have been observed to engage in two distinct flight patterns while foraging: long flights that
655 extend for several uninterrupted minutes and short sally flights lasting less than one minute
656 ([Cramer et al. 2001](#)). These bats possess relatively short and broad wings, an adaptation that
657 enhances their maneuverability, particularly in environments filled with obstacles ([Marinello &](#)
658 [Bernard 2014](#)). However, this wing morphology comes with a trade-off, as it makes continuous
659 flight over extended distances energetically costly ([Norberg & Rayner 1987](#); [Kalko et al. 1999](#)).
660 *Trachops cirrhosus* hunts for prey in continuous flight, presumably depending on prey availability.
661 Prey is usually taken from the substrate (gleaning mode) in a brief landing or may be caught
662 occasionally on the wing (aerial mode) ([Kalko et al. 1999](#)). *Trachops cirrhosus* is a carnivorous bat
663 that feeds on a wide variety of prey species, including insects, frogs, lizards, and other small
664 vertebrates ([Gardner 1977](#); [Pine and Anderson 1979](#); [Barclay et al. 1981](#); [Tuttle & Ryan 1981](#);
665 [Bonato and Facure 2000](#); [Bonato et al. 2004](#); [Giannini and Kalko 2005](#); [Page and Jones 2016](#)).
666 Additionally, it has been observed consuming fruits and seeds ([Whitaker & Findley 1980](#);
667 [Humphrey et al. 1983](#); [Cramer et al. 2001](#)). Foraging areas of 3 to 12 ha and commuting distances
668 between roost and foraging areas are < 2 km ([Kalko et al. 1999](#)). The emergence time and activity
669 peak of *T. cirrhosus* coincided with the maximum calling activity of the Tungara frogs,
670 Leptodactylidae, ([Tuttle & Ryan 1981](#); [Ryan et al. 1983](#)). The number and duration of long flights
671 reduce as the calling declines; giving way to an increased frequency of short flights, which might

672 also indicate a switch from frogs to other prey such as insects ([Belwood 1990](#); [Kalko et al. 1996](#),
673 [1999](#)). This bat is very flexible in its responses to prey calls by updating acoustic information with
674 echo acoustic and gustatory cues, as it approaches potential prey, enabling bats to avoid
675 potentially lethal mistakes ([Page and Jones 2016](#)). Captive studies show that cues can also be
676 learned socially and transmitted across individuals ([Jones et al. 2013](#); [Page and Jones 2016](#); [Flores](#)
677 [et al. 2020](#)).

678

679 Very little is known about the reproductive biology of *T. c. cirrhosus*. Females give birth to one
680 offspring at a time coinciding with the start of the rainy season ([Flores and Page 2017](#)), but the
681 gestation period length is unknown. Females of this species have been reported to be pregnant in
682 April to March and December ([Villa-R 1967](#); [Alvarez-Castañeda and Álvarez 1991](#)). In Brazil,
683 [Trajano \(1984\)](#) suggested a polyestrous reproductive pattern, with two annual birth peaks, one
684 before and the other after August. In Trinidad and Tobago, [Goodwin and Greenhall \(1961\)](#) found
685 a colony of *T. cirrhosus* composed of 6 individuals of both sexes, including pregnant females in
686 March ([Bredt et al. 1999](#)). The social structure of *T. cirrhosus* is still not fully understood, but a
687 recent six-year study in Panama showed evidence of female philopatry and preferred co-roosting
688 associations in both sexes; kin-biased associations were also detected among pairs of females but
689 not males ([Flores et al. 2020](#)).

690

691 During the mating season, reproductive males have enlarged testes and create an odorous
692 substance that is smeared on their forearm, called forearm crust. [Flores and Page \(2017\)](#) and
693 [Flores et al. \(2019\)](#) discovered that fringe-lipped males scratch their body with one hind claw,
694 including the area around a prominent mid-ventral chest gland, insert the same hind claw into the
695 mouth, and then repeatedly lick the forearm. Apparently, this substance is not related to female
696 preferences since two-thirds of females selected the scent of a male without forearm crust, but it
697 would play a fundamental role in male-male interactions ([Flores et al. 2019](#)).

698

699 *Trachops ehrhardti* Felten, 1956

700

701 *Trachops cirrhosus ehrhardti* Felten, 1956b:369. Type locality "Joinville, Sta. Catarina,
702 Brazil."

703

704 **Distribution and habitat:** Southeastern Brazil. Specimens are known from the humid
705 environments of the Atlantic Forest of the states of Santa Catarina, Parana, Sao Paolo, Mina Gerais,
706 Rio de Janeiro and Espiritu Santo (Figure 7).

707

708 Diagnosis: Medium-size bat (FA: 54–60 mm; GLS 26.90–27.70 mm). Smaller than *Trachops*

709 *cirrhosus* (Table 5). The ventral fur from the base of the hair shows a lighter shade of brown that

710 gradually transitions to an ashy color at the tips. Dorsal fur is characterized by a reddish-brown

711 to cinnamon-brown hue. The base of the hair appears whitish, creating a contrast with the slightly

712 ashy tone at the tips. Underparts are light brownish with a grayish tint. This coloration is

713 attributed to the presence of light-colored tips on the hairs, and there are white-tipped hairs

714 specifically found on the animal's underparts. The pinnae are hairy, with marked folds. Lips and

715 chin are ornamented with wart-like protuberances and ears are large and clothed with hairs

716 projecting conspicuously beyond anterior margins as in *Trachops cirrhosus* ([Goldman 1925](#)).

717 Skull is noticeably smaller in comparison to *T. cirrhosus*. Braincase is smaller, forming an angle

718 with a less pronounced rostrum than in *T. cirrhosus*, however, this character shows more degree

719 of variation. Sagittal crest is not developed. In the analyzed skulls, which belong to the type series,

720 it is observed that the lingual edges of the w-shaped stylar shelf are longer. The molar crowns are

721 relatively longer, and in the dorsal view, the parastyle, mesostyle, and metastyle of the second and

722 third upper molars are further away from the maxillary bone. The formed cusps are further apart

723 than in *T. cirrhosus*, giving them a broader appearance. These characters could be important to

724 identify individuals from the eastern areas of Brazil where there could be contact between *T.*

725 *cirrhosus* and *T. ehrhardti* (Figure 4).

726

727 **Natural history:** To the best of our knowledge, precise data on the natural history of this
728 population is currently lacking, although it is expected to share similarities with *T. cirrhosus*. This
729 species inhabits the Atlantic Forest, which encompasses both lowland and montane systems along
730 the Atlantic coast of southeastern Brazil, as well as the contiguous moist-subtropical forest of the
731 Parana basin ([Pavan et al. 2016](#)). Similar to *T. cirrhosus*, it is likely that they seek refuge in caves,
732 hollow trees, culverts, and buildings, often in small groups comprising a few tens of individuals.
733 The species might prey on insects, frogs, lizards, and other small vertebrates. Currently, no
734 information is available regarding their reproductive behavior.

735

736 **Remarks:** The species was described by [Felten \(1956b\)](#) based on 3 specimens collected in 1908
737 by W. Ehrhardt at Joinvile in the Brazilian state of Santa Catarina, considerably expanding the
738 southern limit of distribution of the species in South America. The only distinctive characteristic
739 of the subspecies mentioned by [Felten \(1956b\)](#) is its size, notably smaller in relation to animals
740 from the northern part of South America and similar in size to the former subspecies *T. c. coffini*.
741 In 2019, in a degree dissertation from the Federal University of Espírito Santo (see Fonseca,
742 unpublished data), it was proposed, based on an integrative approach to morphological,
743 ecological, and phylogenetic evidence, that *T. cirrhosus ehrhardti* should be elevated to the species
744 category; however, the species has not been formally described nor has the taxonomy been
745 validated.

746

747 **Comparisons:** The size and shape of the skull of the two species is similar, but in *Trachops*
748 *ehrhardti* it is smaller on average. In *T. cirrhosus*, the skull is larger and more elongated than in *T.*
749 *ehrhardti*, and the braincase is more elevated above the rostrum. However, this character shows
750 a degree of variation. *T. cirrhosus* presents a faint notch in the cutting edge of the upper incisors
751 while is broad, with an open groove leading to a distinct notch in the cutting edge in *T. ehrhardti*
752 ([Goldman 1925](#)), but this characteristic is also variable. The first lower premolar 1 (p1) in *T.*

753 *ehrhardti* is wider overall compared to the same teeth in *T. cirrhosus* which is taller than wider.
754 Molariforms toothrow in *T. cirrhosus* is longer than in *T. ehrhardti*, *Trachops cirrhosus* mandible is
755 broader and more robust than in *T. ehrhardti*. In *T. cirrhosus*, the dentary is tall and has a
756 contracted premolar toothrow, and an expanded molar toothrow, with the last molar being closer
757 to the fulcrum, a high coronoid process, and an expanded angular process. This could be
758 associated with a higher bite force ([Nogueira et al. 2009](#)). Regarding the width of the cranium, 3
759 measurements are broader in *cirrhosus* than *ehrhardti* (i.e. Breadth of brain case, Mastoid process
760 breadth, and Zygomatic breadth).

761

762

763 **Acknowledgments**

764 We extend our gratitude to the FSPI–Doctoral Schools Project of the French Embassy in Ecuador,
765 supported by the Ministry of Europe and Foreign Affairs. This work has greatly benefited from
766 the “Investissement d’Avenir” grants overseen by the Agence Nationale de la Recherche (CEBA,
767 ANR-10-LABX-25-01; TULIP, ANR-10-LABX-0041). We are thankful to Marisa Surovy (American
768 Museum of Natural History), Darrin Lunde (National Museum of Natural History), Nicolás Reyes-
769 Amaya (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt), Oscar E.
770 Murillo-García (Universidad del Valle), and Edith Montalvo (Museo de Historia Natural Gustavo
771 Orcés-V.) for providing access to invaluable specimens. We would also like to thank Adam
772 Ferguson and Bruce Paterson from the Field Museum of Natural History, Marie L. Campbell and
773 Joseph Cook from the Museum of Southwestern Biology, Jacqueline Miller and Burton Lim from
774 the Royal Ontario Museum, and Dr. Irina Ruf from the Senckenberg Naturmuseum Frankfurt for
775 their generosity in providing tissue samples. For their work on the mtDNA sequencing and
776 assembly, we express our profound thanks to Alexandra Bialonski and Marike Petersen from the
777 Bernhard Nocht Institute for Tropical Medicine. We also want to acknowledge Ruben D. Jarrín
778 from Pontificia Universidad Católica del Ecuador and Anika Vogel from the Senckenberg
779 Research Institute for their photographic contributions. Santiago F. Burneo deserves a special

780 mention for granting access to specimens under his care at QCAZ and his help with the maps
781 presented on this manuscript. Our sincere appreciation goes to Diego Tirira and the anonymous
782 reviewers whose insights and comments have significantly enhanced this manuscript.

783

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1231 **TABLES**

1232

1233 **Table 1.** Estimates of evolutionary divergence across sequence pairs between groups are
1234 presented. The number of base differences per site, calculated by averaging over all sequence
1235 pairs between groups, is depicted below the diagonal and scaled as percentages.

1236

	<i>T. c. cirrhosus</i>	<i>T. c. coffini</i>	<i>T. c. ehrhardti</i>	Outgroup
<i>T. c. cirrhosus</i>		0.0013	0.0018	0.0023
<i>T. c. coffini</i>	5.6%		0.0022	0.0025
<i>T. c. ehrhardti</i>	8.2%	8.6%		0.0025
Outgroup	17.7%	17.8%	17.8%	

1237

1238

1239 **Table 2.** Estimates of evolutionary divergence across sequence pairs within groups
1240 Standard error estimate(s) are shown in the second column and were obtained by a bootstrap
1241 procedure (1000 replicates).

1242

	Distance %	S.E. (%)
<i>T. c. cirrhosus</i>	5.5	0.0
<i>T. c. coffini</i>	1.9	0.0
<i>T. c. ehrhardti</i>	0.0	0.0
Outgroup	0.1	0.0

1243

1244
1245
1246**Table 3.** Measurements (mm) and body masses (g) of *Trachops c. cirrhosus*, *T. c. coffini*

and *T. c. ehrhardtii*. Descriptive measures: minimum–maximum; arithmetic mean (standard deviation).

