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Cryptic diversity in common mustached bats *Pteronotus* cf. *parnellii* (Mormoopidae) in French Guiana and Brazilian Amapa

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The common mustached bat (*Pteronotus parnellii*) is a mormoopid bat living in caves in lowland rainforests throughout the north and eastern Neotropics, including several Caribbean islands. Recent studies have shown that this taxon is certainly a composite of several cryptic species, especially in the western part of the Guianan Shield, where molecular reconstructions and bioacoustics point to the presence of at least two cryptic species that may not be related to genuine *P. parnellii*, native to Jamaica. We examined here over 200 bioacoustically identified individuals to show that two phonic types live in sympatry in French Guiana with no overlap in frequencies of echolocation calls. Morphological variation in some skull characters showed consistent and significant differences between the two phonic types, whereas external measurements alone were unable to discriminate between groups. Two mitochondrial markers analyzed in a selection of each of these phonic types were further used to evidence that they represent two genetically discrete groups, and to assign them to the existing molecular clades described elsewhere. Molecular comparisons with reference specimens sampled near the type localities of *P. parnellii* and *P. rubiginosus* further suggest that the 53 kHz phonic type found in French Guiana and Amapa (Brazil) should be assigned to the later species, while the 59 kHz phonic type represents an undescribed species.

*Key word*s: cryptic species, bioacoustics, mitochondrial DNA, Guianan Shield

INTRODUCTION

The Mormoopidae is a widely distributed family of Neotropical insectivorous bats ranging from the southwestern United States to southern Brazil, including many islands in the Antilles. The Mormoopidae is composed of two genera, *Mormoops* and *Pteronotus* (Simmons, 2005). One species, the common mustached bat (*Pteronotus parnellii*) is the only high-duty cycle echolocating bat in the Neotropics, i.e. one that uses constant frequency (CF) calls to orientate itself (Schnitzler and Kalko, 1998). This species was described by Gray (1843) using animals originating in Jamaica, but it is often viewed as a widespread species living across most of the Antilles, Central and tropical South America (e.g., Simmons, 2005). Eight subspecies have been described throughout this wide range, including some former continental species that are now considered as synonyms of *P. parnellii* (reviewed in Herd, 1983; and Simmons, 2005).

However, recent phylogenetic studies revealed that populations of the common mustached bat (CMB) are not homogeneous and bear much hidden biodiversity across their geographic range. Using sequences of the cytochrome *b* gene (Cyt *b*), Lewis-Oritt *et al.* (2001) showed that animals from the type locality in Jamaica are genetically very distinct (11% sequence divergence) from specimens in Suriname or Guyana, while similar levels of

divergence separate some bats from Suriname and those from Guyana or Mexico. By using an improved geographic sampling and combining mitochondrial and nuclear genes, Davalos (2006) confirmed the large molecular divergence between *P. parnellii* sampled in the Antilles (Jamaica, Puerto Rico and Hispaniola), and mainland lineages. One of these divergent lineages was located in French Guiana and Suriname, and the other in Mexico, Honduras and Guyana. Based on genetic, morphological and distributional data, Davalos (2006) and Van Den Bussche and Weyandt (2003) proposed that the mainland CMB might represent cryptic species different from Jamaican *P. parnellii*. Davalos (2006) further suggested that the name *P. rubiginosus* (Wagner, 1843) would be appropriate to name the continental lineage represented by CMB from French Guiana, Guyana, Suriname, Mexico and Honduras.

More recently, Clare *et al.* (2013) analyzed mitochondrial and nuclear gene variation together with morphological and some acoustic data to show that the CMB found in Central and South America represent four independent, biological species, and confirmed that the name *P. parnellii* should be restricted to bats from Jamaica and perhaps other islands in the Greater Antilles. These Jamaican CMB emitted CF echolocation calls at ca. 61 kHz (Clare *et al*., 2013). These authors further used DNA barcodes of the cytochrome oxydase 1 gene (CO1) to circumscribe four major clades of continental CMB that may each represent a distinct species. The correlation of these molecular clades with morphological characters was good, but none of the individual measurements were able to discriminate all clades. Using this integrated approach, Clare *et al.* (2013) reached the following taxonomic conclusions for continental taxa: (i) their clade 1 (or Group 1) is comprised of all CMB sampled in Central America (from Panama to southern Mexico) and are relatively small (mean forearm length, FA = 59.9 mm). They emit CF echolocation calls at about 62 kHz and could be named *P. mesoamericanus*; (ii) their clade 2 (Group 2) is comprised of CMB sampled in Venezuela, Trinidad and western Guyana and are medium-sized (mean FA = 62.4 mm). They emit CF calls at about 59 kHz (although no call from continental animals could be obtained), and would be an unnamed species (*P.* sp2); (iii) their clade 3 (Group 3) includes specimens from Guyana and Suriname that are medium-sized (mean FA = 63.2 mm) and may represent another unnamed species (*P.* sp3); (iv) their clade 4 (Group 4) includes specimens from the same area as those of clade 3 (Guyana and Suriname), but are significantly larger (mean FA = 65.2 mm), and represent a forth unnamed species (*P.* sp4). The CF calls recorded from free-flying CMB from Guyana were at 53–54 kHz, but as no match with genetically identified animals could be obtained, Clare *et al.* (2013) were unable to associate these call characteristics with either clade 3 or clade 4. During a study of acoustic identification in French Guiana, Barataud *et al*. (2013) found two different phonic types in CMB and suggested that two cryptic species might coexist in sympatry.

In this study, we describe bioacoustic variation of over 200 CMB sampled in French Guiana and nearby Amapa State in Brazil, to show that two distinct phonic types live in sympatry in extended parts of this geographic range. We also characterize the molecular identity of these two phonic types and link them to published samples or clades to make our taxonomic recommendations. Morphological characters, although not completely discriminant between the two phonic groups, are also described to aid their identification in the field or for museum specimens.

Materials and methods

Sampling

Mormoopid bats were sampled from 14 localities of French Guiana and Amapa (Fig. 1). Capture methods included essentially mist nets set either at the entrance of caves or across nearby corridors such as trails in the forest. Mist nets of 2.6 × 6 m and 2.6 × 10 m were employed at ground level. At Cacao (locality 3 in Fig. 1), we used a three-frame harp trap (AUSTBAT Research Equipment, Victoria, Australia), with a catching surface of 1.0 m^2. This trap was erected across a trail acting as a corridor for bats flying out of a nearby cave system.

External measurements and ultrasonic calls were recorded for all captured bats after which they were released. Prior to release, a small biopsy punch (Worthington-Wilmer and Barratt, 1996) was used to collect tissues from some individuals for DNA analyses. A selection of 25 euthanized specimens was preserved as scientific vouchers herein used to obtain cranial measurements. These voucher specimens were euthanized according to ASM guidelines (Gannon and Sikes, 2007), fixed in 10% buffered formalin, and stored in 70% ethanol (Appendix I).

Morphology

Gender and reproductive status were acquired from external characteristics (e.g., enlarged nipples or testis) or from gross examination of dissected specimens (Racey, 2009). All specimens reported here were adults as indicated by completely fused phalangeal epiphyses. The following external measurements were taken with a dial calliper accurate to 0.1 mm: forearm length (FA), metacarpal of third digit (MC3), metacarpal of fourth digit (MC4), total length of fourth digit (D4), and tibia length (TI). Digit measurements were taken from the right wing held flat on a solid surface with the wrist extended.

