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Paul M. Velazco

Division of Mammals
Department of Zoology
Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496
U.S.A.

Department of Biological Sciences
University of Illinois at Chicago
Chicago, Illinois 60680-4348
U.S.A.

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Morphological Phylogeny of the Bat Genus *Platyrrhinus* Saussure, 1860 (Chiroptera: Phyllostomidae) with the Description of Four New Species

Paul M. Velazco

Abstract

Platyrrhinus, comprising 10 species of broad-nosed bats, is one of the most diverse genera in the Neotropical family Phyllostomidae. To evaluate the content and limits of this genus, the phylogenetic relationships among these species and other closely related taxa were examined using a data set of 60 morphological characters including external, cranial, dental, and postcranial characters. Four species (*Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes caraccioli*) of the family Phyllostomidae were used as outgroups to test the monophyly of *Platyrrhinus* and to resolve intrageneric relationships.

Parsimony analysis resulted in two most parsimonious trees. The results support *Platyrrhinus* monophyly with a bootstrap value of 84% and a Bremer support of 3. Three synapomorphies are recognized for the genus. The results also support the recognition of *P. umbratus* as a junior synonym of *P. dorsalis,* the division of *P. dorsalis* into three distinct species, and the discovery of two new species previously considered part of *P. helleri* and *P. vittatus.* Taxonomic diagnoses of all the species of *Platyrrhinus* based on character optimizations as well as descriptions of four new species are presented. This revision brings the total number of species of *Platyrrhinus* to 14, making it the most speciose genus in the family Phyllostomidae.

Introduction

The genus *Platyrrhinus* Saussure, 1860, belongs to the family Phyllostomidae (Mammalia: Chiroptera). The distribution of this family is restricted to the Neotropics. Morphologically, it is characterized by the presence of a noseleaf, developed in most of its members, as well as the presence of two synapomorphic characters that differentiate it from the other Microchiropterans: oviductal folds restricted to the extramural oviduct (Hood & Smith, 1982) and friction lock in the digits of feet (Simmons & Quinn, 1994; Simmons, 1998). Within the Phyllostomidae, *Platyrrhinus* is placed in the subfamily Stenodermatinae, which is diagnosed by a combination of the presence of short and flattened muzzle, short and wide nose leaf, narrow uropatagium, lack of tail, and frequent presence of facial and/or dorsal stripes (Linares, 1986; Albuja, 1999). This subfamily also has two synapomorphic characters: a single common uterine lumen, without remnants of cornual lumina, and the oviducts enter the fundic border of the uterine body near the midsagittal line (Hood & Smith, 1982).

The species of *Platyrrhinus* (Fig. 1) are thought to be monophyletic (Owen, 1987; Lim, 1993; Wetterer et al., 2000). *Platyrrhinus* is diagnosed from other Stenodermatinae by a combination of three characters: two accessory cusps on the posterior face of P4, presence of three upper molars, and presence of a fringe of hair on the edge of the uropatagium. Although other genera also have these characters, no other genus possesses all three (Lim, 1993; Albuja, 1999).

Ten nominal species of *Platyrrhinus* are commonly recognized (Owen, 1987; Koopman, 1993; Nowak, 1999). The distributional range of