Variable	<i>T. cirrhosus</i> <i>cirrhosus</i> (N = 202)	<i>T. cirrhosus coffini</i> (N = 31)	<i>T. cirrhosus</i> <i>ehrhartii</i> (N = 5)
Breadth of brain case (BB)	11.07–12.97; 11.60 (0.28)	10.33–12.03; 11.49 (0.26)	11.30–11.50; 11.40 (0.10)
Palatal width at canines (C-C)	5.72–6.85; 6.22 (0.21)	5.26–6.68; 5.98 (0.26)	5.4–5.80; 5.63 (0.21)
Condylarcanine length (CCL)	22.23–26.79; 25.01 (0.71)	20.93–26.12; 24.17 (0.86)	
Condyloincisive length (CIL)	23.30–27.95; 26.03 (0.69)	21.87–26.78; 25.10 (0.79)	23.90–24.50; 24.20 (0.30)
Coronoid height (COH)	4.97–6.80; 5.85 (0.30)	4.79–6.28; 5.42 (0.31)	
Dentary length (DENL)	17.41–20.48; 18.97 (0.60)	16.11–19.93; 18.15 (0.67)	
Greatest length of skull (GLS)	26.13–31.24; 29.21 (0.79)	24.70–30.02; 28.27 (0.88)	26.90–27.70; 27.20 (0.44)
Breadth across upper molars (M2-M2)	9.15–11.03; 10.14 (0.32)	8.34–10.86; 9.77 (0.38)	9.80
Mandibular toothrow length (MANDL)	10.71–12.40; 11.42 (0.34)	7.61–11.78; 10.92 (0.54)	
Molariform toothrow (MLTRL)	6.68–7.81; 7.22 (0.21)	6.07–7.67; 6.96 (0.26)	
Mastoid (process) breadth (MPW)	12.78–14.96; 13.70 (0.41)	11.40–14.31; 13.21 (0.46)	13–13.40; 13.20 (0.20)
Maxillary toothrow (MTRL)	9.50–11.33; 10.51 (0.32)	8.57–10.93; 10.11 (0.40)	9.60–10; 9.8 (0.20)
Post orbital constriction breadth (PB)	4.85–5.76; 5.34 (0.17)	4.66–5.71; 5.11 (0.18)	5
Palatal length (PL)	10.12–12.72; 11.40 (0.47)	8.92–12.42; 11.00 (0.52)	
Zygomatic breadth (ZB)	12.46–15.97; 14.53 (0.48)	12.06–15.70; 13.96 (0.58)	13.3–14.10; 13.77 (0.42)
Braincase height (BCH)	9.24–12.20; 10.84 (0.47)	9.39–12.25; 10.63 (0.42)	
Calcar length (CL)	9.19–18.21; 13.29 (1.52)	10.84–16.55; 13.64 (1.30)	11.62
Forearm length (FA)	53.36–64.70; 59.23 (2.25)	49.57–62.11; 57.88 (2.51)	53.99–60; 57.29 (2.43)
Hindfoot length (HF)	12.40–23; 17.38 (2.35)	13.92–22; 17.66 (2.04)	11.47–16.01; 13.74 (3.21)
Metacarpal III (MET-III)	35.31–52.88; 48.18 (2.49)	37.56–53.40; 47.63 (2.27)	39.45–52.30; 47.56 (4.91)
Metacarpal IV (MET-IV)	37.12–55.48; 50.24 (2.56)	37.98–54.43; 49.34 (2.36)	40.57–53.30; 49.51 (5.18)
Metacarpal V (MET-V)	39.04–58.86; 53.53 (2.73)	41.15–58.13; 53.25 (2.20)	42.85–55.60; 51.79 (5.2)
Tibia length (TiL)	16.82–29.69; 25.90 (1.84)	20.38–28.90; 24.94 (1.45)	20.61–25.16; 23.09 (1.66)
Tail length (T)	10–28; 16.93 (3.25)	10–22; 16.11 (2.75)	14.38
Total length (TL)	59.70–128; 96.16 (11.35)	56.25–107; 91.09 (15.94)	
Ear length (E)	23.07–39; 31.10	20–39; 31 (4.06)	27.65–31; 29.33

1247

Weight (W)	(4.06) 16–55; 34.48 (7.74)	22–46; 33.19 (6.99)	(2.37)
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For Review Only

1248

Table 4. Loadings, eigenvalues and percentage of variance for 2 principal components1249 from a PCA of the 13 linear measurements for adult specimens of *Trachops*.

Variables	PC1	PC2
Breadth of brain case (BB)	.554	.280
Palatal width at canines (C-C)	.778	.314
Condylloincisive length (CIL)	.919	.068
Greatest length of skull (GLS)	.919	.071
Breadth across upper molars (M2-M2)	.756	.293
Mastoid (process) breadth (MPW)	.820	.212
Molariform toothrow (MLTRL)	.872	.067
Post orbital constriction breadth (PB)	.383	.698
Zygomatic breadth (ZB)	.864	.128
Forearm length (FA)	.743	-.180
Metacarpal III (MET-III)	.690	-.555
Metacarpal IV (MET-IV)	.800	-.515
Metacarpal V (MET-V)	.786	-.546
Eigenvalues	7.787	1.731
% of explained variance	59.9	13.3
% of cumulative variance	59.9	73.2

1250

Review Only

1251

Table 5. Measurements (mm) and body masses (g) of *Trachops cirrhosus* and *T. ehrhardti*.

1252

Descriptive measures: minimum–maximum; arithmetic mean (standard deviation)

<i>Variable</i>	<i>T. cirrhosus</i> <i>N</i> = 233	<i>T. ehrhardti</i> <i>N</i> = 5
Breadth of brain case (BB)	10.33–12.97; 11.56 (0.28)	11.30–11.50; 11.40 (0.10)
Palatal width at canines (C-C)	5.26–6.85; 6.13 (0.26)	5.40–5.80; 5.63 (0.21)
Condylocanine length (CCL)	20.93–26.79; 24.70 (0.87)	
Condylloincisive length (CIL)	21.87–27.95; 25.67 (0.85)	23.90–24.50; 24.20 (0.30)
Coronoid height (COH)	4.79–6.80; 5.71 (0.36)	
Dentary length (DENL)	16.11–20.48; 18.70 (0.72)	
Greatest length of skull (GLS)	24.70–31.24; 28.86 (0.94)	26.90–27.70; 27.20 (0.44)
Breadth across upper molars (M2-M2)	8.34–11.03; 10 (0.39)	9.80
Mandibular toothrow length (MANDL)	10.06–12.40; 11.05 (0.40)	
Molariform toothrow (MLTRL)	6.07–7.81; 7.12 (0.27)	
Mastoid (process) breadth (MPW)	11.40–14.96; 13.51 (0.49)	13–13.40; 13.20 (0.20)
Maxillary toothrow (MTRL)	8.57–11.33; 10.36 (0.40)	9.60–10; 9.8 (0.20)
Post orbital constriction breadth (PB)	4.66–5.76; 5.25 (0.21)	5
Palatal length (PL)	8.92–12.72; 11.25 (0.53)	
Zygomatic breadth (ZB)	12.06–15.97; 14.31 (0.59)	13.3–14.10; 13.77 (0.42)
Braincase height (BCH)	9.24–12.25; 10.76 (0.46)	
Calcar length (CL)	9.19–18.21; 13.41 (1.44)	11.62
Forearm length (FA)	49.57–64.70; 58.71 (2.43)	53.99–60; 57.29 (2.43)
Hindfoot length (HF)	12.40–23; 17.49 (2.24)	11.47–16.01; 13.74 (3.21)
Metacarpal III (MET-III)	35.31–53.40; 47.93 (2.41)	39.45–52.30; 47.56 (4.91)
Metacarpal IV (MET-IV)	37.12–55.48; 49.93 (2.51)	40.57–53.30; 49.51 (5.18)
Metacarpal V (MET-V)	39.04–58.86; 53.42 (2.54)	42.85–55.60; 51.79 (5.2)
Tibia length (TiL)	16.82–29.69; 25.57 (1.76)	20.61–25.16; 23.09 (1.66)
Tail length (T)	10–28; 16.61 (3.08)	14.38
Total length (TL)	56.25–128; 94.13 (11.39)	
Ear length (E)	20–39; 31.81 (3.61)	27.65–31; 29.33 (2.37)
Weight (W)	16–55; 34.07 (7.48)	

1253

1254 **Figure Legends**

1255

1256 **Figure 1.** Adult *Trachops cirrhosus* captured in Parque Nacional Yasuní, Orellana, Ecuador. Note
1257 the conspicuous finger-like dermal projections on the chin and lips. Photo: Rubén D. Jarrín.

1258

1259 **Figure 2.** Collecting localities of the *Trachops* specimens analyzed in this study. The localities are
1260 shown in the Supplementary Table 1. Black symbols represent *Trachops cirrhosus*, gray symbols
1261 represent *Trachops coffini*, and white symbols represent *Trachops ehrhardti*. Circles are
1262 specimens that were measured only, squares are sequenced only, and diamonds are both.

1263

1264 **Figure 3.** Maximum Likelihood phylogeny of *Trachops* based on complete mitochondrial genomes
1265 (nucleotide sequences). The tree was reconstructed in RAxML under the GTR+G+I model using 57
1266 complete mitogenomes including outgroups. Shaded semicircles on the nodes indicate ML
1267 bootstrap support (as a percentage) and Bayesian posterior probabilities from a congruent
1268 Bayesian Inference Analysis (see insert key).

1269

1270 **Figure 4.** Dorsal, ventral, and lateral views of the skulls and lateral view of the mandibles of
1271 *Trachops cirrhosus cirrhosus* (left); *T. c. coffini* (middle), and *T. c. ehrhardti* (right) Photos: Rubén
1272 D. Jarrín (QCAZ 11818); M. Alejandra Camacho (NMNH 244262); Anika Vogel (SMF 11718).

1273

1274 **Figure 5.** Principal components (PC's) from a PCA based on 13 measurements from 238
1275 individuals. Samples: *Trachops cirrhosus cirrhosus* (red circles), *T. c. coffini* (blue circles), and *T. c.*
1276 *ehrhardti* (green circles).

1277

1278 **Figure 6.** Principal components analysis of 6 geographic groups and 238 specimens of *Trachops*
1279 of the 13 cranial measurements considered in the morphometric analysis. Meaning of Geographic
1280 abbreviation areas: **CAm** - Central America; **WSAm** - West South America; **ESAm** - East South

1281 America; **NEC/NWV**, NE Colombia and NW Venezuela; **GS** - the Guiana Shield; and **AF** - Atlantic
1282 Forest.

1283

1284 **Figure 7.** Emended distributions of *Trachops cirrhosus* and *Trachops ehrhardti*. Black circles and
1285 crosses (• and ×) represent the recorded locations of *Trachops cirrhosus*. White circles and plus
1286 signs (o and+) correspond to the recorded locations of *Trachops ehrhardti*. The crosses and plus
1287 signs are the data collected by Fonseca (2019), sourced from <https://github.com/bsf07/Defesa.git>.

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For Review Only

1290 **FIGURES**

1291

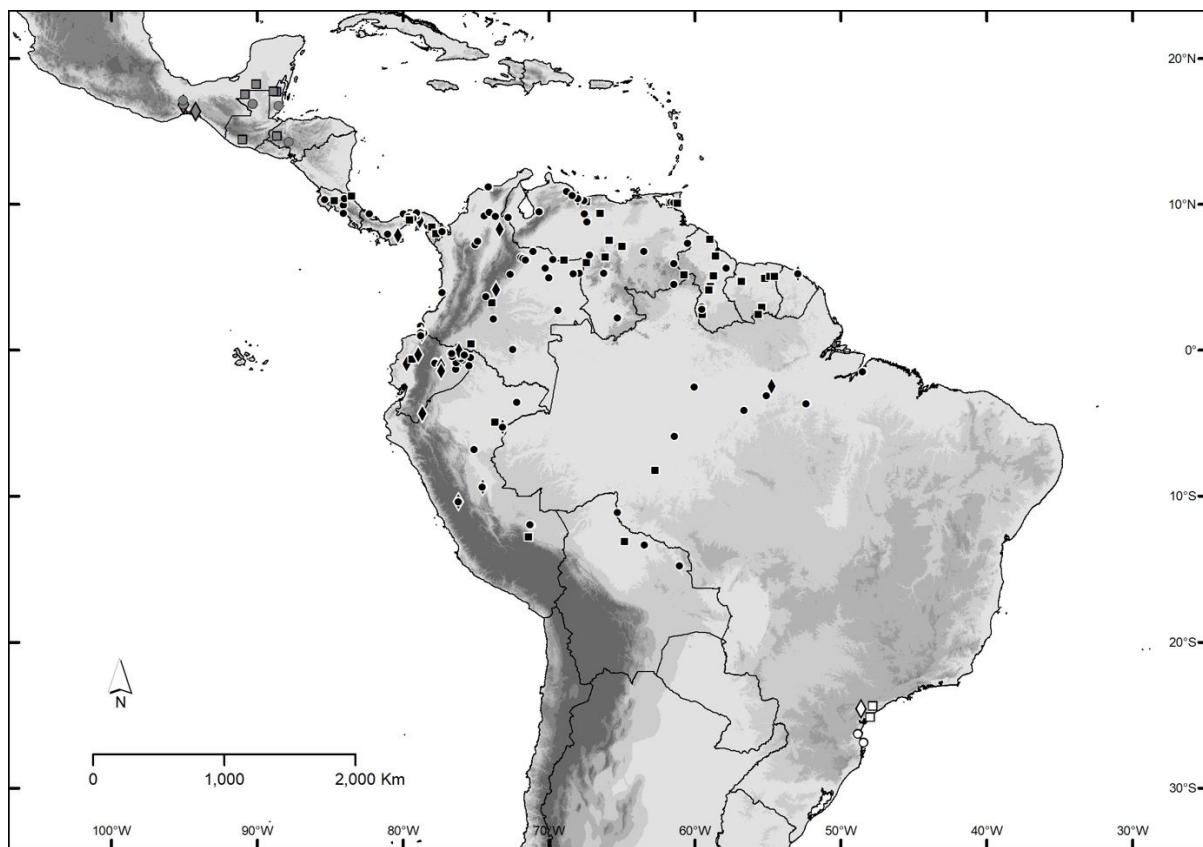
1292 • These figures are only referential. All the figures are presented in TIFF format in separate.