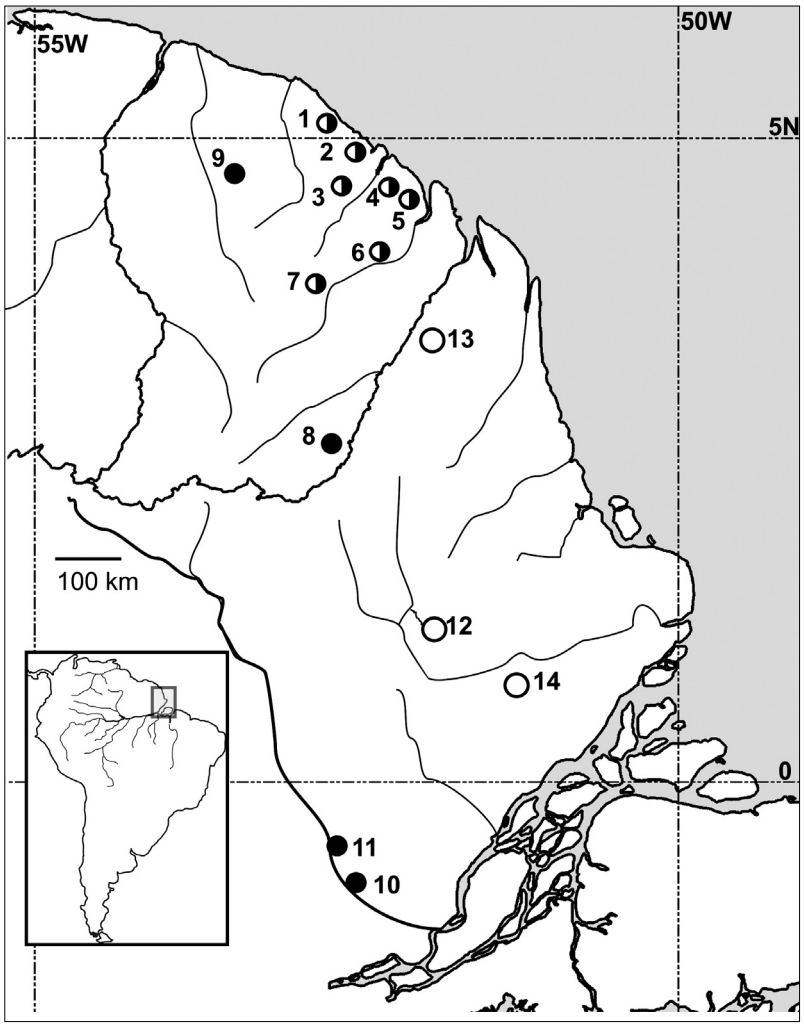

FIG. 1. Map of French Guiana (localities 1 to 9) and Amapa, Brazil (10 to 14) locations where bats of the 53 kHz (white circles) and the 59 kHz phonic types (black circles) have been characterized through bioacoustics, skull morphometry and/or molecular genetics. Localities harbouring both phonic types in sympatry are indicated by a pie circle. 1 — Macouria River, municipality of Tonate, 05°02'N, 52°30'W; 2 — Quartier Torcy, municipality of Roura, 04°50'N, 52°16'W; 3 — Cacao, municipality of Roura, 04°34'N, 52°27'W; 4 — Trésor Natural Preservation, municipality of Roura, 04°37'N, 52°17'W; 5 — Grotte Mathilde, municipality of Regina, 04°31'N, 52°07'W; 6 — Montagne des Gouffres, municipality of Regina, 04°20'N, 52°16'W; 7 — Saut-Pararé, municipality of Regina, 04°02'N, 52°42'W; 8 — Montagne Cacao by Haute Camopi, municipality of Camopi, 02°20'N, 53°12'W; 9 — La Trinité, municipality of Saint Elie, 04°61'N, 53°40'W; 10 — Iratapuru village, near to Laranjal do Jari, Jari river, 00°37'S, 52°31'W; 11 — Itapeuara village, near to Laranjal do Jari, Jari river, 00°29'S, 52°41'W; 12 — P. N. Tumucumaque, Rio Mutum, municipality of Calçoene, 01º23'N, 51º55'W; 13 — P. N. Tumucumaque, Rio Anoteie, municipality of Oiapoque, 03º13'N; 52º01'W; 14 — Aricari farm/BR156 road, km 147, municipality of Tartarugalzinho, 00º56'N, 51º14'W

Skull and dental measurements were taken with a dial caliper (accurate to 0.05 mm) following the methods detailed in Gutierrez and Molinari (2008) and Simmons and Voss (1998) except when noted: greatest length of skull (bone-to-bone: GLS) and greatest length of skull including the upper incisors (GLSI), braincase depth (BRD), maxillary toothrow length (MTL), condylo-incisive (CIL) and condylo-canine lengths (CCL), palatal length (distance between the posterior palatal notch and the lateral border of the incisors PL), length of upper molars (M^1M^3), zygomatic breadth (ZB), mastoid breadth (MB), outer breadth across molars (BaM), mandibular toothrow length (MDT), mandibular condylo-canine length (MCC), coronoid height of mandible (CRH). For comparing the French Guianan material with topotypic material of *P. rubiginosus*, we examined a museum specimen (MZUSP-35152) caught at Cuiabá, Mato Grosso, Brazil. This city is located 180 km east-north-east from Cáiçara, which is the type-locality of *P. rubiginosus* defined by Gardner (2007) as being near the city of Caceres at 16°04'S, 57°43'W.

To differentiate between phonic types, we performed two discriminant function analyses (DFA; Statistica 6.0, StatSoft Inc., USA): one based on the three external measurements taken in all 201 recorded bats (FA, MC3 and MC4; only a fraction of them had more external measurements taken), and one based on 14 cranial measurements (M^1M^3, GLS, GLSI, CIL, CCL, ZB, MB, MTL, BaM, CRH, PL, MDT, MCC, BRD) of 23

vouchered specimens. Each bat was classified a priori according to its recorded phonic type (53 or 59 kHz), except for the Mato Grosso specimen which was left unclassified prior to analyses. To reduce the number of cranial variables entered into the discriminant function, we computed a stepwise discriminant function, where only those first variables contributing the most to the discrimination of the two groups are entered. Univariate statistical tests for comparing measurements or acoustic calls between groups included Mann-Whitney nonparametric test, as implemented by the software PAleontological STatistics (PAST — Hammer *et al.*, 2011).

Bioacoustics

Echolocation calls were recorded for animals both kept in tissue bags and upon release with Pettersson bat detectors (models D240X, D500X, D1000X: Pettersson Elektronik AB, Uppsala, Sweden) and stored using a Edirol R-05 (Roland AG, Itingen, Switzerland) recorder. Calls were analyzed with BatSound Pro 3.31 (Pettersson Elektronik AB, Uppsala, Sweden) based on spectrograms with Hanning window at a sampling rate of 44,100 Hz and fast fourier transformat (FFT) size of 512. Two to five calls were analysed for each animal, and for each recorded call the [second] harmonic containing most energy was identified from the power spectrum and measurements taken from the constant frequency (CF) component of the call, as detailed in previous studies (Schnitzler and Kalko, 1998).