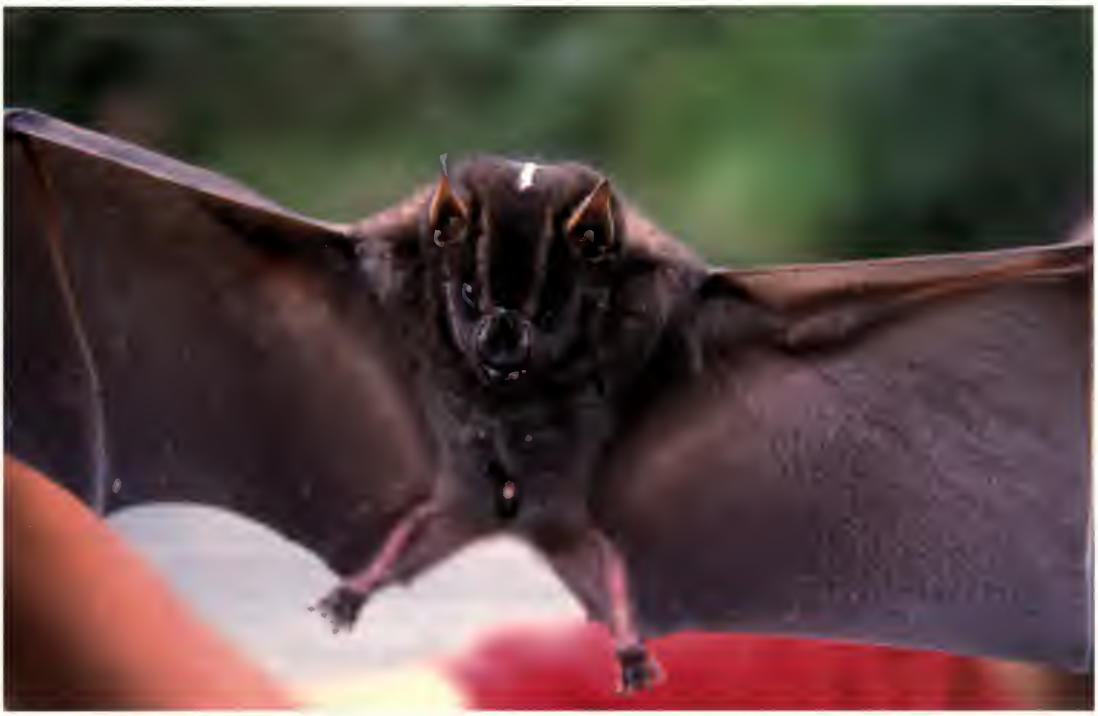

FIG. 1. Frontal view of *Platyrrhinus* sp. nov. (FMNH 172108); adult male photographed at Pillahuata in the Cultural zone of the Manu Biosphere Reserve, Cuzco, Peru, by P. M. Velazco.

Platyrrhinus includes North, Central, and South America, from southern Mexico to Bolivia, Paraguay, Uruguay, and southeastern Brazil (Sanborn, 1955; Cabrera, 1957; Jones & Carter, 1976; Hall, 1981; Koopman, 1982, 1993). Some species of this genus are widely distributed—for example, *P. helleri* is distributed from southern Mexico to Peru, Bolivia, and Brazil as well as Trinidad and Tobago (Koopman, 1982; Ferrell & Wilson, 1991).

The genus *Platyrrhinus* presents difficulties both in terms of its diagnosis and in how many species it comprises. The present work seeks to elucidate the phylogenetic relationships among the members of *Platyrrhinus*. To do so, cladistic analyses of discrete morphological characters were conducted. External, cranial, dental, and postcranial skeletal characters were examined. The results from these analyses offer a new interpretation of morphological diversity within the genus and a reassessment of the hypotheses of relationships presented by Owen (1987), Lim (1993), Baker et al. (2000, 2003), and Wetterer et al. (2000).

Background

All the species of *Platyrrhinus* Saussure, 1860, described before 1990 were recognized under the genus *Vampyrops* Peters, 1865. Gardner and Ferrell (1990) reviewed the nomenclatural history of these bats and determined that *Platyrrhinus* and *Vampyrops* were synonymous and that *Platyrrhinus* had priority over *Vampyrops*.

Koopman (1993) recognized 10 nominal species of *Platyrrhinus*: *P. aurarius* (Handley & Ferris, 1972), endemic to the Guianan Shield (southern Venezuela, Guyana, and Suriname); *P. brachycephalus* (Rouk & Carter, 1972), distributed in the Amazon and the coasts of northern South America and adjacent islands (northern Brazil, Colombia to Guyana, Ecuador, Peru, and Bolivia); *P. chocoensis* Alberico and Velasco, 1991, distributed in the Chocó region (western Colombia, in lowlands between the western slope of the Andes Cordillera and the Pacific coast); *P. dorsalis* (Thomas, 1900), distributed on both slopes of the Andes Cordillera and Central America (Panama to Peru and Bolivia); *P. helleri* (Peters, 1866), dis-

tributed from Central America (Oaxaca and Veracruz [Mexico]), south to Peru, Bolivia, the Amazon of Brazil, and Trinidad and Tobago; *P. infuscus* (Peters, 1880), distributed on the eastern slope of the north part of the Andes Cordillera and in the Amazon (Colombia to Peru, Bolivia, and northwestern Brazil); *P. lineatus* (É. Geoffroy, 1810), distributed in the Pampean subregion, Amazon, and the eastern slope of the north part of the Andes Cordillera (Colombia to Peru, Bolivia, Uruguay, northern Argentina, and southern and eastern Brazil); *P. recifinus* (Thomas, 1901), distributed in the highlands and coast of eastern Brazil and the Amazon (eastern Brazil); *P. umbratus* (Lyon, 1902), distributed in the eastern slope of the northern Andes Cordillera, north coast of South America and adjacent islands, and the Pacific coast of Ecuador and Colombia (Panama, Colombia, and northern Venezuela); and *P. vittatus* (Peters, 1860), distributed on the eastern slope of the north part of the Andean Cordillera, north coast and islands of South America, and Central America (Costa Rica to Venezuela and from Peru to Bolivia) (Koopman 1982, 1993; Alberico 1990; Lim & Engstrom, 2000).