1293



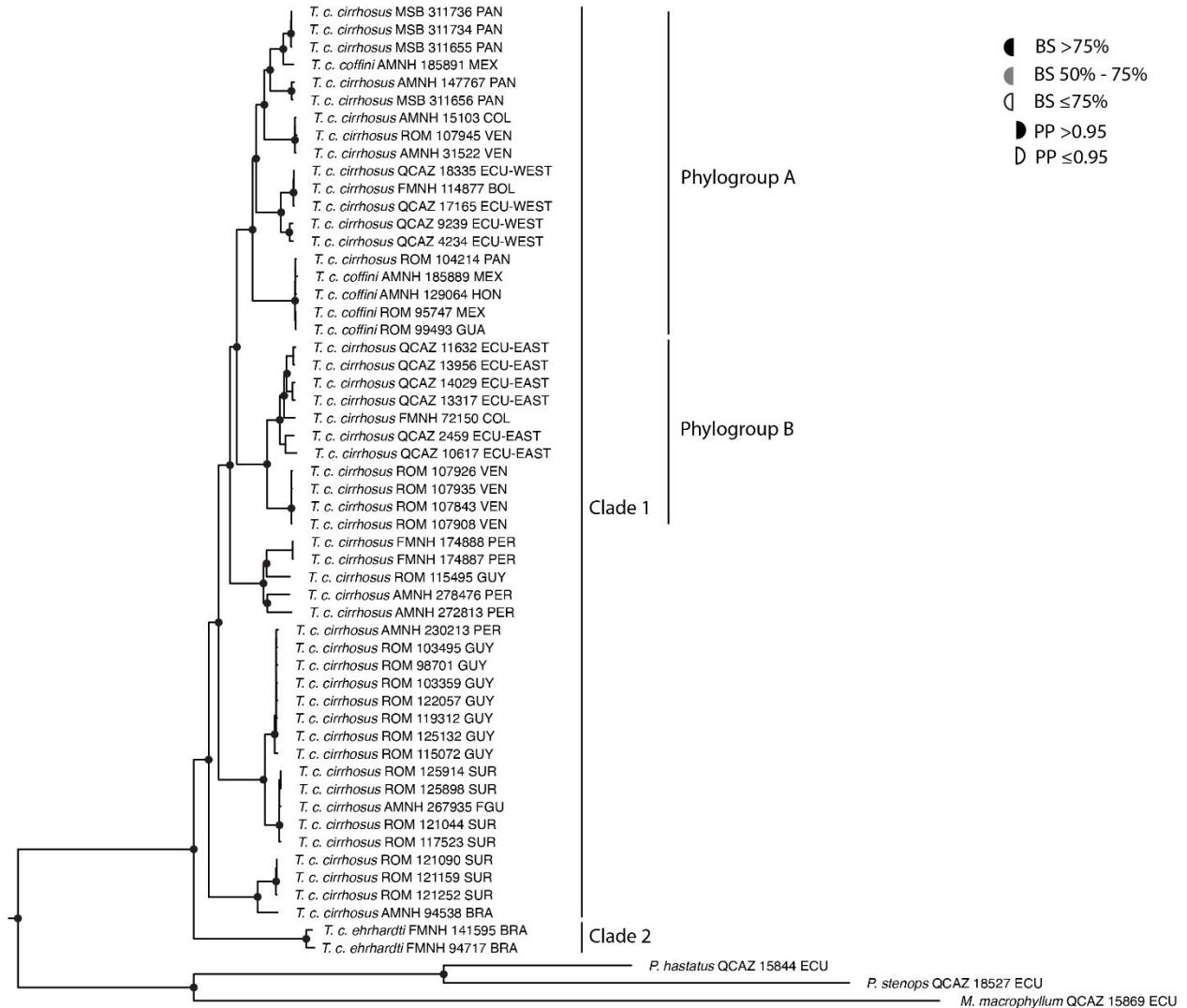
1294

1295 **Figure 1.** Adult *Trachops cirrhosus* captured in Parque Nacional Yasuní, Orellana, Ecuador. Note
1296 the conspicuous finger-like dermal projections on the chin and lips. Photo: Rubén D. Jarrín.



1297

1298 **Figure 2.** Collecting localities of the *Trachops* specimens analyzed in this study. The localities are
1299 shown in the Supplementary Table 1. Black symbols represent *Trachops cirrhosus*, gray symbols
1300 represent *Trachops coffini*, and white symbols represent *Trachops ehrhardti*. Circles are
1301 specimens that were measured only, squares are sequenced only, and diamonds are both.
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Figure 3. Maximum Likelihood phylogeny of *Trachops* based on complete mitochondrial genomes

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(nucleotide sequences). The tree was reconstructed in RAxML under the GTR+G+I model using 57

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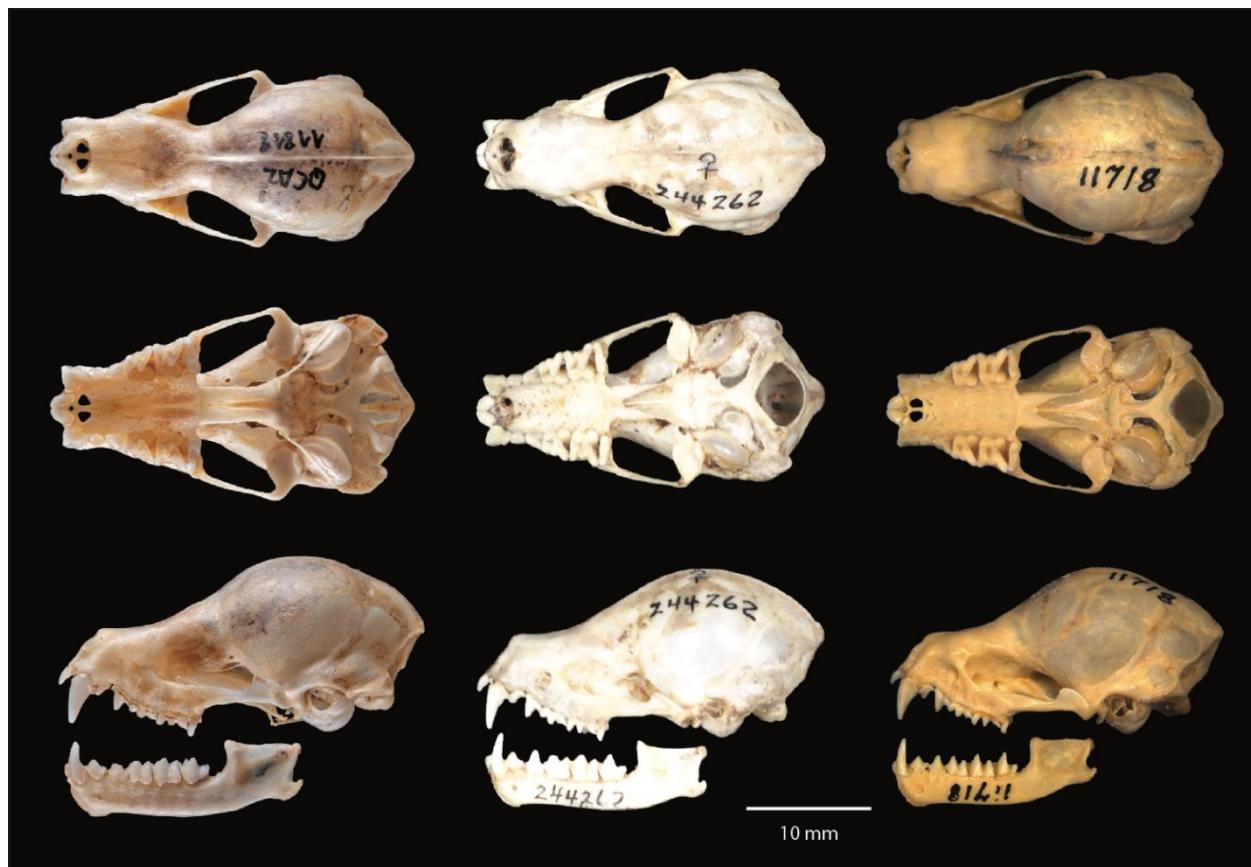
complete mitogenomes including outgroups. Shaded semicircles on the nodes indicate ML

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bootstrap support (as a percentage) and Bayesian posterior probabilities from a congruent

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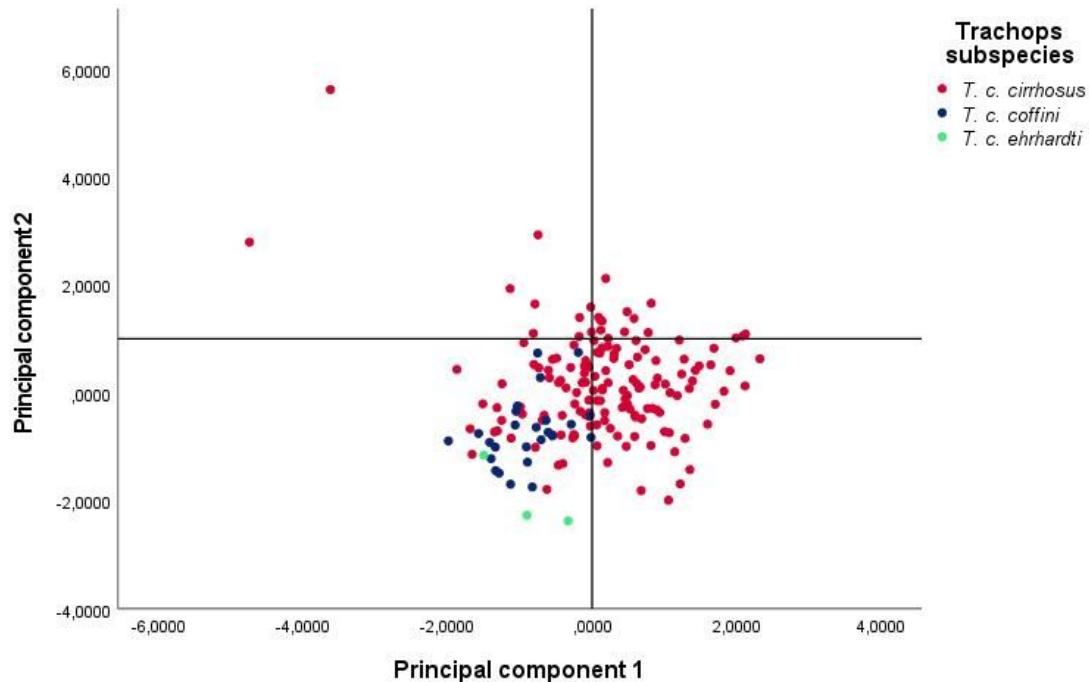
Bayesian Inference Analysis (see insert key).



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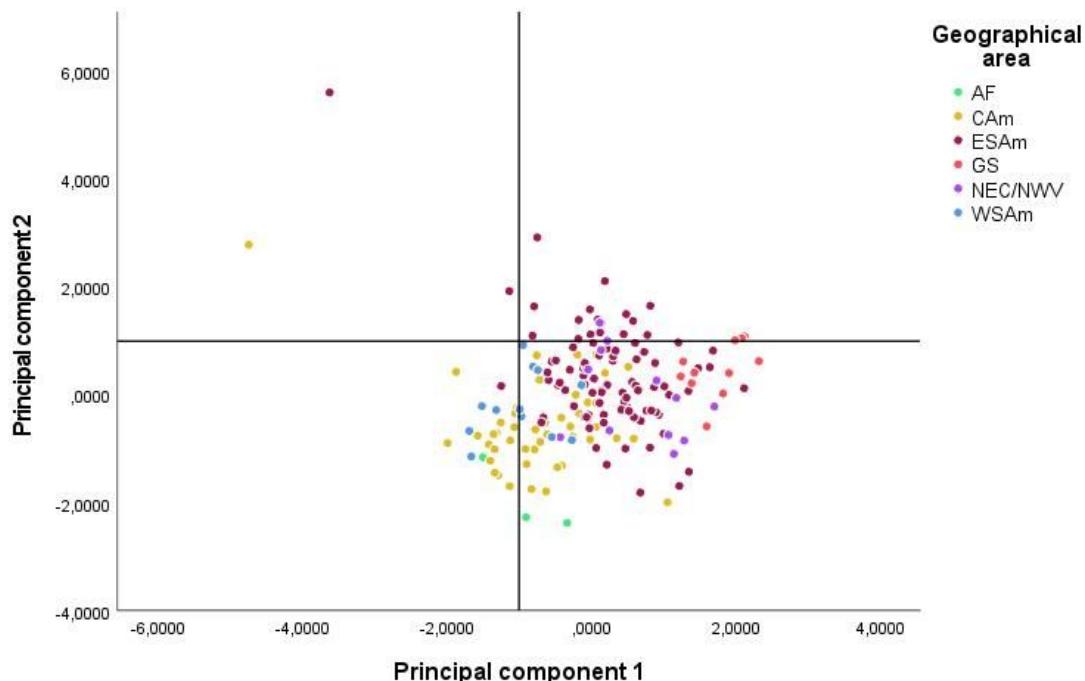
1311 **Figure 4.** Dorsal, ventral, and lateral views of the skulls and mandibles of
1312 *Trachops cirrhosus cirrhosus* (left); *T. c. coffini* (middle), and *T. c. ehrhardti* (right) Photos: Rubén
1313 D. Jarrín (QCAZ 11818); Alejandra Camacho (NMNH 244262); Anika Vogel (SMF 11718).

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1316 **Figure 5.** Principal components (PC's) from a PCA based on 13 measurements from 238
1317 individuals. Samples: *Trachops cirrhosus cirrhosus* (red circles), *T. c. coffini* (blue circles), and *T. c.*
1318 *ehrhardti* (green circles).



1319

1320 **Figure 6.** Principal components analysis of 6 geographic groups and 238 specimens of *Trachops*
1321 of the 13 cranial measurements considered in the morphometric analysis. Meaning of Geographic
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1324 Forest.

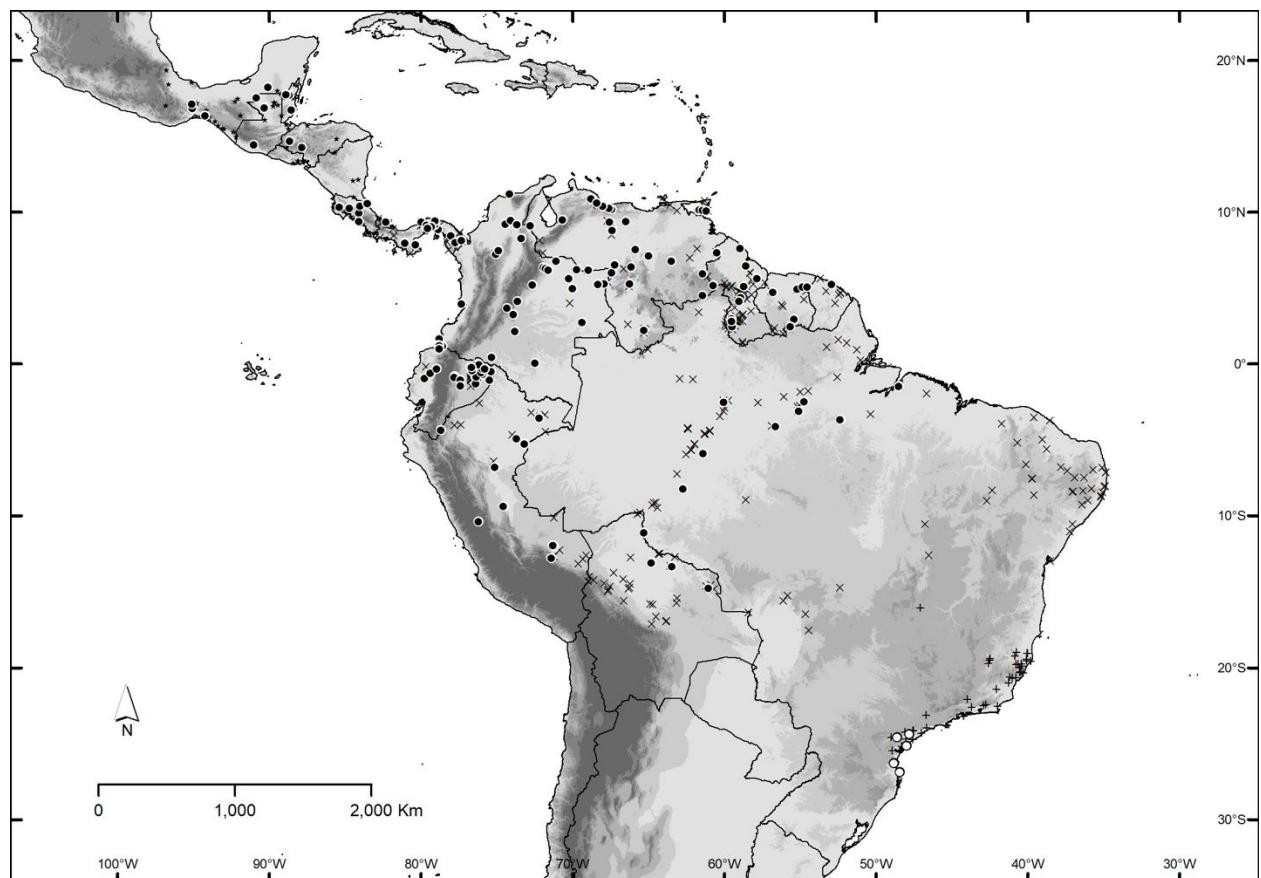


Figure 7. Emended distributions of *Trachops cirrhosus* and *Trachops ehrhardti*. Black circles and

crosses (• and ×) represent the recorded locations of *Trachops cirrhosus*. White circles and plus

signs (o and+) correspond to the recorded locations of *Trachops ehrhardti*. The crosses and plus

signs are the data collected by Fonseca (2019), sourced from <https://github.com/bsf07/Defesa.git>.