Molecular

DNA was extracted from 95% ethanol-preserved tissues with the NucliSENS EasyMag robot (Biomérieux, Craponne, France) following manufacturer's recommendations for biopsy extraction. Two mitochondrial genes were targeted: the cytochrome b (Cyt *b*), amplified using the two pairs of primers MVZ05/NEW12 and UMMZ13/UMMZ04 (Jansa *et al.*, 1999, Dávalos and Jansa, 2004) and yielding two overlapping fragments for a full coverage of the gene, and the cytochrome oxydase 1 (CO1), amplified as recommended in barcoding screening (Borisenko *et al.*, 2008; Clare *et al*., 2013). After amplification, PCR products were sent for purification and sequencing at Cogenics (Takeley, UK), using the same primers as for amplifications. Sequences were aligned and checked manually with MEGA 5.1 (Tamura *et al.*, 2011) for absence of gaps or stop codons, to ensure that these were not pseudogenes. Besides the French Guianan, Amapa and the *rubiginosus* specimen from Mato Grosso (MZUSP-35152), the Cyt *b* and CO1 sequences were acquired from three additional specimens from Jamaica, for the sake of having comparative materials from near the type-locality of *P. parnellii*. All sequences obtained in this study have been deposited in GenBank and are listed by their accession number in Appendix I.

Phylogenetic relationships between samples were evaluated using maximum likelihood (ML), neighbor-joining (NJ), and Bayesian procedures. The GTR model (Tavaré, 1986), with gamma (G) rate parameter and a proportion of invariant sites (I) was identified with MEGA 5.1 as the best fitting nucleotide substitution model for both genes. Ten thousand replicates were used for maximum likelihood analyses in Mega 5.1, yielding support values of Bootstrap Percentage (BP). The Bayesian approach was carried out with MrBAYES 3.2 (Ronquist *et al.*, 2012). Markov Chain Monte Carlo (MCMC) simulations were run twice independently for 10 million generations with four simultaneous chains, using a sample frequency of 1,000 and a burn-in of 2,500 trees; support values are indicated by Posterior Probabilities (PP), and were calculated from the remaining trees. Intra and inter-clade haplotypic and nucleotidic variabilities were calculated with ARLEQUIN 3.5 (Excoffier and Lischer, 2010). Pairwise genetic distances were calculated with MEGA 5.1 using the K2P model in order to be easily comparable with other similar studies.

For the sake of clarity and for facilitating comparisons with previous works, we indicate in Appendix II the names we used for the sequences retrieved from GenBank, their approximate localities and voucher numbers. For the present work, we have generated 30 sequences (20 CO1 and 10 Cyt *b*) and we have used 47 sequences (21 CO1 and 26 Cyt *b*) retrieved from GenBank.

Results

Bioacoustics

Grotte Mathilde (locality 5; Fig. 1) is a cave surrounded by primary rainforest located ca. 40 km south-east from Cayenne. At this locality, we verified that CMB held individually in cotton-bags emitted ultrasonic calls that had CF characteristics indiscernible from those emitted when flying (upon release). Differences measured for each bat recorded in the bag and upon release were negligible (standard deviation less than 0.2 kHz), which validates the assignation of all handled bats into their respective phonic types. Based on these acoustic assignations, 63 CMB caught at Grotte Mathilde emitted ultrasound with a CF component around 53 kHz (called hereafter the 53 kHz phonic type), and 57 bats had CF calls at around 59 kHz (i.e., the 59 kHz phonic type).

We then addressed the population variability of the CF component of both phonic types in samples from Grotte Mathilde (the same 120 individuals), Cacao (87), and Haute-Camopi (38), where these phonic types were recorded in sympatry. At those three sites the two distinct phonic types were clearly discernible with no intermediate CF value (Table 1). At any location, the difference between the highest CF value in the 53 kHz phonic type and the lowest in the 59 kHz phonic type was at least 2.3 kHz (Grotte Mathilde), whereas the difference in mean CF values between each phonic type varied between 5.45 kHz (Cacao) and 6.13 kHz (Haute Camopi). At the regional scale, all individuals from 6 different localities in French Guiana were assigned to their respective phonic type (53 or 59 kHz), and again CF calls showed minimal variability within each group (53.4 ± 0.62 kHz, n = 130; 59.2 ± 0.68, n = 127; respectively). No overlap was observed between

TABLE 1. Variability of the constant frequency (CF) component of echolocation calls for two phonic types of common mustached bats caught in sympatry in French Guiana. Values are expressed in kHz and correspond to the frequency containing maximum energy (FME), with mean, standard deviation (SD), minimum (min) and maximum (max) values; *n* is the number of bats recorded

Locality	Phonic type (kHz)	*n*	$\bar{x}$	SD	min	max
Cacao	53	47	53.79	0.31	53.1	54.3
Cacao	59	40	59.24	0.53	57.6	60.1
Grotte Mathilde	53	63	53.10	0.65	51.6	54.5
Grotte Mathilde	59	57	59.10	0.72	56.8	59.9
Haute-Camopi	53	21	52.85	0.55	51.5	53.9
Haute-Camopi	59	17	58.98	0.59	58.3	60.0

phonic types (Fig. 2). The recorded CF component of all handled or free-flying CMB thus provides an easy and reliable character for recognizing the two phonic types in French Guiana.

Molecular Systematics and Taxonomy

The CO1 barcode fragment (657 bp) was sequenced in 14 vouchered specimens from the area of sympatry of Grotte Mathilde and whose ultrasonic calls were also known. The alignment of these sequences resulted in five distinct haplotypes. Two were unique to the six 53 kHz phonic type CMB, and three unique to the eight 59 kHz animals. Haplotypes from the two phonic types differ by a mean K2P distance of 4.9%. Haplotypes differed by one mutation (0.06% net distance) and by up to nine mutations (0.56% net distance) within the 53 and 59 kHz phonic types, respectively.

The more global phylogenetic analyses of DNA barcodes (CO1 fragments) included five distinct sequences from French Guiana, two from Brazilian Amapa, one from Brazilian Mato Grosso, and the unique haplotype found in three CMB from Jamaica, as well as 17 published CO1 sequences from various localities in Suriname, Guyana, Venezuela, El Salvador and Mexico (Clare *et al.*, 2011, 2013). Phylogenetic analyses indicate that the French Guianan and Amapa bats of each phonic type also segregate in two monophyletic clusters (Fig. 3). Noteworthy, the CO1 sequence of the Mato Grosso specimen MZUSP-35152 is nested within the cluster containing all CMB identified as *Pteronotus* sp4 by Clare *et al.* (2013), within less than 0.1% K2P distance. Each major clade in the phylogenetic tree (denoted as *P.* sp3 and *P.* sp4) contains animals from various localities of Suriname and Guyana (Appendix II), and both are well supported by high bootstrap and PP values (Fig. 3). These two clades show low intraspecific variability (< 1.4% K2P) and form closely related, sister taxa differing by a mean of 5.1% K2P distance. Also apparent on the phylogenetic tree is a cluster of four CO1 sequences containing CMB from Mexico (ROM-95741), El

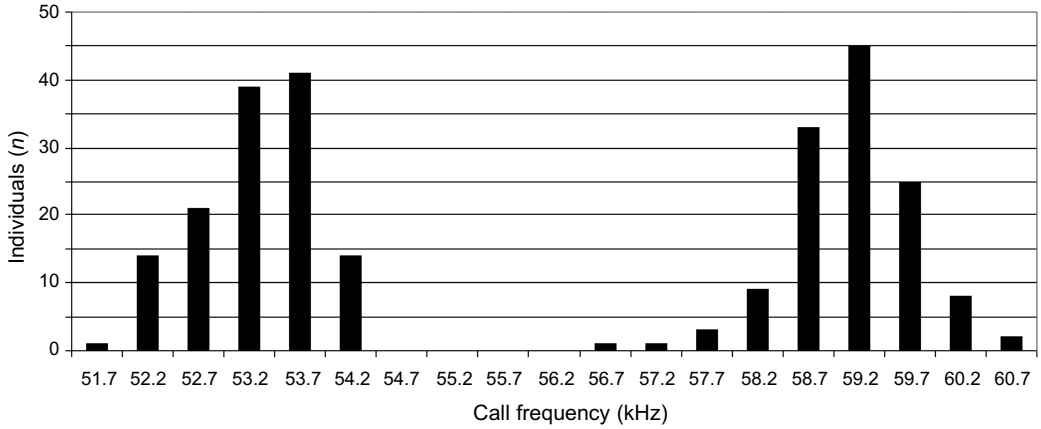

FIG. 2. Histograms of constant frequency (CF) values emitted by 257 common mustached bats caught in French Guiana. The median constant frequency value (CF) emitted by 130 individuals of the first phonic type (left) was 53.5 kHz (SD = 0.62 kHz), and that of the 127 individuals of the second phonic type (right) was 59.3 kHz (SD = 0.68 kHz)

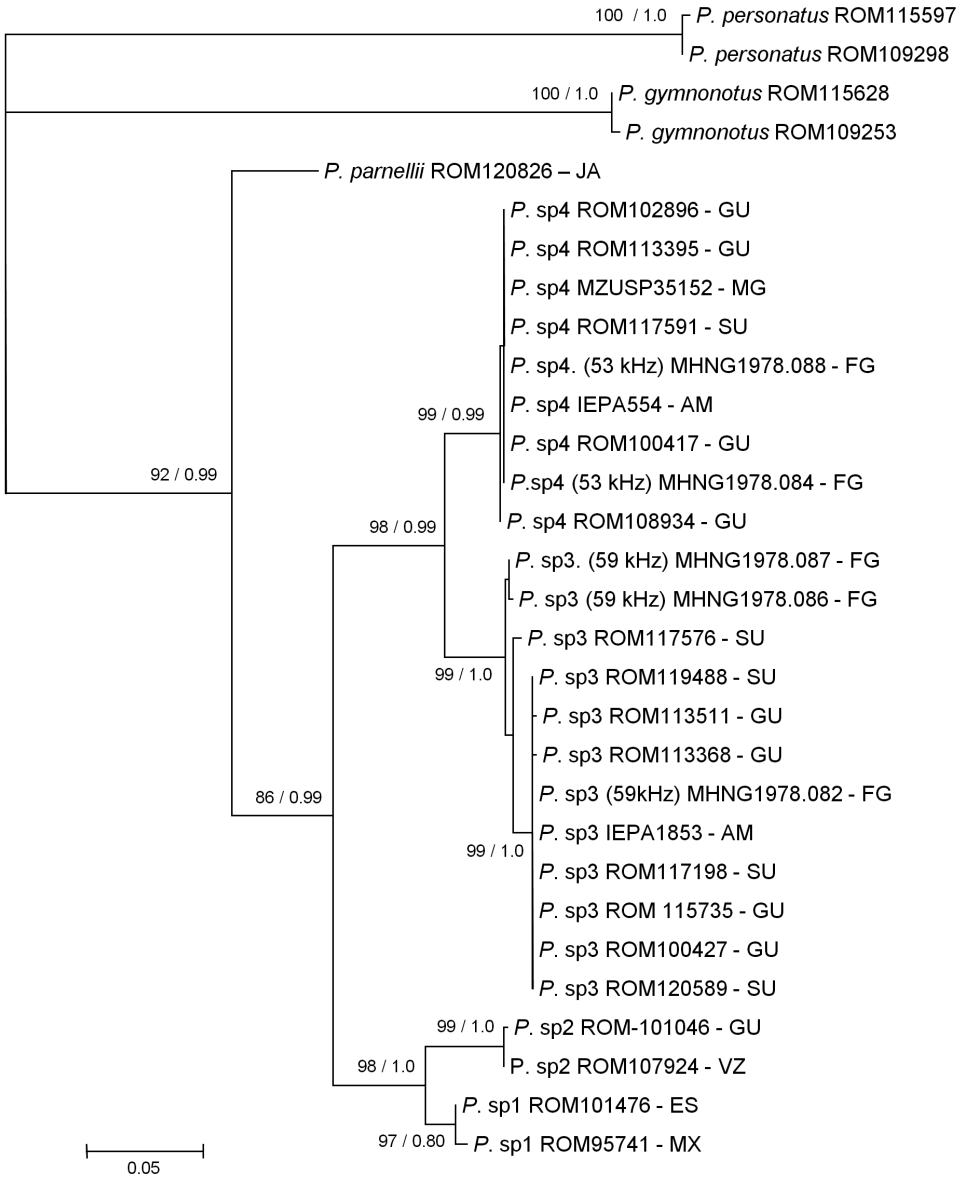

FIG. 3. Maximum likelihood tree showing the phylogenetic relationships among 26 CO1 barcodes of common mustached bats from Amapa (AM), Mato Grosso (MG), French Guiana (FG), Guyana (GU), Suriname (SU), Venezuela (VZ), El Salvador (ES), Mexico (MX), and Jamaica (JA). Bootstrap support from ML and posterior probabilities (PP) from a Bayesian analysis are shown above and below major nodes, respectively. Labels for continental CMB are composed of the same species names as in Clare *et al*. (2013) followed by specimen reference (see Appendices I and II). The tree was rooted with sequences of *P. personatus* and *P. gymnonotus*. Specimens (with voucher numbers) were assigned to *Pteronotus* sp1 to sp4 according to Clare *et al*. (2013). The phonic type of the individually recorded bats is also given in the label

Salvador (101476), Venezuela (107924), and western Guyana (101046) and corresponding to *P.* sp1 and *P.* sp2 of Clare *et al.* (2013). This second group is sister to the other species (*P.* sp3 and *P.* sp4) from the Guianan Shield. The CO1 haplotype from Jamaica (ROM-120826) representing *P. parnellii* is external to the clade containing *P.* sp1 to *P.* sp4 (Fig. 3) and differs from continental CMB by a mean K2P of 11.4%.