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1331 **Appendix 1.** List of specimens used in the present study including voucher identification,
 1332 GenBank accession number, taxonomic information, and general features of the mitogenome
 1333 assemblies.

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Museum number	GenBank Accession number	Species	Nº of reads	Mean coverage	Nº of mtDNA reads	mtDNA length	GC content (%)
AMNH-15103	Pending	T. cirrhosus	4324942	104,79	29909	16584	37,58
AMNH-31522	Pending	T. cirrhosus	2236998	37,01	10356	16601	37,58
AMNH-94538	Pending	T. cirrhosus	2151243	23,34	5747	16591	37,37
AMNH-129064	Pending	T. cirrhosus	2740862	79,92	22336	16595	37,58
AMNH-147767	Pending	T. cirrhosus	2789364	7,54	1891	16598	37,58
AMNH-185889	Pending	T. cirrhosus	3336996	17,44	4212	16596	37,25
AMNH-185891	Pending	T. cirrhosus	4357962	101,3	22996	16625	37,3
AMNH-230213	Pending	T. cirrhosus	4526938	399,14	90418	16622	37,66
AMNH-267935	Pending	T. cirrhosus	3494936	164,35	37044	16621	37,53
AMNH-272813	Pending	T. cirrhosus	5430224	147,99	33 493	16655	37,58
AMNH-278476	Pending	T. cirrhosus	5304394	57,21	12932	16653	37,59
FMNH-72150	Pending	T. cirrhosus	7428142	7,64	1773	16578	37,35
FMNH-114877	Pending	T. cirrhosus	7529998	82,99	18741	16598	37,36
FMNH-174887	Pending	T. cirrhosus	5776246	1 237,67	282126	16743	37,7
FMNH-174888	Pending	T. cirrhosus	5550234	282,11	64164	16713	37,68
MSB-311655	Pending	T. cirrhosus	4271430	68,59	15555	16600	37,58
MSB-311656	Pending	T. cirrhosus	4543408	261,75	59681	16602	37,58
MSB-311734	Pending	T. cirrhosus	4944460	169,89	38553	16603	37,37
MSB-311736	Pending	T. cirrhosus	5215900	62,19	14095	16603	37,37
QCAZ-2459	Pending	T. cirrhosus	3690346	54,62	12560	16630	37,46
QCAZ-4234	Pending	T. cirrhosus				16822	37,60
QCAZ-9239	Pending	T. cirrhosus	3751390	157,88	35638	16623	37,47
QCAZ-10617	Pending	T. cirrhosus	5240730	7,99	1829	16620	37,47
QCAZ-11632	Pending	T. cirrhosus	6075978	111,02	25064	16571	37,31
QCAZ-13317	Pending	T. cirrhosus				16619	37,50
QCAZ-13956	Pending	T. cirrhosus	5352738	29,08	6658	16621	37,35
QCAZ-14029	Pending	T. cirrhosus	6361566	104,18	23674	16619	37,42
QCAZ-17165	Pending	T. cirrhosus	6480538	20,02	4522	16614	37,34
QCAZ-18335	Pending	T. cirrhosus	4985186	83	18723	16579	37,35
ROM-95747	Pending	T. cirrhosus	5305082	299,46	67789	16624	37,32
ROM-98701	Pending	T. cirrhosus	5550346	43,24	9792	16612	37,67
ROM-99493	Pending	T. cirrhosus	3211086	79,6	18085	16621	37,31
ROM-103359	Pending	T. cirrhosus	4896612	14,83	3326	16317	36,24
ROM-103495	Pending	T. cirrhosus	4853726	522,78	118097	16621	37,59
ROM-104214	Pending	T. cirrhosus	4148188	39,36	9909	16582	37,3
ROM-107843	Pending	T. cirrhosus	4250814	17,87	4049	16617	37,41

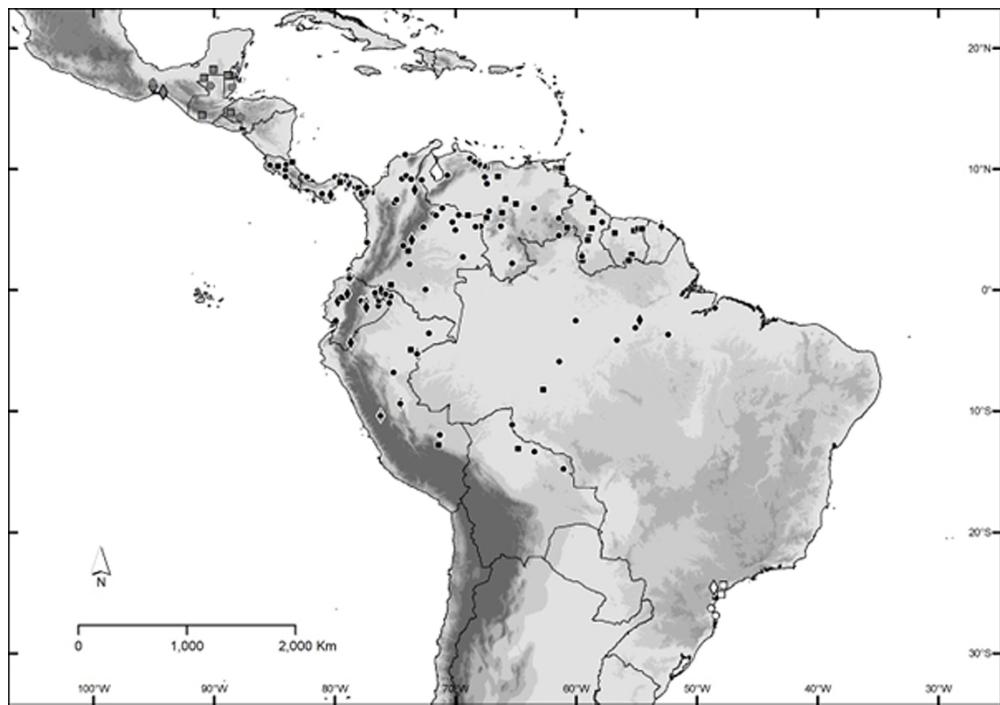
ROM-107908	Pending	T. cirrhosus	3634508	67,38	15210	16593	37,4
ROM-107926	Pending	T. cirrhosus	3176256	169,41	38250	16602	37,41
ROM-107935	Pending	T. cirrhosus	3613554	260,21	58765	16607	37,39
ROM-107945	Pending	T. cirrhosus	4380050	281,34	63704	16637	37,65
ROM-115072	Pending	T. cirrhosus	6091173	10,53	2211	16577	37,29
ROM-115495	Pending	T. cirrhosus	7436128	21,57	4895	16624	37,42
ROM-117523	Pending	T. cirrhosus				16749	37,6
ROM-119312	Pending	T. cirrhosus	4225778	167,44	37808	16611	37,67
ROM-121044	Pending	T. cirrhosus	4673024	426,56	96388	16613	37,56
ROM-121090	Pending	T. cirrhosus	4051452	46,35	10501	16622	37,65
ROM-121159	Pending	T. cirrhosus	6174610	1006,61	227410	16594	37,62
ROM-121252	Pending	T. cirrhosus	4190554	197,92	44724	16615	37,69
ROM-122057	Pending	T. cirrhosus	4946730	215,59	49150	16622	37,67
ROM-125132	Pending	T. cirrhosus	5841756	217,79	48522	16631	37,65
ROM-125898	Pending	T. cirrhosus	5053904	26,77	6039	16589	37,51
ROM-125914	Pending	T. cirrhosus	5364036	132,02	29962	16606	37,53
FMNH-94717	Pending	T. erhardti	3597194	8,72	1996	16618	37,03
FMNH-141595	Pending	T. erhardti	4767214	20,62	4716	16619	37,3
		Average	4731900,47	138,74	36649,90	16615,22	37,46
		Standar deviation	1242366,47	172,72	52650,26	60,37	0,22

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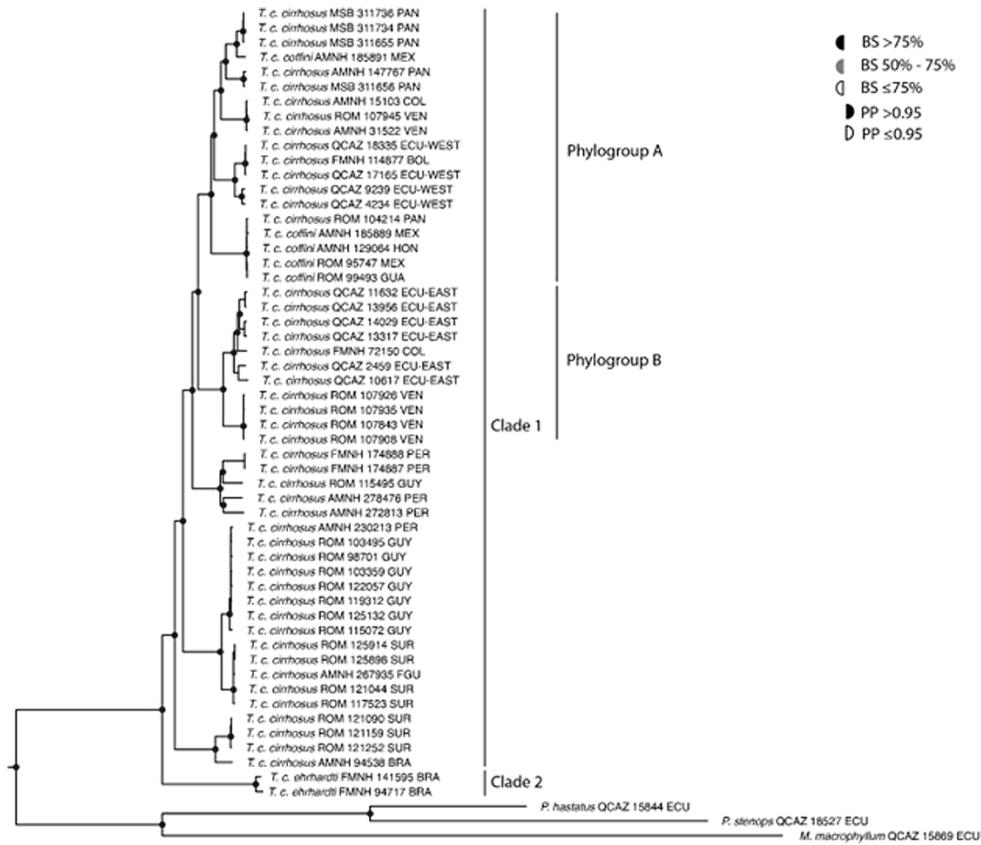
Adult *Trachops cirrhosus* captured in Parque Nacional Yasuní, Orellana, Ecuador. Note the conspicuous finger-like dermal projections on the chin and lips. Photo: Rubén D. Jarrín.

649x979mm (28 x 28 DPI)



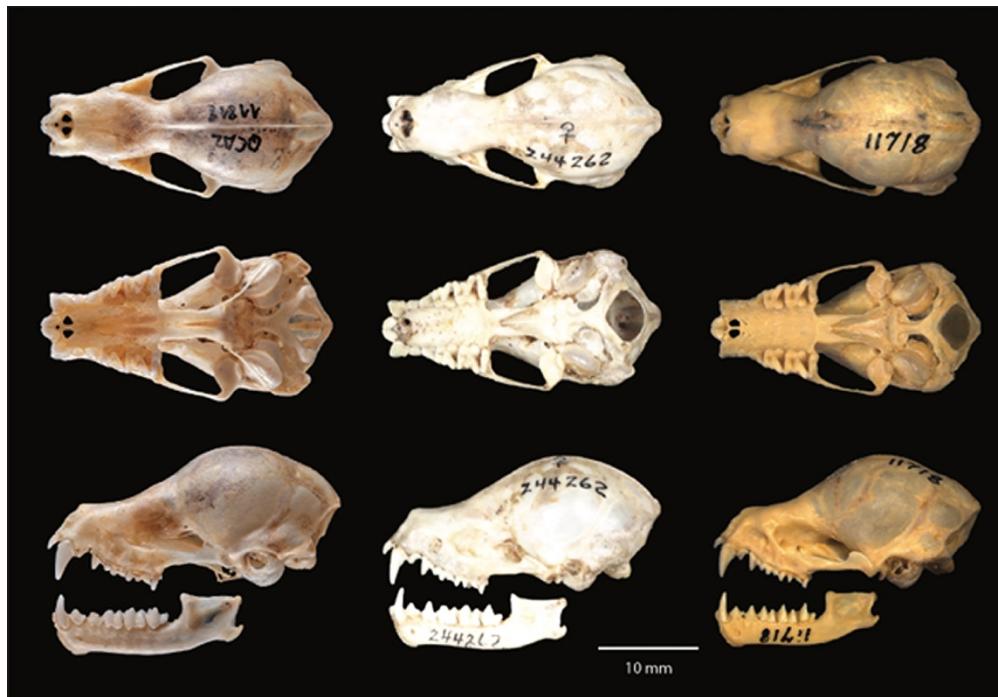
Collecting localities of the *Trachops* specimens analyzed in this study. The localities are shown in the Supplementary Table 1. Black symbols represent *Trachops cirrhosus*, gray symbols represent *Trachops coffini*, and white symbols represent *Trachops ehrhardti*. Circles are specimens that were measured only, squares are sequenced only, and diamonds are both.