The phylogenetic analysis of 36 Cyt *b* sequences (for 32 mormoopid and four outgroup taxa) provides a novel image of the relationships of *P. parnellii* and its sister taxa (Fig. 4). All sequences of the 59 kHz phonic type bats cluster with the putative species *P.* sp3, while those of the 53 kHz phonic type group within *P.* sp4, both with strong support (BP of 91 and 99, respectively; 1.0 PP — Fig. 4). The latter putative species also includes the single specimen from

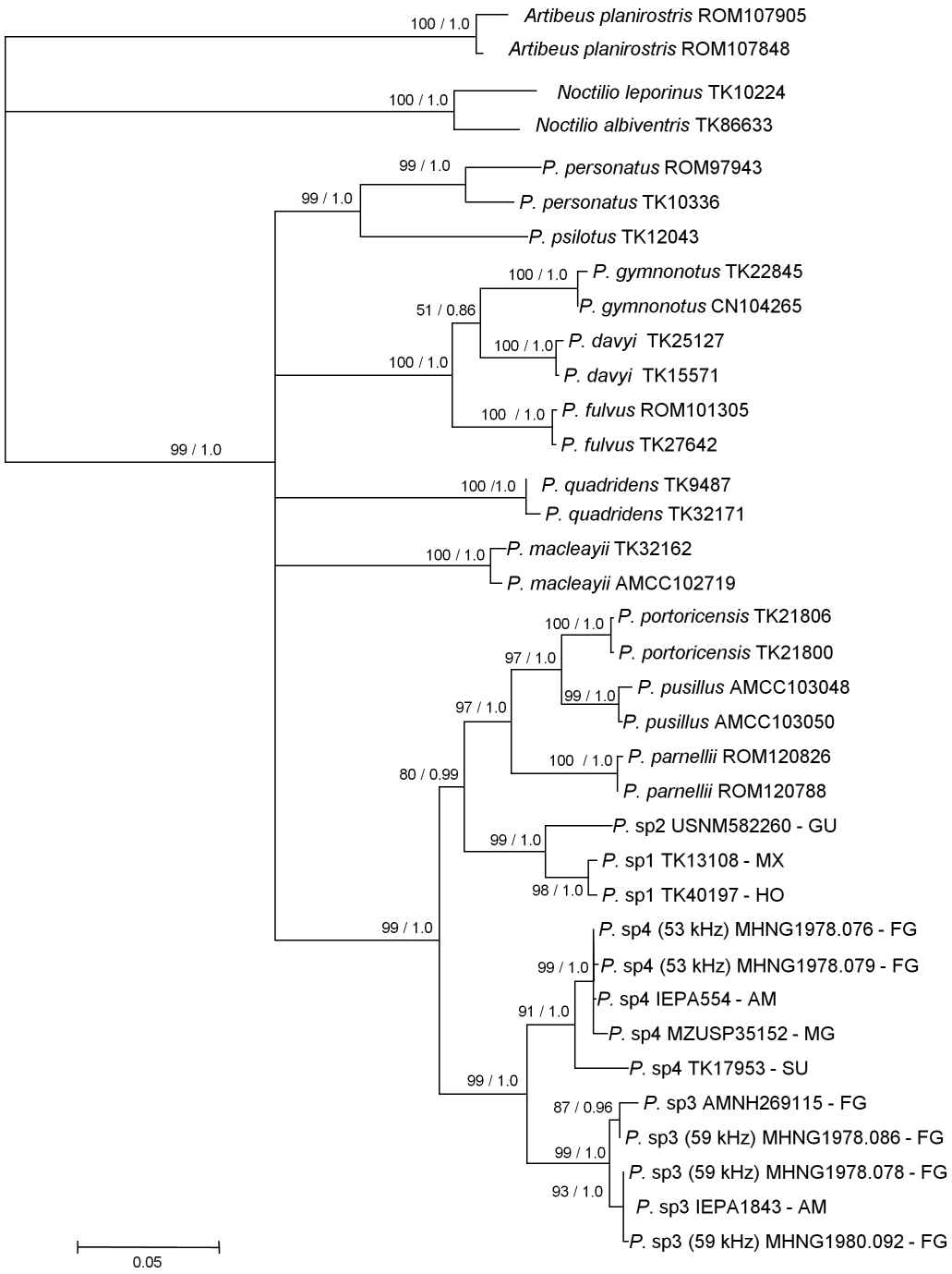

FIG. 4. Maximum likelihood tree showing the phylogenetic relationships among 31 Cyt *b* sequences of *Pteronotus* specimens from Central, South America and the Caribbean region. The legend is the same as for Fig. 3 except that the tree was rooted with sequences of *Artibeus* and *Noctilio*. Branches poorly supported (BP less than 80 in ML or PP less than 0.8 in Bayesian analysis) were collapsed into a polytomy. The country of origin is indicated after each specimen number for the continental CMB (*P.* sp1 to sp4) with the same abbreviations as in Fig. 3 and with HO — Honduras

near the type-locality of *rubiginosus*. Average divergence within these two clades was 1.0 and 1.6% nucleotides, respectively. Each clade included animals caught in sympatry in French Guiana or Amapa, and appears as each other's closest relative (at 6.6% K2P) in all reconstructions (Fig. 4).

The putative species *P.* sp2 (from western Guyana) and *P.* sp1 (Mexico and Honduras) form another pair of closely related taxa and group in a clade (99 BP, 1.0 PP) which is sister to a well-supported group (97 BP, 1.0 PP) containing the Antillean species *P. parnellii* (Jamaica), *P. pusillus*

(Dominican Republic), and *P. portoricensis* (Puerto Rico). All four putative species and the Antillean CMB cluster in a large, well supported clade (99 BP, 1.0 PP) which forms a polytomy together with the seven remaining species of *Pteronotus* (*macleayii*, *quadridens*, *fulvus*, *davyi*, *gymnonotus*, *psilotus*, and *personatus*).

External and Cranial Morphology

External measurements indicated that females are slightly larger than males in both phonic types, but differences were mostly insignificant (data not shown), and hence we pooled genders for other comparisons. Differences among phonic types sampled across French Guiana were in turn all highly significant (Table 2) with individuals of the 53 kHz phonic type being on average larger than those of the 59 kHz phonic type.

Although mean values differ, the ranges of the external measurements overlapped broadly (data not shown). Similarly, the three external variables (FA, MC3, MC4) recorded on all CMB and retained to discriminate the two phonic types were insufficient to identify each phonic type with confidence, although the discriminant function analysis (DFA) is highly significant ($F_{196} = 67.168$, *d.f.* = 3, $P < 0.001$). Indeed, 19 out of 110 individuals identified by their CF component as 59 kHz phonic type and 12 out of 89 identified as 53 kHz phonic type were misclassified by this discriminant function (results not shown). Interestingly, the male individual from Mato Grosso (MZUSP-35132) is classified as a 53 kHz phonic type (posterior probability = 0.76) with this simple function. Results were similar if sexes were separated or pooled in the discriminant analyses. Clearly none of these external characters taken alone or in combination can be used for reliable phonic type discrimination.

Cranial and dental measurements also indicate that 53 kHz CMB are larger than 59 kHz bats and, despite small sample sizes, differ significantly from each other (Table 3). Contrary to external characters, most cranial measurements do not overlap between individuals of the two phonic types (Table 3), but these results should be considered preliminary due to the small number of skulls examined.