1407x979mm (28 x 28 DPI)



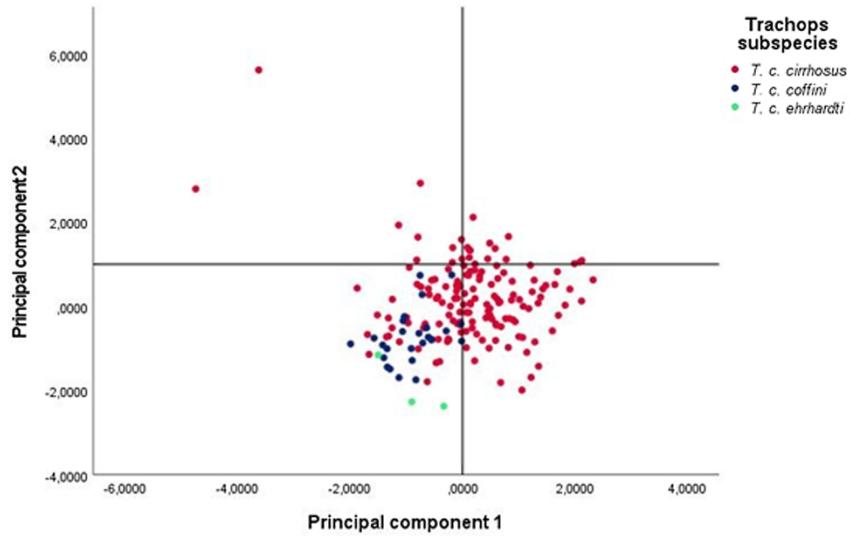
Maximum Likelihood phylogeny of *Trachops* based on complete mitochondrial genomes (nucleotide sequences). The tree was reconstructed in RAxML under the GTR+G+I model using 57 complete mitogenomes including outgroups. Shaded semicircles on the nodes indicate ML bootstrap support (as a percentage) and Bayesian posterior probabilities from a congruent Bayesian Inference Analysis (see insert key).

1041x910mm (28 x 28 DPI)



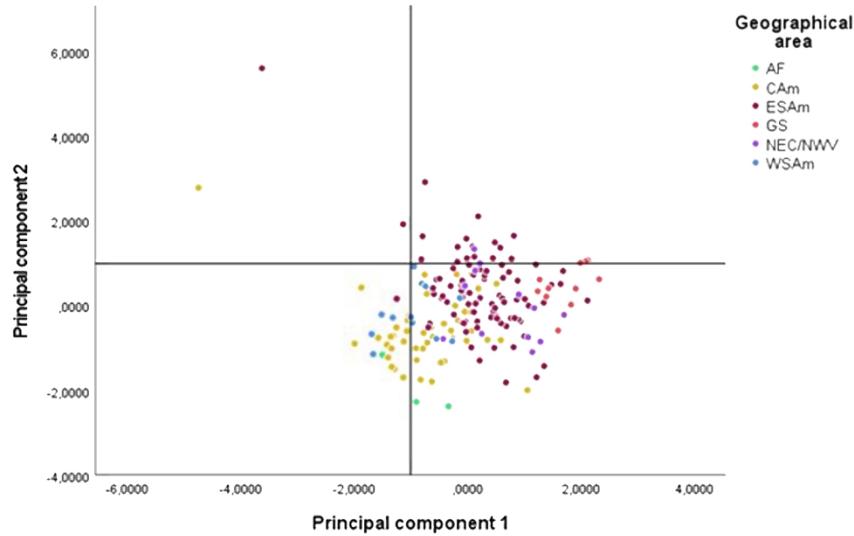
Dorsal, ventral, and lateral views of the skulls and lateral view of the mandibles of *Trachops cirrhosus* (left); *T. c. coffini* (middle), and *T. c. ehrhardti* (right) Photos: Rubén D. Jarrín (QCAZ 11818); M. Alejandra Camacho (NMNH 244262); Anika Vogel (SMF 11718).

1415x979mm (28 x 28 DPI)



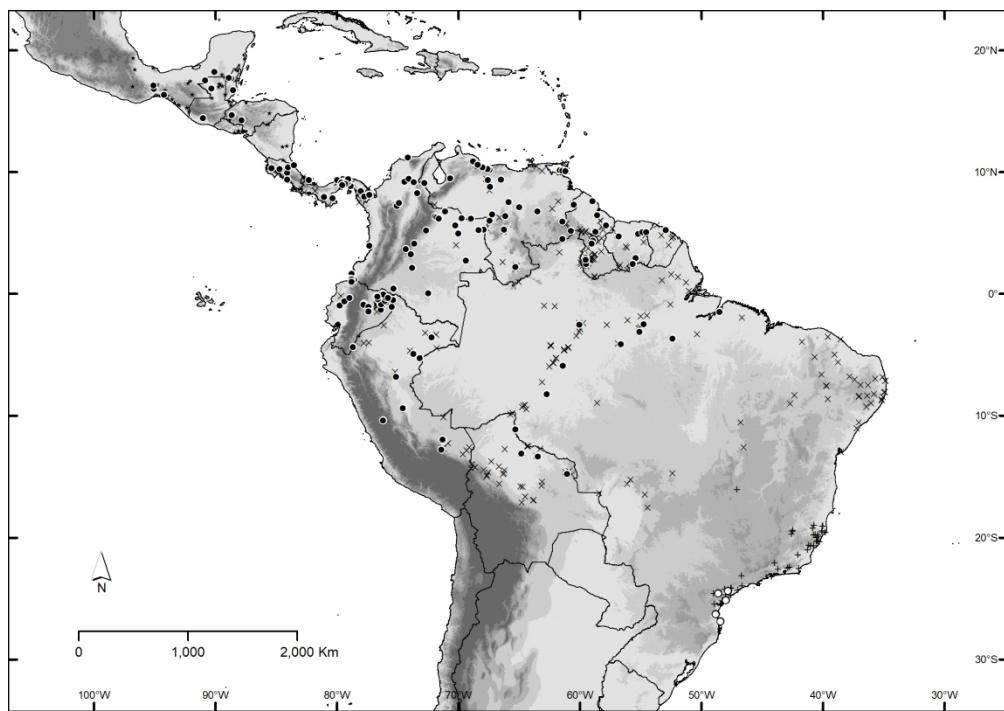
Principal components (PC's) from a PCA based on 13 measurements from 238 individuals. Samples: *Trachops cirrhosus* (*T. c. cirrhosus*), *T. c. coffini* (*T. c. coffini*), and *T. c. ehrhardti* (*T. c. ehrhardti*).

1469x979mm (28 x 28 DPI)



Principal components analysis of 6 geographic groups and 238 specimens of *Trachops* of the 13 cranial measurements considered in the morphometric analysis. Meaning of Geographic abbreviation areas: CAm - Central America; WSAm - West South America; ESAm - East South America; NEC/NWV, NE Colombia and NW Venezuela; GS - the Guiana Shield; and AF - Atlantic Forest.

1469x979mm (28 x 28 DPI)



Emended distributions of *Trachops cirrhosus* and *Trachops ehrhardti*. Black circles and crosses (• and □) represent the recorded locations of *Trachops cirrhosus*. White circles and plus signs (□ and +) correspond to the recorded locations of *Trachops ehrhardti*. The crosses and plus signs are the data collected by Fonseca (2019), sourced from <https://github.com/bsf07/Defesa.git>.

199x139mm (300 x 300 DPI)

Supplementary Table 1. Specimens, samples, biorepositories and geographic information.

Museum	# voucher	Unique	Measured	Treatment	Species
ROM	120475	ROM-120475	No	Sequenced	<i>Trachops cirrhosus</i>
AMNH	278284	AMNH-278284	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	278402	AMNH-278402	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	278668	AMNH-278668	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	278748	AMNH-278748	No	Sequenced	<i>Trachops cirrhosus</i>
USNM	583009	USNM-583009	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	209349	AMNH-209349	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	209350	AMNH-209350	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	209348	AMNH-209348	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	209351	AMNH-209351	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	210679	AMNH-210679	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	210680	AMNH-210680	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	210681	AMNH-210681	Yes	Measured	<i>Trachops cirrhosus</i>
FMNH	114877	FMNH-114877	No	Sequenced	<i>Trachops cirrhosus</i>
USNM	584479	USNM-584479	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	530956	USNM-530956	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	530957	USNM-530957	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	92252	AMNH-92252	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	94536	AMNH-94536	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	94537	AMNH-94537	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	549355	USNM-549355	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	549354	USNM-549354	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	361534	USNM-361534	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	361533	USNM-361533	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	460090	USNM-460090	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	94538	AMNH-94538	Yes	Both	<i>Trachops cirrhosus</i>
AMNH	95500	AMNH-95500	Yes	Measured	<i>Trachops cirrhosus</i>
FMNH	235204	FMNH-235204	No	Sequenced	<i>Trachops cirrhosus</i>
SMF	11716	SMF-11716	Yes	Measured	<i>Trachops cirrhosus</i>
SMF	11717	SMF-11717	Yes	Measured	<i>Trachops cirrhosus</i>
SMF	11718	SMF-11718	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	200992	USNM-200992	Yes	Measured	<i>Trachops cirrhosus</i>
AMNH	256301	AMNH-256301	Yes	Both	<i>Trachops cirrhosus</i>
FMNH	141595	FMNH-141595	No	Sequenced	<i>Trachops cirrhosus</i>
FMNH	94717	FMNH-94717	No	Sequenced	<i>Trachops cirrhosus</i>
IAvH-M	954	IAvH-M-954	Yes	Measured	<i>Trachops cirrhosus</i>
IAvH-M	1331	IAvH-M-1331	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	499295	USNM-499295	Yes	Measured	<i>Trachops cirrhosus</i>
USNM	499764	USNM-499764	Yes	Measured	<i>Trachops cirrhosus</i>
IAvH-M	9466	IAvH-M-9466	Yes	Measured	<i>Trachops cirrhosus</i>
IAvH-M	9628	IAvH-M-9628	Yes	Measured	<i>Trachops cirrhosus</i>

IAvH-M	9470	IAvH-M-9470	Yes	Measured	Trachops cirrhosus
IAvH-M	10098	IAvH-M-10098	Yes	Measured	Trachops cirrhosus
IAvH-M	9976	IAvH-M-9976	Yes	Measured	Trachops cirrhosus
FMNH	92309	FMNH-92309	No	Sequenced	Trachops cirrhosus
FMNH	92311	FMNH-92311	No	Sequenced	Trachops cirrhosus
USNM	281054	USNM-281054	Yes	Measured	Trachops cirrhosus
IAvH-M	7141	IAvH-M-7141	Yes	Measured	Trachops cirrhosus
IAvH-M	10622	IAvH-M-10622	Yes	Measured	Trachops cirrhosus
IAvH-M	9970	IAvH-M-9970	Yes	Measured	Trachops cirrhosus
IAvH-M	7850	IAvH-M-7850	Yes	Measured	Trachops cirrhosus
IAvH-M	8109	IAvH-M-8109	Yes	Measured	Trachops cirrhosus
IAvH-M	8110	IAvH-M-8110	Yes	Measured	Trachops cirrhosus
USNM	281926	USNM-281926	Yes	Measured	Trachops cirrhosus
USNM	281927	USNM-281927	Yes	Measured	Trachops cirrhosus
USNM	281049	USNM-281049	Yes	Measured	Trachops cirrhosus
USNM	281050	USNM-281050	Yes	Measured	Trachops cirrhosus
USNM	281037	USNM-281037	Yes	Measured	Trachops cirrhosus
USNM	281038	USNM-281038	Yes	Measured	Trachops cirrhosus
USNM	281039	USNM-281039	Yes	Measured	Trachops cirrhosus
USNM	281040	USNM-281040	Yes	Measured	Trachops cirrhosus
USNM	281045	USNM-281045	Yes	Measured	Trachops cirrhosus
IAvH-M	11372	IAvH-M-11372	Yes	Measured	Trachops cirrhosus
UV	2745	UV-2745	Yes	Measured	Trachops cirrhosus
UV	2746	UV-2746	Yes	Measured	Trachops cirrhosus
AMNH	15103	AMNH-15103	No	Sequenced	Trachops cirrhosus
IAvH-M	2218	IAvH-M-2218	Yes	Measured	Trachops cirrhosus
IAvH-M	11316	IAvH-M-11316	Yes	Measured	Trachops cirrhosus
FMNH	88070	FMNH-88070	No	Sequenced	Trachops cirrhosus
UV	5549	UV-5549	Yes	Measured	Trachops cirrhosus
AMNH	142158	AMNH-142158	Yes	Both	Trachops cirrhosus
UV	6996	UV-6996	Yes	Measured	Trachops cirrhosus
AMNH	255713	AMNH-255713	Yes	Both	Trachops cirrhosus
FMNH	71533	FMNH-71533	No	Sequenced	Trachops cirrhosus
FMNH	72150	FMNH-72150	No	Sequenced	Trachops cirrhosus
UV	5550	UV-5550	Yes	Measured	Trachops cirrhosus
IAvH-M	2921	IAvH-M-2921	Yes	Measured	Trachops cirrhosus
IAvH-M	8332	IAvH-M-8332	Yes	Measured	Trachops cirrhosus
IAvH-M	8333	IAvH-M-8333	Yes	Measured	Trachops cirrhosus
USNM	562764	USNM-562764	Yes	Measured	Trachops cirrhosus
USNM	562763	USNM-562763	Yes	Measured	Trachops cirrhosus
USNM	565808	USNM-565808	Yes	Measured	Trachops cirrhosus
USNM	568489	USNM-568489	Yes	Measured	Trachops cirrhosus
FMNH	137225	FMNH-137225	No	Sequenced	Trachops cirrhosus

USNM	526241	USNM-526241	Yes	Measured	Trachops cirrhosus
FMNH	124102	FMNH-124102	No	Sequenced	Trachops cirrhosus
QCAZ	9239	QCAZ-9239	Yes	Both	Trachops cirrhosus
MEPN	5676	MEPN-5676	Yes	Measured	Trachops cirrhosus
QCAZ	9237	QCAZ-9237	Yes	Measured	Trachops cirrhosus
QCAZ	2341	QCAZ-2341	Yes	Measured	Trachops cirrhosus
QCAZ	9238	QCAZ-9238	Yes	Measured	Trachops cirrhosus
MEPN	2014	MEPN-2014	Yes	Measured	Trachops cirrhosus
MEPN	3014	MEPN-3014	Yes	Measured	Trachops cirrhosus
QCAZ	18335	QCAZ-18335	Yes	Both	Trachops cirrhosus
USNM	528489	USNM-528489	Yes	Measured	Trachops cirrhosus
QCAZ	17164	QCAZ-17164	Yes	Measured	Trachops cirrhosus
QCAZ	17165	QCAZ-17165	No	Sequenced	Trachops cirrhosus
QCAZ	285	QCAZ-285	Yes	Measured	Trachops cirrhosus
QCAZ	3290	QCAZ-3290	Yes	Measured	Trachops cirrhosus
QCAZ	11818	QCAZ-11818	Yes	Both	Trachops cirrhosus
MEPN	5603	MEPN-5603	Yes	Measured	Trachops cirrhosus
QCAZ	18016	QCAZ-18016	Yes	Measured	Trachops cirrhosus
QCAZ	13876	QCAZ-13876	Yes	Measured	Trachops cirrhosus
QCAZ	13877	QCAZ-13877	Yes	Measured	Trachops cirrhosus
QCAZ	13415	QCAZ-13415	Yes	Measured	Trachops cirrhosus
QCAZ	13596	QCAZ-13596	Yes	Measured	Trachops cirrhosus
QCAZ	7937	QCAZ-7937	Yes	Measured	Trachops cirrhosus
QCAZ	8171	QCAZ-8171	Yes	Measured	Trachops cirrhosus
QCAZ	8172	QCAZ-8172	Yes	Measured	Trachops cirrhosus
QCAZ	8079	QCAZ-8079	Yes	Measured	Trachops cirrhosus
QCAZ	13956	QCAZ-13956	No	Sequenced	Trachops cirrhosus
QCAZ	14029	QCAZ-14029	No	Sequenced	Trachops cirrhosus
QCAZ	3289	QCAZ-3289	Yes	Measured	Trachops cirrhosus
QCAZ	1116	QCAZ-1116	Yes	Measured	Trachops cirrhosus
MEPN	5125	MEPN-5125	Yes	Measured	Trachops cirrhosus
MEPN	4477	MEPN-4477	Yes	Measured	Trachops cirrhosus
QCAZ	1475	QCAZ-1475	Yes	Measured	Trachops cirrhosus
QCAZ	10617	QCAZ-10617	Yes	Both	Trachops cirrhosus
QCAZ	4234	QCAZ-4234	Yes	Both	Trachops cirrhosus
MEPN	2013	MEPN-2013	Yes	Measured	Trachops cirrhosus
MEPN	4555	MEPN-4555	Yes	Measured	Trachops cirrhosus
MEPN	4482	MEPN-4482	Yes	Measured	Trachops cirrhosus
QCAZ	7228	QCAZ-7228	Yes	Measured	Trachops cirrhosus
QCAZ	6850	QCAZ-6850	Yes	Measured	Trachops cirrhosus
QCAZ	6855	QCAZ-6855	Yes	Measured	Trachops cirrhosus
QCAZ	6870	QCAZ-6870	Yes	Measured	Trachops cirrhosus
QCAZ	13317	QCAZ-13317	No	Sequenced	Trachops cirrhosus

QCAZ	11632	QCAZ-11632	Yes	Both	Trachops cirrhosus
QCAZ	7051	QCAZ-7051	Yes	Measured	Trachops cirrhosus
QCAZ	7578	QCAZ-7578	Yes	Measured	Trachops cirrhosus
QCAZ	10172	QCAZ-10172	Yes	Measured	Trachops cirrhosus
QCAZ	587	QCAZ-587	Yes	Measured	Trachops cirrhosus
QCAZ	5070	QCAZ-5070	Yes	Measured	Trachops cirrhosus
QCAZ	2459	QCAZ-2459	Yes	Both	Trachops cirrhosus
AMNH	267935	AMNH-267935	Yes	Both	Trachops cirrhosus
AMNH	266079	AMNH-266079	Yes	Measured	Trachops cirrhosus
AMNH	267926	AMNH-267926	Yes	Measured	Trachops cirrhosus
AMNH	267928	AMNH-267928	Yes	Measured	Trachops cirrhosus
AMNH	267930	AMNH-267930	Yes	Measured	Trachops cirrhosus
AMNH	267934	AMNH-267934	Yes	Measured	Trachops cirrhosus
AMNH	267936	AMNH-267936	Yes	Measured	Trachops cirrhosus
AMNH	266080	AMNH-266080	No	Sequenced	Trachops cirrhosus
AMNH	266089	AMNH-266089	Yes	Measured	Trachops cirrhosus
FMNH	65184	FMNH-65184	No	Sequenced	Trachops cirrhosus
ROM	99493	ROM-99493	No	Sequenced	Trachops cirrhosus
USNM	244252	USNM-244252	Yes	Measured	Trachops cirrhosus
USNM	244254	USNM-244254	Yes	Measured	Trachops cirrhosus
USNM	244256	USNM-244256	Yes	Measured	Trachops cirrhosus
USNM	244262	USNM-244262	Yes	Measured	Trachops cirrhosus
USNM	244264	USNM-244264	Yes	Measured	Trachops cirrhosus
USNM	244266	USNM-244266	Yes	Measured	Trachops cirrhosus
USNM	244268	USNM-244268	Yes	Measured	Trachops cirrhosus
USNM	244269	USNM-244269	Yes	Measured	Trachops cirrhosus
USNM	582290	USNM-582290	Yes	Measured	Trachops cirrhosus
ROM	98701	ROM-98701	No	Sequenced	Trachops cirrhosus
ROM	115072	ROM-115072	No	Sequenced	Trachops cirrhosus
ROM	115495	ROM-115495	No	Sequenced	Trachops cirrhosus
ROM	122057	ROM-122057	No	Sequenced	Trachops cirrhosus
ROM	125132	ROM-125132	No	Sequenced	Trachops cirrhosus
USNM	582292	USNM-582292	Yes	Measured	Trachops cirrhosus
USNM	582291	USNM-582291	Yes	Measured	Trachops cirrhosus
ROM	103359	ROM-103359	No	Sequenced	Trachops cirrhosus
ROM	103495	ROM-103495	No	Sequenced	Trachops cirrhosus
AMNH	182717	AMNH-182717	Yes	Measured	Trachops cirrhosus
ROM	119312	ROM-119312	No	Sequenced	Trachops cirrhosus
USNM	337270	USNM-337270	Yes	Measured	Trachops cirrhosus
USNM	339719	USNM-339719	Yes	Measured	Trachops cirrhosus
USNM	339720	USNM-339720	Yes	Measured	Trachops cirrhosus
USNM	337289	USNM-337289	Yes	Measured	Trachops cirrhosus
AMNH	129065	AMNH-129065	Yes	Measured	Trachops cirrhosus

AMNH	129072	AMNH-129072	Yes	Measured	Trachops cirrhosus
AMNH	129080	AMNH-129080	Yes	Measured	Trachops cirrhosus
AMNH	129081	AMNH-129081	Yes	Measured	Trachops cirrhosus
AMNH	129090	AMNH-129090	Yes	Measured	Trachops cirrhosus
AMNH	129732	AMNH-129732	Yes	Measured	Trachops cirrhosus
AMNH	129736	AMNH-129736	Yes	Measured	Trachops cirrhosus
AMNH	129064	AMNH-129064	No	Sequenced	Trachops cirrhosus
AMNH	129730	AMNH-129730	Yes	Measured	Trachops cirrhosus
ROM	95747	ROM-95747	No	Sequenced	Trachops cirrhosus
AMNH	185891	AMNH-185891	Yes	Both	Trachops cirrhosus
AMNH	185886	AMNH-185886	Yes	Both	Trachops cirrhosus
AMNH	185889	AMNH-185889	Yes	Both	Trachops cirrhosus
AMNH	185887	AMNH-185887	Yes	Measured	Trachops cirrhosus
AMNH	185888	AMNH-185888	Yes	Measured	Trachops cirrhosus
AMNH	185890	AMNH-185890	Yes	Measured	Trachops cirrhosus
USNM	332697	USNM-332697	Yes	Measured	Trachops cirrhosus
USNM	332698	USNM-332698	Yes	Measured	Trachops cirrhosus
USNM	332699	USNM-332699	Yes	Measured	Trachops cirrhosus
USNM	332700	USNM-332700	Yes	Measured	Trachops cirrhosus
USNM	554264	USNM-554264	Yes	Measured	Trachops cirrhosus
USNM	464596	USNM-464596	Yes	Measured	Trachops cirrhosus
USNM	464597	USNM-464597	Yes	Measured	Trachops cirrhosus
ROM	104214	ROM-104214	No	Sequenced	Trachops cirrhosus
USNM	311960	USNM-311960	Yes	Measured	Trachops cirrhosus
MSB	311736	MSB-311736	No	Sequenced	Trachops cirrhosus
MSB	311734	MSB-311734	No	Sequenced	Trachops cirrhosus
MSB	311655	MSB-311655	No	Sequenced	Trachops cirrhosus
MSB	311656	MSB-311656	No	Sequenced	Trachops cirrhosus
USNM	309362	USNM-309362	Yes	Measured	Trachops cirrhosus
USNM	309364	USNM-309364	Yes	Measured	Trachops cirrhosus
USNM	309367	USNM-309367	Yes	Measured	Trachops cirrhosus
USNM	309368	USNM-309368	Yes	Measured	Trachops cirrhosus
USNM	309369	USNM-309369	Yes	Measured	Trachops cirrhosus
USNM	309370	USNM-309370	Yes	Measured	Trachops cirrhosus
AMNH	178902	AMNH-178902	Yes	Both	Trachops cirrhosus
AMNH	143757	AMNH-143757	Yes	Measured	Trachops cirrhosus
AMNH	147767	AMNH-147767	Yes	Both	Trachops cirrhosus
AMNH	42564	AMNH-42564	Yes	Measured	Trachops cirrhosus
USNM	575470	USNM-575470	Yes	Measured	Trachops cirrhosus
USNM	312982	USNM-312982	Yes	Measured	Trachops cirrhosus
USNM	312983	USNM-312983	Yes	Measured	Trachops cirrhosus
USNM	312984	USNM-312984	Yes	Measured	Trachops cirrhosus
USNM	312985	USNM-312985	Yes	Measured	Trachops cirrhosus

USNM	174884	USNM-174884	Yes	Measured	Trachops cirrhosus
USNM	305199	USNM-305199	Yes	Measured	Trachops cirrhosus
USNM	305200	USNM-305200	Yes	Measured	Trachops cirrhosus
USNM	305201	USNM-305201	Yes	Measured	Trachops cirrhosus
USNM	309178	USNM-309178	Yes	Measured	Trachops cirrhosus
USNM	309179	USNM-309179	Yes	Measured	Trachops cirrhosus
USNM	309180	USNM-309180	Yes	Measured	Trachops cirrhosus
USNM	309181	USNM-309181	Yes	Measured	Trachops cirrhosus
FMNH	92672	FMNH-92672	No	Sequenced	Trachops cirrhosus
AMNH	233227	AMNH-233227	Yes	Both	Trachops cirrhosus
AMNH	236002	AMNH-236002	Yes	Measured	Trachops cirrhosus
AMNH	272813	AMNH-272813	Yes	Both	Trachops cirrhosus
AMNH	273176	AMNH-273176	Yes	Both	Trachops cirrhosus
AMNH	272820	AMNH-272820	Yes	Measured	Trachops cirrhosus
AMNH	272821	AMNH-272821	Yes	Measured	Trachops cirrhosus
AMNH	74026	AMNH-74026	Yes	Measured	Trachops cirrhosus
AMNH	278476	AMNH-278476	No	Sequenced	Trachops cirrhosus
AMNH	76162	AMNH-76162	Yes	Measured	Trachops cirrhosus
AMNH	76163	AMNH-76163	Yes	Measured	Trachops cirrhosus
AMNH	76164	AMNH-76164	Yes	Measured	Trachops cirrhosus
AMNH/MUSM	13277	AMNH/MUSM-13277	Yes	Measured	Trachops cirrhosus
AMNH/MUSM	13278	AMNH/MUSM-13278	Yes	Measured	Trachops cirrhosus
AMNH/MUSM	13279	AMNH/MUSM-13279	Yes	Measured	Trachops cirrhosus
AMNH/MUSM	13280	AMNH/MUSM-13280	Yes	Measured	Trachops cirrhosus
AMNH/MUSM	15286	AMNH/MUSM-15286	Yes	Measured	Trachops cirrhosus
AMNH/MUSM	15287	AMNH/MUSM-15287	Yes	Measured	Trachops cirrhosus
USNM	566489	USNM-566489	Yes	Measured	Trachops cirrhosus
USNM	566490	USNM-566490	Yes	Measured	Trachops cirrhosus
USNM	566491	USNM-566491	Yes	Measured	Trachops cirrhosus
FMNH	174887	FMNH-174887	No	Sequenced	Trachops cirrhosus
FMNH	174888	FMNH-174888	No	Sequenced	Trachops cirrhosus
AMNH	230213	AMNH-230213	Yes	Both	Trachops cirrhosus
USNM	364272	USNM-364272	Yes	Measured	Trachops cirrhosus
ROM	125898	ROM-125898	No	Sequenced	Trachops cirrhosus
ROM	125914	ROM-125914	No	Sequenced	Trachops cirrhosus
ROM	126156	ROM-126156	No	Sequenced	Trachops cirrhosus
ROM	117523	ROM-117523	No	Sequenced	Trachops cirrhosus
ROM	121252	ROM-121252	No	Sequenced	Trachops cirrhosus
ROM	121044	ROM-121044	No	Sequenced	Trachops cirrhosus
ROM	121090	ROM-121090	No	Sequenced	Trachops cirrhosus
ROM	121159	ROM-121159	No	Sequenced	Trachops cirrhosus
AMNH	175602	AMNH-175602	No	Sequenced	Trachops cirrhosus
AMNH	256313	AMNH-256313	Yes	Measured	Trachops cirrhosus
AMNH	180034	AMNH-180034	Yes	Measured	Trachops cirrhosus