A discriminant function analysis including all 14 cranial characters is highly significant ($F_7 = 20.23$, *d.f.* = 14, $P < 0.001$) and classified all 22 skulls in their correct phonic type (results not shown). Again the skull of the Mato Grosso *Pteronotus* (specimen MZUSP-35152) is classified a posteriori as a 53 kHz phonic type with a posterior probability of 1.0 in the preformed DFA based on cranial measurements (data not shown).

Discussion

Our study confirms and extends the recent survey of Clare *et al.* (2013) who evidenced a high level of cryptic diversity in CMB throughout Central and South America. Clare *et al.* (2013) used both mitochondrial (CO1) and nuclear (Dby-7 on y-chromosome and RAG2 on autosome) genes — together with external and skull morphometry — and came to the conclusion that four cryptic species were found in continental CMB. By using multiple lines of new evidence (ultrasonic calls, fine-scale distribution, morphometry, molecular markers) we provide a better understanding for two sympatric species of *Pteronotus* found in the eastern parts of the Guianan Shield.

Our results clearly support the existence of two phonic types among CMB living in French Guiana and Brazilian Amapa, a result which was already noticed by Barataud *et al*. (2013) in French Guiana. Each phonic type emits constant frequency calls at

Table 2. External measurements (in mm) for common mustached bats of the 53 kHz and 59 kHz phonic types from French Guiana. The last column correspond to measurements of the specimen MZUSP-35152 from Cuiabá, Mato Grosso, Brazil. Abbreviations of measurements as defined in Materials and Methods; *n* = number of bats measured, n.a. = not available

Character	53 kHz			59 kHz			*P*-value	MZUSP-35152
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD		
FA	89	64.2	0.13	111	61.8	0.12	< 0.001	63.6
MC3	89	52.8	0.16	111	50.5	0.13	< 0.001	52.6
MC4	89	50.9	0.19	111	49.1	0.15	< 0.001	50.9
D4	89	77.0	0.36	111	75.3	0.32	< 0.01	n.a.
TI	44	25.6	0.18	76	24.0	0.11	< 0.001	25.6
Body mass (g)	43	23.9	0.19	65	21.7	0.16	< 0.001	n.a.
Wingspan	9	418.0	7.60	14	398.0	8.90	< 0.001	n.a.

TABLE 3. Cranial and dental measurements (in mm) in French Guianan common mustached bats: eight individuals of the 53 kHz phonic type and 14 individuals of the 59 kHz phonic type. Mann-Whitney tests of differences between the phonic types are all significant at $P < 0.001$. The far right column is for specimen MZUSP-35152, from Cuiabá, Mato Grosso, Brazil (see text for further details). Abbreviations of measurements as defined in Materials and Methods

Character	53 kHz			59 kHz			MZUSP-35152
	$\bar{x}$	min	max	$\bar{x}$	min	max	
GLS	22.85	22.25	23.30	21.80	21.46	22.20	23.04
GLSI	23.54	22.94	24.30	22.38	21.74	22.83	23.65
CIL	22.55	22.22	22.90	21.48	21.03	22.11	22.15
CCL	21.48	20.96	21.90	20.27	19.90	20.70	21.50
PL	11.47	11.15	11.72	10.82	10.58	11.08	11.24
ZB	13.56	13.30	13.85	12.98	12.50	13.40	13.00
BaM	8.76	8.55	8.94	8.35	8.14	8.80	8.62
MCC	16.71	16.45	17.07	15.59	15.20	15.91	16.44
MTL	10.21	10.00	10.44	9.54	9.22	9.83	9.75
M^1M^3	5.95	5.72	6.09	5.59	5.41	5.76	5.60
MDT	11.56	11.35	11.77	10.87	10.57	11.11	11.08

non-overlapping ranges (Fig. 2). Indeed both sexes of the 53 kHz phonic type emit around 53 kHz with very limited variation between individuals and across regions (extremes 51.5–54.5 kHz — Table 1). Likewise, CMB of the 59 kHz phonic type emits CF components at around 59 kHz (range 56.8–60.1 kHz — Table 1) in all recorded localities. We also showed that these CF components of CMB echolocation calls did not differ when recorded in flight or when held captive in cotton bags. Thus the two phonic types in French Guiana differ by a small but consistent variation in CF calls (53.4 ± 0.6 kHz versus 59.2 ± 0.7 kHz), and are easy to identify via their echolocation calls.

The two phonic types are found throughout French Guiana and Brazilian Amapa (Fig. 1), but further bioacoustic studies are needed to understand their exact distribution in this region. Where they are found in sympatry, both phonic types occur in comparable numbers (for example 38 versus 47 at Cacao, or 49 versus 39 at Grotte Mathilde, for the 59 kHz and 53 kHz phonic types, respectively), suggesting that they can coexist in similar habitats without major ecological competition. Indeed, they may both occupy the few cave roosts existing in this area, while exploiting a different trophic niche of their habitat, as was evidenced in other sympatric, sibling species that share roosts (e.g., Arlettaz *et al.*, 1997).

Molecular analyses of two mitochondrial genes (CO1 and Cyt *b* — Figs. 3 and 4) consistently identify these two phonic types in the clades defined by Clare *et al.* (2013). The sequences of 59 kHz phonic type bats correspond to clade 3, which is considered as a putative species *P.* sp3, while the 53 kHz phonic type sequences cluster within clade 4 (*P.* sp4). Both phonic types are closely related (mean 6.6% K2P distance for the Cyt *b* and 5.1% for CO1), sister clades in all phylogenetic reconstructions and present little genetic variation within clades (Figs 3 and 4). Although sample sizes of CMB characterized by both bioacoustics and genetic data are still limited (14 individuals), there is complete concordance between phonic types and molecular clades, indicating that no mitochondrial gene flow or secondary admixture occurred between animals of both phonic types, even when they share roosts. By combining Y-chromosome and mitochondrial DNA sequences, Clare *et al.* (2013) found only one possible hybrid individual in a sample of 61 specimens. Our results therefore fully corroborate the conclusions of Clare *et al.* (2013) who considered that *Pteronotus* sp3 and sp4 represent independent, biological species. Interestingly, Clare *et al.* (2011) identified molecularly nearly the same number of *P.* sp3 ($n = 143$) and *P.* sp4 ($n = 151$) individuals in a large survey (355 barcoded bats) of CMB sampled in Suriname and Guyana, a pattern of relative abundance similar to what we found in French Guiana.

Morphologically, these two species differ in size, the 53 kHz phonic type being significantly larger than the 59 kHz type in all external (Table 2) and cranial (Table 3) characters measured. These differences in body size and in echolocation calls parameters are consistent with expectations from the scaling effect of size (Jones, 1999), where larger species tend to emit calls at lower frequencies when compared to smaller ones. Unfortunately, these morphological differences, although highly significant, do not allow for an unambiguous separation of both phonic types, as most external characters show

large measurement overlaps. Clare *et al.* (2013) also found that the forearm length of their Group 3 (59 kHz type) was smaller than their Group 4 (53 kHz), although the measured values were largely overlapping. Clearly, ultrasound recording is a much more reliable and less invasive method to identify living CMB of both phonic types in French Guiana and Amapa. Individual measurements of skull characters exhibit little overlap (Table 3) and thereby allow for a complete discrimination of all specimens in a simple discriminant analysis, though with a limited number of specimens investigated. Again, this result is consistent with Clare *et al*. (2013) analyses of skull differences among the four putative species (*P.* sp1 to *P.* sp4), where 60 to 90% of specimens were correctly assigned to their respective group.