AMNH	175603	AMNH-175603	Yes	Measured	Trachops cirrhosus
AMNH	175600	AMNH-175600	No	Sequenced	Trachops cirrhosus
ROM	107843	ROM-107843	No	Sequenced	Trachops cirrhosus
USNM	388865	USNM-388865	Yes	Measured	Trachops cirrhosus
USNM	388869	USNM-388869	Yes	Measured	Trachops cirrhosus
USNM	407611	USNM-407611	Yes	Measured	Trachops cirrhosus
USNM	407614	USNM-407614	Yes	Measured	Trachops cirrhosus
USNM	373534	USNM-373534	Yes	Measured	Trachops cirrhosus
USNM	373539	USNM-373539	Yes	Measured	Trachops cirrhosus
AMNH	235556	AMNH-235556	Yes	Measured	Trachops cirrhosus
AMNH	235557	AMNH-235557	Yes	Measured	Trachops cirrhosus
AMNH	235551	AMNH-235551	No	Sequenced	Trachops cirrhosus
USNM	517312	USNM-517312	Yes	Measured	Trachops cirrhosus
ROM	107935	ROM-107935	No	Sequenced	Trachops cirrhosus
ROM	107908	ROM-107908	No	Sequenced	Trachops cirrhosus
ROM	107926	ROM-107926	No	Sequenced	Trachops cirrhosus
USNM	388852	USNM-388852	Yes	Measured	Trachops cirrhosus
USNM	388856	USNM-388856	Yes	Measured	Trachops cirrhosus
USNM	444405	USNM-444405	Yes	Measured	Trachops cirrhosus
USNM	385510	USNM-385510	Yes	Measured	Trachops cirrhosus
USNM	385511	USNM-385511	Yes	Measured	Trachops cirrhosus
AMNH	31522	AMNH-31522	Yes	Both	Trachops cirrhosus
AMNH	31520	AMNH-31520	Yes	Measured	Trachops cirrhosus
AMNH	31521	AMNH-31521	Yes	Measured	Trachops cirrhosus
USNM	444404	USNM-444404	Yes	Measured	Trachops cirrhosus
USNM	371556	USNM-371556	Yes	Measured	Trachops cirrhosus
USNM	371557	USNM-371557	Yes	Measured	Trachops cirrhosus
USNM	419151	USNM-419151	Yes	Measured	Trachops cirrhosus
USNM	419153	USNM-419153	Yes	Measured	Trachops cirrhosus
USNM	419242	USNM-419242	Yes	Measured	Trachops cirrhosus
USNM	444396	USNM-444396	Yes	Measured	Trachops cirrhosus
USNM	444398	USNM-444398	Yes	Measured	Trachops cirrhosus
ROM	107945	ROM-107945	No	Sequenced	Trachops cirrhosus
USNM	444382	USNM-444382	Yes	Measured	Trachops cirrhosus
USNM	371559	USNM-371559	Yes	Measured	Trachops cirrhosus
USNM	371560	USNM-371560	Yes	Measured	Trachops cirrhosus
USNM	419248	USNM-419248	Yes	Measured	Trachops cirrhosus
TOTALS		238	22	Both	
			216	Measured	
			56	Sequenced	

subspecies	Country	State/Province
coffini	Belize	Orange Walk County
coffini	Belize	Orange Walk District
coffini	Belize	Orange Walk District
coffini	Belize	Orange Walk District
coffini	Belize	Orange Walk District
coffini	Belize	Stann Creek
cirrhosus	Bolivia	Beni
cirrhosus	Bolivia	Santa Cruz
cirrhosus	Brazil	Amazonas
cirrhosus	Brazil	Amazonas
cirrhosus	Brazil	Amazonas
cirrhosus	Brazil	Para
cirrhosus	Brazil	Rondonia
ehrhardti	Brazil	Santa Catarina
ehrhardti	Brazil	Sao Paulo
ehrhardti	Brazil	Sao Paulo
ehrhardti	Brazil	Sao Paulo
cirrhosus	Colombia	Antioquia
cirrhosus	Colombia	Arauca
cirrhosus	Colombia	Arauca

cirrhosus	Colombia	Arauca
cirrhosus	Colombia	Bolívar
cirrhosus	Colombia	Caquetá
cirrhosus	Colombia	Casanare
cirrhosus	Colombia	Cesar
cirrhosus	Colombia	Córdoba
cirrhosus	Colombia	Guainía
cirrhosus	Colombia	Guainía
cirrhosus	Colombia	Magdalena
cirrhosus	Colombia	Meta
cirrhosus	Colombia	Nariño
cirrhosus	Colombia	Norte de Santander
cirrhosus	Colombia	Putumayo
cirrhosus	Colombia	Putumayo
cirrhosus	Colombia	Valle del Cauca
cirrhosus	Colombia	Vichada
cirrhosus	Colombia	Vichada
cirrhosus	Colombia	Vichada
cirrhosus	Costa Rica	Guanacaste
cirrhosus	Costa Rica	Heredia
cirrhosus	Costa Rica	Heredia
cirrhosus	Costa Rica	Limon
cirrhosus	Costa Rica	Limón

cirrhosus	Costa Rica	Puntarenas
cirrhosus	Costa Rica	Puntarenas
cirrhosus	Ecuador	Esmeraldas
cirrhosus	Ecuador	Guayas
cirrhosus	Ecuador	Los Ríos
cirrhosus	Ecuador	Los Ríos
cirrhosus	Ecuador	Los Ríos
cirrhosus	Ecuador	Napo
cirrhosus	Ecuador	Napo
cirrhosus	Ecuador	Napo
cirrhosus	Ecuador	Orellana
cirrhosus	Ecuador	Pastaza
cirrhosus	Ecuador	Pichincha
cirrhosus	Ecuador	Sucumbios
cirrhosus	Ecuador	Sucumbios
cirrhosus	Ecuador	Sucumbios
cirrhosus	Ecuador	Sucumbíos

cirrhosus	Ecuador	Sucumbíos
cirrhosus	Ecuador	Zamora Chinchipe
cirrhosus	French Guiana	Cayenne
cirrhosus	French Guiana	Paracou
coffini	Guatemala	Chimaltenango
coffini	Guatemala	El Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
coffini	Guatemala	Peten
cirrhosus	Guyana	Barima-Waini
cirrhosus	Guyana	Barima-Waini
cirrhosus	Guyana	Cuyuni-Mazaruni
cirrhosus	Guyana	Essequibo Islands-West Demerara
cirrhosus	Guyana	Potaro-Siparuni
cirrhosus	Guyana	Potaro-Siparuni
cirrhosus	Guyana	Upper Demerara-Berbice
cirrhosus	Guyana	Upper Demerara-Berbice
cirrhosus	Guyana	Upper Demerara-Berbice
cirrhosus	Guyana	Upper Takutu - Upper Essequibo
cirrhosus	Guyana	Upper Takutu-Upper Essequibo
cirrhosus	Guyana	Upper Takutu-Upper Essequibo
cirrhosus	Guyana	Upper Takutu-Upper Essequibo
cirrhosus	Guyana	Upper Takutu-Upper Essequibo
coffini	Honduras	Lempira

coffini	Honduras	Lempira
coffini	Mexico	Campeche
coffini	Mexico	Oaxaca
cirrhosus	Panama	Bocas Del Toro
cirrhosus	Panama	Bocas Del Toro
cirrhosus	Panama	Canal Zone
cirrhosus	Panama	Canal Zone
cirrhosus	Panama	Darien
cirrhosus	Panama	Los Santos
cirrhosus	Panama	Panama
cirrhosus	Panama	Panama
cirrhosus	Panama	Panama
cirrhosus	Panama	Veraguas
cirrhosus	Panama	

cirrhosus	Panama	
cirrhosus	Peru	Huanuco
cirrhosus	Peru	Huanuco
cirrhosus	Peru	Loreto
cirrhosus	Peru	Madre De Dios
cirrhosus	Peru	Madre De Dios
cirrhosus	Peru	Madre De Dios
cirrhosus	Peru	Madre de Dios
cirrhosus	Peru	Madre de Dios
cirrhosus	Peru	Pasco
cirrhosus	Peru	Pasco
cirrhosus	Suriname	Brokopondo
cirrhosus	Suriname	Brokopondo
cirrhosus	Suriname	Para
cirrhosus	Suriname	Sipaliwini
cirrhosus	Trinidad and T	Trinidad
cirrhosus	Trinidad and T	Trinidad
cirrhosus	Trinidad and T	Trinidad

cirrhosus	Trinidad and T	Trinidad
cirrhosus	Trinidad and T	Trinidad
cirrhosus	Venezuela	Amazonas
cirrhosus	Venezuela	Apure
cirrhosus	Venezuela	Apure
cirrhosus	Venezuela	Aragua
cirrhosus	Venezuela	Bolivar
cirrhosus	Venezuela	Carabobo
cirrhosus	Venezuela	Carabobo
cirrhosus	Venezuela	Carabobo
cirrhosus	Venezuela	Falcon
cirrhosus	Venezuela	Falcon
cirrhosus	Venezuela	Falcon
cirrhosus	Venezuela	Guarico
cirrhosus	Venezuela	Trujillo
cirrhosus	Venezuela	Trujillo
cirrhosus	Venezuela	Zulia

Verbatim Precise Locality	Latitude	Longitude
Lamanai Lodge	17.752072	-88.656762
Ka'Kabish Archaeological Reserve	17.767250	-88.867436
Ka'Kabish Archaeological Reserve	17.767250	-88.867436
Ka'Kabish Archaeological Reserve	17.767250	-88.867436
Ka'Kabish Archaeological Reserve	17.767250	-88.867436
Cockscomb Basin Wildlife Sanctuary	16.773611	-88.532500
ca. 1.5 kilometers below Costa Marquez, Itenez River	-13.334992	-63.439769
ca. 1.5 kilometers below Costa Marquez, Itenez River	-13.334992	-63.439769
Baures River mouth	-11.094083	-65.281711
ca. 4 kilometers above Costa Marques, Itenez River	-13.334992	-63.439769
ca. 5 kilometers northwest of Grande River mouth	-13.334992	-63.439769
ca. 5 kilometers northwest of Grande River mouth	-13.334992	-63.439769
ca. 5 kilometers northwest of Grande River mouth	-13.334992	-63.439769
El Beni, Mamore, Camino Vilches	-13.066700	-64.800000
National Park Kempff Mercado, El Refugio	-14.766389	-61.034722
Manaus, 80 Km N (By Road)	-2.510833	-60.017500
Manaus, 80 Km N (By Road)	-2.510833	-60.017500
Rosarinho. Rio Madeira	-5.8753	-61.3903
Tauari, Tapajos River	-3.083333	-55.100000
Tauari, Tapajos River	-3.083333	-55.100000
Altamira, 17 Km S (By Road), Caverna Do Tatajuba	-3.630000	-52.350000
Altamira, 52 Km SSW, E Bank Rio Xingu	-3.650000	-52.370000
Belem, Fazenda Velha	-1.444722	-48.501389
Belem, Station A Ian	-1.444722	-48.501389
Belem, Varzea	-1.444722	-48.501389
Tapajos River, Igarape Brabo	-2.466667	-54.750000
Tapajos River, Inajatuba	-4.115556	-56.609722
Rondonia, Cachoeira Nazare, Rio Ji-Parana	-8.225000	-62.726667
Joinville	-26.293056	-48.827778
Joinville	-26.293056	-48.827778
Joinville	-26.293056	-48.827778
Mount Hansa	-26.881944	-48.451389
Bairro do Betari, Gruta do Betari	-24.586389	-48.593889
Ilha do Cardoso.	-25.133300	-47.966700
Primeiro Morro.	-24.366700	-47.816700
25 Km South, 22 Km West from Zaragoza, La Tirana	7.261694	-75.028628
26 Km South, 22 Km West from Zaragoza, Aljibes	7.258047	-75.047181
Zaragoza, 25 Km S, 22 Km W, At La Tirana	7.485089	-74.867306
Zaragoza, 25 Km S, 22 Km W, At La Tirana	7.485089	-74.867306
Finca La Tormenta, Caño Salas	6.8121111	-71.0755
Caño Juriepe, Finca La Aurora, Bosques de Juriepe	6.2339722	-69.716333