In an effort to assign an appropriate taxonomic name to the two putative cryptic species (phonic types) present in French Guiana, we included one CMB (MZUSP-35152; see Appendix I) sampled at 180 km from the type locality of *rubiginosus* (i.e., in Mato Grosso — Wagner, 1843). This taxon name was suggested by Davalos (2006) for CMB living in eastern South America, but because there are clearly more than one species of CMB living in this region, it was unclear if this name would be applicable. In all comparisons, MZUSP-35152 was unambiguously part of the 53 kHz phonic type (= *P.* sp4). Indeed, despite extensive geographic distance separating samples of *P.* sp4 from French Guiana and the Mato Grosso (over 2,000 km), both mitochondrial markers show little genetic differentiation (Figs. 3 and 4). Morphologically, the relatively large external measurements of this Mato Grosso CMB also fits the range of variation displayed by CMB of the 53 kHz phonic type in French Guiana (Table 2) and matches skull dimensions typical of specimens from this phonic type (Table 3).

The holotype of *rubiginosus* held in Munich (Germany) under accession number ZSM-45 is unfortunately not available for molecular nor for cranial comparisons, as the skull has not been extracted from the dry specimen (Smith, 1972). Wagner's (1843: 367) description of *rubiginosus* was limited to "*Chilonycteris* cinnamomeo-rufescens; auriculis elongatis, angustatis, acuminatis; patagio interfemorali amplissimo truncate", which would translate as "*Chilonycteris* of cinnamon-brown colour, elongated ears, tapered, pointed; patagium interfemoral very broad, truncated"; this description would fit any CMB from South or Central America. Furthermore Wagner (1843) gave the forearm length of his type specimen as <Antibrachium 2''3'''>, which would correspond to ca. 59 mm if his units of measurement were Prussian Zolls (see Pine *et al*., 2013). This value is, however, doubtful, as D. C. Carter measured recently the forearm of Wagner's holotype at 64.2 mm (Smith, 1972: 75). Such a large forearm is more in line with larger 53 kHz animals that we measured in French Guyana and Brazil. Thus, if we assume that the analysed Mato Grosso individual (MZUSP-35152) also represents genuine *rubiginosus*, then this taxon name is available to designate the 53 kHz phonic type (*P*. sp4 or clade 4 as in Clare *et al.*, 2013) and would extend its geographic range beyond the Guianan Shield.

The smaller CMB of the 59 kHz phonic type and representing *P.* sp3 are even more difficult to classify. So far, these animals are found only on the Guianan Shield (French Guiana, Brazilian Amapa, Guyana and Suriname — Clare *et al.*, 2013 and Fig. 1) where no endemic taxa have been named. This phonic type most probably represents a new cryptic species in the CMB complex, as suggested earlier. At a broader geographical scale, a third taxon of CMB denoted *P.* sp2 is characterized by CF calls around 59 kHz and is found in the north-western part of the Guianan Region (Guyana and the Venezuelan states of Amazonas and Bolivar — Clare *et al.*, 2013). Representatives of this third cryptic species are genetically distinct from the 53 and 59 kHz phonic types from French Guiana in all reconstructions (Figs. 3 and 4) and certainly represent another cryptic species, related to the Central American *P.* sp1 (= *P. mesoamericanus* in Clare *et al.*, 2013). We did not sample *P.* sp2 in French Guiana or Brazil, and as no complete morphological or bioacoustic data are available it is premature to name it properly. Clearly, reference material from other type localities of CMB taxa and more specimens characterized with multiple methods are needed before all cryptic species within the CMB complex can be critically reviewed for an adequate systematic arrangement. The existence of at least three cryptic species of CMB living in the Guianan Shield, some of which may live in strict sympatry and share roosts (Fig. 1) has important implications for their conservation, as their exact distribution, ecological needs and abundance are largely unknown.

Regarding the biogeography of the genus *Pteronotus* in general, the Cyt *b* phylogenetic tree (Fig. 4) suggests that there is no proper *P. parnellii* lineage in continental CMB. Indeed *P. parnellii* from Jamaica is sister to other insular species such as *P. pusillus* (Hispaniola) and *P. portoricensis* (Puerto

Rico) and this Antillan lineage is thus distinct from any of the putative continental taxa. Additional molecular characters are however needed to test whether the four continental CMB cryptic species (*Pteronotus* sp1 to sp4) are monophyletic or else if *P.* sp1 and *P.* sp2 are more closely related to some Antillean species (*parnellii*, *pusillus*, *portoricensis*). Davalos (2006) presented a similar branching pattern as ours regarding Cyt *b* sequences but the author was cautious enough to call all insular and continental CMB taxa as '*P. parnellii*', whereas we here recognize *P. pusillus* (Hispaniola), *P. portoricensis* (Puerto Rico), *P.* sp1 (Hondura and Mexico), *P.* sp2 (Guyana), and *P.* sp3 and sp4 (Guyana, Suriname, French Guiana, Brazilian Amapa) as distinct species. Clearly, more work combining different kinds of characters is needed for linking Pteronotus sp1 to sp4 to traditional names (*fuscus*, *mesoamericanus*, *mexicanus*, *paraguanensis*, *rubiginosus*) in Central and South America, a taxonomic issue which is not yet solved.

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Appendix I

Specimens examined are housed in the following institutions: Muséum d'Histoire Naturelle de Genève (MHNG), collection of Pierre-Charles Dominique housed at the Laboratoire d'Ecologie du Muséum at Brunoy, France (MNHN-PCD), Instituto de Pesquisas Cientificas e Technologicas do Estado do Amapa, at Macapa (IEPA); Museum of Zoology of the University at Sao Paulo (MZUSP); Royal Ontario Museum at Toronto (ROM). For each taxon, specimens are listed according to country, political division, locality, coordinates, and museum catalog number (except for R266, which was released after recording). When available, GenBank accession number of both sequenced genes (CO1 and Cyt *b*) are given in parentheses after the catalog number

Pteronotus rubiginosus (*P.* sp4) — Brazil: Amapa: Parque Nacional Montanhas do Tumucumaque, Rio Mutum, Calçoene: IEPA-554 (CO1 KF636800, Cyt *b* KF636804); Mato Grosso: Cuiabá MZUSP-35152 (CO1 KF636799, Cyt *b* KF636801). French Guiana: municipality of Roura: Cacao MHNG-1983.064 and 65; 1979.073; municipality of Regina: Grotte Mathilde MHNG-1978.076 (CO1 KF636795; Cyt *b* KF636803), 1978.079 (CO1 KF636797; Cyt *b* KF636802), 1978.080 (CO1 KF636798), 1978.083 (CO1 KF636796), 1978.084 (CO1 KF636794), 1978.088 (CO1 KF636793).

Pteronotus sp3 — Brazil: Amapa: Iratapuru village, near to Laranjal do Jari, Jari river: IEPA-1843 (CO1 KF636815, Cyt *b* KF636817). French Guiana: municipality of Roura: Cacao MHNG-1980.091 and 92 (CO1 KF636813, Cyt *b* KF636816), 1983.043, 58 and 69; Trésor Natural Preservation R266 (CO1 KF636814); municipality of Regina: Grotte Mathilde MHNG-1980.094, 1978.077 (CO1 KF636809), 1978.078 (CO1 KF636811, Cyt *b* KF636818), 1978.081 (CO1 KF636810), 1978.082 (CO1 KF636805), 1978.085 (CO1 KF636807), 1978.086 (CO1 KF636806, Cyt *b* KF636819), 1978.087 (CO1 KF636812), 1978.089 (CO1 KF636808); municipality of Regina: camp inselberg des Nouragues (04°02'N, 52°42'W) MNHN-PCD-433, 485, 1088, 1095, 1228, 1229 and 1230.

Pteronotus parnellii — Jamaica: Saint Elisabeth, Oxford Cave (18°09'N, 77°05'W) ROM-120788 (Cyt *b* KF636822); Saint Andrew, 10 km N of Kingston (18°05'N, 76°43'W) ROM-120826 (CO1 KF636820, Cyt *b* KF636821)

Appendix II

Reference list of the *Pteronotus* spp. sequences used in Figs. 3 and 4. The first column lists the taxon name used in this paper, followed by GenBank and voucher numbers, and the approximate location of origin of the specimen. Sp1 to sp4 are taxon names given by Clare *et al.* (2013) to designate genetically and morphologically distinct continental common mustached bats. The acronyms TK (Museum of Texas Tech University), ROM (Royal Ontario Museum), AMNH (American Museum of Natural History), AMCC (Ambrose Monell Cryo Collection, at New York) and USNM (United States National Museum) designate the institutions housing the sequenced specimens

Name used in this paper	GenBank	Specimen/Voucher	Country/Locality
P. davyi	AF338669	TK-15571	Dominica: St. Joseph Parish, mouth of Layou River
P. davyi	AF338671	TK-25127	Trinidad and Tobago: Trinidad, Nariva, Arena Reserve
P. fulvus	JF446541	ROM-101305	El Salvador: Ahuachapan, El Imposible, El Refugio

Appendix II. Continued

Name used in this paper	GenBank	Specimen/Voucher	Country/Locality
P. fulvus	AF338672.	TK-27642	Mexico: Jalisco, Chamela
P. gymnonotus	EF080590	ROM-115628	Guyana: Essequibo Islands-West Demerara
P. gymnonotus	EF080591	ROM-109253	Guyana: Potaro-Siparuni
P. gymnonotus	JF447432	ROM-104265	Panama: Parque Nacional Altos de Campana
P. gymnonotus	AF338674	TK-22845	Peru: Huanuco Department, Leoncia Prado
P. macleayii	AF338683	TK-32162	Cuba: Guantanamo Province, Guantanamo Bay Naval Station
P. macleayii	AY604461	AMCC102719	Jamaica; St Claire Cave, St Catherine Parish
P. mesoamericanus (sp1)	JF448266	ROM-101476	El Salvador: Santa Ana, Parque Nacional Montecristo, Los Planes
P. mesoamericanus (sp1)	AF338662	TK-40197	Honduras: Valle, 8.5 mi SSW San Lorenzo
P. mesoamericanus (sp1)	AF338664	TK-13108	Mexico: Vera Cruz, 14 km N 22 km E Cordoba
P. mesoamericanus (sp1)	JF448279	ROM-95741	Mexico: Campeche, 44 km S of Constitucion
P. parnellii	AY604456	AMCC102714	Jamaica; St Claire Cave, St Catherine Parish
P. parnellii	AF338661	TK-27704	Jamaica: St. Ann's Parish, 24 km W St. Ann's Bay
P. personatus	EF080596	ROM-115597	Guyana: Essequibo Islands-West Demerara
P. personatus	EF080597	ROM-109298	Guyana: Potaro-Siparuni
P. personatus	JF455427	ROM-97943	Guyana: Upper Takutu, Karanambo
P. personatus	AF338679	TK-10336	Suriname: Nickerie, Grassalco
P. personatus	AF338678	TK-19079	Venezuela: Bolivar, 0.5 km E El Manteco
P. portoricensis	AF338665	TK-21800	Puerto Rico: Naguabo, Caribbean National Forest
P. portoricensis	AF338666	TK-21806	Puerto Rico: Naguabo, Caribbean National Forest
P. psilotus	AF338680	TK-12043	Mexico: Oaxaca, Tehuantepec
P. pusillus	AY604455	AMCC103048	Dominican Republic: La Entrada de Cabrera, Maria Trinidad Sanchez
P. pusillus	AY604454	AMCC103050	Dominican Republic: La Entrada de Cabrera, Maria Trinidad Sanchez
P. quadridens	AF338681	TK-32171	Cuba: Guantanamo Province, Guantanamo Bay Naval Station
P. quadridens	AF338682	TK-9487	Jamaica: St. Catherine Parish, St. Clair Cave
P. rubiginosus (sp4)	JF448246	ROM-100417	Guyana: East Berbice-Corentyne
P. rubiginosus (sp4)	EF080592	ROM-108916	Guyana: Potaro-Siparuni
P. rubiginosus (sp4)	EF080593	ROM-108934	Guyana: Potaro-Siparuni
P. rubiginosus (sp4)	JF448388	ROM-102896	Guyana: Upper Takutu-Upper Essequibo, Takutu
P. rubiginosus (sp4)	JF448455	ROM-113395	Guyana: Upper-Demerara-Berbice, Pibiri
P. rubiginosus (sp4)	AF330807	TK-17953	Suriname: Marowiejne, Oelemarie
P. rubiginosus (sp4)	EU096920	ROM-117591	Suriname: Sipaliwini
P. rubiginosus (sp4)	EU096918	ROM-117608	Suriname: Sipaliwini
P. rubiginosus (sp4)	EU096924	ROM-117654	Suriname: Sipaliwini
P. sp2	JF448375	ROM-101046	Guyana: Barima-Waini, Baramita, Old World
P. sp2	AF338668	USNM-582260	Guyana: NW District, Baramita
P. sp2	JF448283	ROM-107924	Venezuela: Bolivar, Hato La Florida, 35 km ESE of Caicara
P. sp3	AY604457	AMNH-269115	French Guiana: Paracou (Sinnamary)
P. sp3	JF448247	ROM-100427	Guyana: East Berbice-Corentyne
P. sp3	JF448433	ROM-111664	Guyana: Potaro-Siparuni
P. sp3	JF448179	ROM-115735	Guyana: Potaro-Siparuni
P. sp3	JF448197	ROM-113511	Guyana: Upper Takutu-Upper Essequibo, Takutu
P. sp3	JF448451	ROM-113368	Guyana: Upper-Demerara-Berbice, Pibiri
P. sp3	JF448457	ROM-113407	Guyana: Upper-Demerara-Berbice, Pibiri
P. sp3	JQ601193	ROM-120589	Suriname: Kutari
P. sp3	EU096921	ROM-117176	Suriname: Sipaliwini
P. sp3	EU096925	ROM-117198	Suriname: Sipaliwini
P. sp3	EU096919	ROM-117576	Suriname: Sipaliwini
P. sp3	HQ919698	ROM-120339	Suriname: Sipaliwini
P. sp3	JQ601320	ROM-119488	Suriname: Tafelberg