Reserva Forestal Protectora Rio Tame, Vereda Sabana de La Venta	6.3843611	-71.926389
Vereda Puna Puna, Hacienda la Envidia	6.3301667	-71.772222
Vereda San Joaquín, finca El Santuario, bosque de vega, cerca de Arauca, 1000ft: Rio Arauca.	6.222532	-71.566834
Arauca, 1000ft: Rio Arauca.	6.203630	-68.964500
Mompox, Norosi	6.203630	-68.964500
PNN Serrania de Chiribiquete, Corregimiento SE río Mesay, Putumayo	9.239653	-74.425617
Vereda Cupiagua, caño abajo de pozo V	0.0741667	-72.451389
Vereda La Manga, finca La Reserva, caño Yaguarapo	5.2262222	-72.626858
Vereda La Manga, finca La Reserva, caño Yaguarapo	6.198954	-71.603834
Corregimiento La Hermosa, finca Nicaragua, bajo de quebrada	5.6641667	-70.2425
Sin descripcion del lugar de colecta-Paz de Ariporo	5	-70
Sin descripcion del lugar de colecta-Paz de Ariporo	5	-70
Rio Guaimaral	9.204211	-73.656131
Rio Guaimaral	9.204211	-73.656131
Valledupar, El Orinoco, Rio Cesar	9.474669	-74.058406
Valledupar, El Orinoco, Rio Cesar	9.474669	-74.058406
Valledupar, Rio Guaimaral	9.204211	-73.656131
Valledupar, Rio Guaimaral	9.204211	-73.656131
Valledupar, Rio Guaimaral	9.204211	-73.656131
Valledupar, Rio Guaimaral	9.204211	-73.656131
Valledupar, Rio Guaimaral	9.204211	-73.656131
Corregimiento El Porveni, Vereda El Peñon, Predio de ODL	9.3963611000	-75.7071944000
Randal Alto (ca. Zancudo). Río Inírida, Guainía	2.766667	-69.366667
Randal Alto (ca. Zancudo). Río Inírida, Guainía	2.766667	-69.366667
Bonda	11.233425	-74.123428
Trocha 1 Km de la Cabaña Duda	2.180033	-73.783108
Rivera del río Tillavá	3.8275556000	-71.2658417000
Meta, Villavicencio, 400m, San Juan de Arama, Los Micos.	3.283330	-73.883300
Quebrada Alegría, Fuente de Materiales Valle	3.717222	-74.296667
Villavicencio, 650m.	4.141944	-73.626667
Inguapí del Guadual, 15 km Tumaco	1.700000	-78.766667
Rio de Oro	8.294119	-73.387344
Putumayo, San Antonio, 185m: Rio Mecaya.	0.466667	-75.333300
Putumayo, San Antonio, 185m: Rio Mecaya.	0.466667	-75.333300
Fuente de materiales, Bahía de Málaga, 40 m Valle	3.976111	-77.325278
PNN El Tuparro, Centro Administrativo	5.309489	-67.894906
PNN El Tuparro, Corregimiento Santa Rita	5.286408	-68.319869
PNN El Tuparro, Corregimiento Santa Rita	5.286408	-68.319869
Refugio Rafael Rodriguez, Hacienda Palo Verde	10.350056	-85.349583
Parque Nacional Braulio Carrillo, San Miguel, 1 Km S, 11.5 Km	9.980775	-84.051450
River Station, Bridge At, La Selva	10.427456	-84.006339
Cano Palma Biological Station	10.600000	-83.530000
Limon, 10ft: Tortuguero, shore opposite.	10.583300	-83.516700

Osa Peninsula, Llorona, Piedra El Arco	9.401969	-84.080308
Puntarenas, Monteverde.	10.300000	-84.700000
Comuna San Francisco de Bogota	1.09343	-78.7063
Estero El Salto, Centro Comunal Awa Mataje	1.200000	-78.561667
San Lorenzo	1.275994	-78.832183
San Lorenzo, Estación La Chiquita	1.23333	-78.76
San Lorenzo, Estación La Chiquita	1.23333	-78.76
Urbina	1.036667	-78.773611
3 km al S de San Miguel (selva)		
Central Hidroeléctrica Marcel Lianado de Wind-Carlas Julio-R	-0.9252312	-79.761266
Santo Domingo, 47 Km S (By Road), Rio Palenque Science Cer	-0.586400	-79.364700
Centro Científico Río Palenque	-0.58884	-79.36106
Centro Científico Río Palenque	-0.58884	-79.36106
Jondachi	-0.79215	-77.7772
Jumandi, 4 km N de Archidona	-0.8721	-77.7914
Gareno, Río Gareno, junto pozo de exploracion Nemora, terri	-1.0485	-77.3774
5 km SW de Marian	-0.083333	-76.350000
Amo C, 101,1 km S de Pompeya Sur	-0.9419245	-76.22474
Parque Nacional Yasuní, Tambococha	-1.02253	-75.448
Parque Nacional Yasuní, Tambococha	-1.02253	-75.448
Parroquia Cononaco, Bloque 16, Repsol YPF-NPF, Km 66, La C	-0.806932	-76.3976
Parroquia Cononaco, Territorio Huaorani, Zona Intangible, fre	-1.2671	-76.3836
Puente de Dosel Chuncho-Yura	-0.643669	-75.9102
Puente de Dosel Pandu	-0.684732	-75.9236
Puente de Dosel Pandu	-0.684732	-75.9236
Vía Nenke-Apaika, orillas del Río Huiririma	-0.64833	-75.9136
Estación Científica Yasuní, Sendero Barizo	-0.67505	-76.3999
Estación Científica Yasuní, Sendero Ceiba, junto a la estación	-0.67616	-76.3959
Parque Nacional Yasuní, Estación Cientifica Yasuní	-0.678193	-76.3966
Yasuní, P.N., El Saladero, km 78	-0.8333333	-76.333333
Caimitoyacu. Cerca de la boca de Suno		
Iripari		
El Edén, Río Napo bajo, cerca a la bocana del Río Yuturi	-0.539787	-76.0237
Comunidad Tarangaro	-1.40062	-77.3835
La Unión del Toachi	-0.31383	-78.9544
Reserva Biológica Limoncocha	-0.400000	-76.633333
Pozo petrolero Paujil		
Río Aguarico. Comunidad Cofán. Záballo	-0.400000	-75.633333
Destacamento Patria, hito 63	-0.46503	-75.3451
Puente del Río Cuyabeno, Hostería Monte Tour, Vía Tarapoa-	-0.0315	-76.32111
Puente del Río Cuyabeno, Hostería Monte Tour, Vía Tarapoa-	-0.0315	-76.32111
Puente del Río Cuyabeno, Hostería Monte Tour, Vía Tarapoa-	-0.0315	-76.32111
Reserva de Producción Faunística Cuyabeno, Santa Elena	-0.315235	-75.9624

Reserva de Producción Faunística Cuyabeno, Jamu Lodge, ori	-0.034808	-76.1644
Záballo	-0.31812	-75.7662
Záballo	-0.31812	-75.7662
Nueva Esmeralda	-0.18383	-76.7334
Reserva Biológica Limoncocha	-0.4079	-76.6206
Shushufindi	-0.18329	-76.6451
Destacamento Shaime, Ríos Shaime y Nangaritza	-4.3344	-78.6807
Paracou	5.283333	-52.916667
Paracou near Sinnamary	5.283333	-52.916667
Chimaltenango, 4400ft: Municipio de Yepocapa, Finca Recred	14.466700	-90.983300
Campo Los Guacamayos, Biotopo Laguna Del Tigre, 40 km N	17.580039	-90.811972
Guyo	16.900561	-90.293000
Baramita, North Side Airstrip	7.371400	-60.495800
Kumaka	7.650000	-58.950000
Mount Roraima, Ridge Camp	5.203125	-60.736975
Shanklands	6.483333	-58.583333
Sandstone, Iwokrama Forest	4.383740	-58.921220
Surama Lake	4.150980	-59.038460
Dubulay Ranch	5.681944	-57.860556
Dubulay Ranch, Region 10, Subregion 2	5.666667	-57.850000
Tropenbos, 20 km SSE of Mabura Hill	5.133306	-58.724472
Tropenbos, 20 km SSE of Mabura Hill	5.133306	-58.724472
Rupununi Savanna	2.999722	-59.499722
1 km upstream From Charwir River Mouth, Rupununi River	2.486389	-59.476389
Dadanawa, 15 Mi E, Weramna-Boco, Savannah Creek	2.824167	-59.525833
Dadanawa, 15 Mi ENE, Comiwari Wau	2.824167	-59.525833
Dadanawa, 15 Mi ENE, Comiwari Wau	2.824167	-59.525833
Dadanawa, 30 Mi ENE, Caribuan Forest	2.824167	-59.525833
Las Flores	14.711836	-88.623428

Las Flores	14.711836	-88.623428
Las Flores	14.300000	-87.833333
44 km S of Constitucion, 44 km S, 70 km E of Escarcega	18.250000	-90.066667
4 miles west of San Pedro Tapanatepec, Ostuta River	16.371111	-94.193056
6 miles north of Matias Romero	16.878889	-95.039444
6 miles north of Matias Romero	16.878889	-95.039444
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6 miles north of Matias Romero	16.878889	-95.039444
Matias Romero, 17 Mi N	16.878889	-95.039444
Matias Romero, 17 Mi N	16.878889	-95.039444
Matias Romero, 17 Mi N	16.878889	-95.039444
Matias Romero, 17 Mi N	16.878889	-95.039444
Palomares, 11.7 Mi S	17.138333	-95.062778
Isla Colon, La Gruta	9.391167	-82.277333
Isla Colon, La Gruta	9.391167	-82.277333
Parque Nacional Soberania	9.074333	-79.659778
Sherman	9.365000	-79.958611
Meteti, Filo del Tallo, Net 2	8.465395	-77.992463
Meteti, Filo del Tallo, Net 3	8.465395	-77.992463
Parque Nacional Darien, Rancho Frio, ANAM Ranger Station,	8.016700	-77.729460
Parque Nacional Darien, Rancho Frio, ANAM Ranger Station,	8.016700	-77.729460
Tacarcuna, Village Camp	8.165417	-77.295806
Tacarcuna, Village Camp	8.165417	-77.295806
Tacarcuna, Village Camp	8.165417	-77.295806
Tacarcuna, Village Camp	8.165417	-77.295806
Tacarcuna, Village Camp	8.165417	-77.295806
La Jagua	7.866667	-80.350000
Summit	9.066667	-79.650000
40 miles east of Panama City, La Cagna River	8.910111	-78.846861
Chilibillo River	9.171977	-79.623222
Nuri [Montijo District]	7.979194	-81.042556
Chepo Road	9.167778	-79.093611

Chilibrillo Cave	9.171977	-79.623222
Mandinga	9.450000	-79.066667
Mandinga	9.450000	-79.066667
Mandinga	9.450000	-79.066667
Pacora	9.079444	-79.290000
Panama City, Chepo Rd.	8.966670	-79.533300
Llullapichis River, tributary of Pachitea River	-9.350000	-74.510000
Llullapichis River, tributary of Pachitea River	-9.370000	-74.550000
Nuevo San Juan, Galvez River	-5.250000	-73.166667
Nuevo San Juan, Galvez River	-5.250000	-73.166667
Nuevo San Juan, Galvez River	-5.250000	-73.166667
Nuevo San Juan, Galvez River	-5.250000	-73.166667
Orosa, Amazon River	-3.533333	-72.183333
Jenaro Herrera	-4.905000	-73.669722
Sarayacu, Ucayali River	-6.783333	-75.116667
Sarayacu, Ucayali River	-6.783333	-75.116667
Sarayacu, Ucayali River	-6.783333	-75.116667
Río Galvez; Nuevo San Juan	-5.250000	-73.166667
Río Galvez; Nuevo San Juan	-5.250000	-73.166667
Río Galvez; Nuevo San Juan	-5.250000	-73.166667
Río Galvez; Nuevo San Juan	-5.250000	-73.166667
Río Galvez; Nuevo San Juan	-5.250000	-73.166667
Río Galvez; Nuevo San Juan	-5.250000	-73.166667
Cocha Salvador	-12.003028	-71.215694
Pakitza	-11.944917	-71.282972
Pakitza	-11.944917	-71.282972
Madre de Dios, Manu, 480m: Maskotania, 13.4 km NNW Ata	-12.771600	-71.385400
Madre de Dios, Manu, 480m: Maskotania, 13.4 km NNW Ata	-12.771700	-71.385500
San Juan	-10.371111	-76.198056
San Juan	-10.371111	-76.198056
Brownsberg Nature Park	4.946690	-55.183450
Brownsberg Nature Park	4.946690	-55.183450
Sabajo, Transect AF1	5.093790	-54.847260
Bakhuis	4.740597	-56.801583
Kasikasima	2.977410	-55.384790
Merian Site 3	5.103570	-54.516580
Upper Palumeu River	2.477050	-55.629410
Upper Palumeu River	2.477050	-55.629410
Cap-de-Ville	10.152500	-61.707500
Fyzabad	10.181111	-61.545833
Parry Lands, Lot 10	10.182222	-61.620833

Penal Rock Road	10.133361	-61.435972
Edwards Trace	10.116194	-61.196833
Pozon, 50 km NE of Puerto Ayacucho	6.050000	-67.416667
Rio Mavaca, 108 Km SSE Esmeralda	2.250000	-65.280000
Rio Mavaca, 108 Km SSE Esmeralda	2.250000	-65.280000
San Juan, 163 Km ESE Pto. Ayacucho, Rio Manapiare	5.300000	-66.220000
San Juan, 163 Km ESE Pto. Ayacucho, Rio Manapiare	5.300000	-66.220000
Hato Cariben, 32 Km NE Pto. Paez, La Villa	6.550000	-67.220000
Hato Cariben, 32 Km NE Pto. Paez, La Villa	6.550000	-67.220000
Rancho Grande	10.216667	-67.416667
Rancho Grande	10.216667	-67.416667
Rancho Grande	10.216667	-67.416667
Maracay, 4 Km NW, El Limon	10.283333	-67.600000
3 km E of Puerto Cabello Del Caura	7.166667	-64.983333
Hata La Cerbatana, 20 km S of Guaniamo	6.433333	-66.116667
Hato La Florida, 35 km Ese of Caicara	7.566667	-65.866667
Hato San Jose, 20 Km W La Paragua	6.820000	-63.480000
Hato San Jose, 20 Km W La Paragua	6.820000	-63.480000
Icabaru, 45 Km NE Icabaru, Santa Lucia De Surukun	4.550000	-61.420000
km. 125, 85 Km SSE El Dorado	5.980000	-61.430000
km. 125, 85 Km SSE El Dorado	5.980000	-61.430000
San Esteban	10.433333	-68.016667
San Esteban	11.233333	-74.133333
San Esteban	10.433333	-68.016667
Riecito, 30 Km S Mirimiri	10.900000	-68.770000
Urama, 19 Km NW Urama, Km 40	10.620000	-68.400000
Urama, 19 Km NW Urama, Km 40	10.620000	-68.400000
Embalse De Guarico, 10 Km N Calabozo	9.020000	-67.430000
Embalse De Guarico, 10 Km N Calabozo	9.020000	-67.430000
Embalse De Guarico, 10 Km N Calabozo	9.020000	-67.430000
Estacion Biologica De Los Llanos, 14 Km SE Calabozo, Nr. Rio	8.820000	-67.370000
Estacion Biologica De Los Llanos, 14 Km SE Calabozo, Nr. Rio	8.820000	-67.370000
Rio Orituco, 10 km W of Chaguramas	9.400000	-66.466667
San Jose De Tiznados, 52 Km NNW Calabozo	9.380000	-67.570000
Valera, 23 Km NNW Valera, Rio Motatan	9.530000	-70.670000
Valera, 23 Km NNW Valera, Rio Motatan	9.530000	-70.670000
El Rosario, 60 Km WNW Encontrados, Boca Del Rio De Oro	9.120000	-72.770000