Sanborn (1955), Gardner and Carter (1972b), and Carter and Rouk (1973) considered *Platyrrhinus umbratus* to be conspecific with *P. dorsalis,* synonymizing the former with the latter. However, Handley (1976) reported that *P. umbratus* differed from *P. dorsalis,* which was followed by Koopman (1993) and Owen (1987). Velazco and Solari (2003) considered *P. aquilus, P. oratus,* and *P. umbratus* as junior synonyms of *P. dorsalis,* and they stated that *P. dorsalis* as it is now recognized is a complex of three taxa. One of these corresponds to *P. dorsalis* (Thomas, 1900), with *aquilus, oratus,* and *umbratus* as junior synonyms; the other two taxa are undescribed species, denoted *P. dorsalis* "Norte" and *P. dorsalis* "Centro-Sur." *Platyrrhinus dorsalis* "Norte" is distributed on both slopes of the Andes in Ecuador and Peru, and *P. dorsalis* "Centro-Sur" is distributed on the eastern slope of the Andes in Peru (Velazco & Solari, 2003).

Tuttle (1970) regarded *Platyrrhinus infuscus* as a junior synonym of *P. vittatus,* but Gardner and Carter (1972b) and Koopman (1978) considered *P. infuscus* distinct from *P. vittatus.* Gardner and Carter (1972a) described *P. nigellus* as a species present in Colombia and probably Ecuador and Peru, but Koopman (1978, 1982), Jones and Carter (1979), and Willig and Hollander (1987) treated *nigellus* as a subspecies of *P. lineatus.* Owen

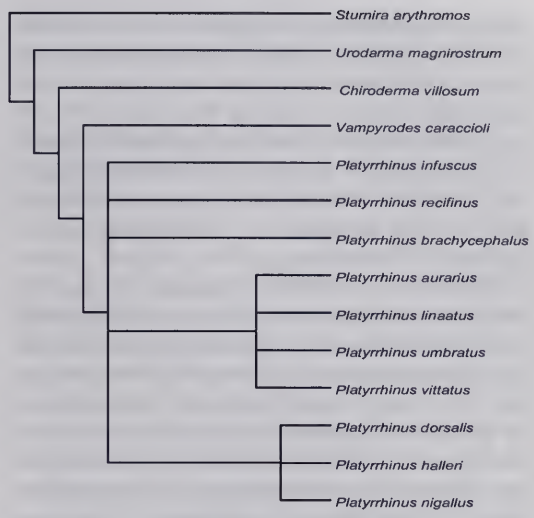

FIG. 2. Owen's (1987; redrawn from Fig. 17) hypothesis of relationships among *Platyrrhinus* species, *Sturnira erythromos, Uroderma magnirostrum, Chiroderma villosum,* and *Vampyrodes caraccioli,* based on a consensus of continuous and discrete characters.

(1987) and Velazco and Solari (2003) recognized *P. nigellus* as a species distinct from *P. lineatus.*

The first explicit hypothesis of phylogenetic relationships within *Platyrrhinus* was presented by Owen (1987; Fig. 2) in the context of his analysis of the subfamily Stenodermatinae. That analysis has been criticized both generally (Lim, 1993) as well as for specific genera included in his analysis (Pacheco & Patterson, 1991). In that analysis, Owen used 22 discrete and 33 continuous external, cranial, and dental characters.

Owen's preferred phylogenetic hypothesis (Owen, 1987; Fig. 2) placed the monotypic genus *Vampyrodes* as a sister genus of *Platyrrhinus.* He considered *Platyrrhinus* to be a monophyletic group and indicated two clades that were not resolved within *Platyrrhinus,* one containing *P. nigellus* + *P. helleri* + *P dorsalis* and the other *P. vittatus* + *P. aurarius* + *P. lineatus* + *P. umbratus.* The relationships of the remaining species in the tree (*P. brachycephalus, P. infuscus,* and *P. recifinus*) also were unresolved. Lim (1993) subsequently argued that Owen (1987) did not judiciously select the best characters for his cladistic analysis and used distance methods not suitable for the reconstruction of evolutionary history.

Lim (1993) used 20 external, cranial, dental, and internal morphological characters to generate a hypothesis of relationships at the generic level for the Stenodermatinae. In this analysis, he ob-

tained *Platyrrhinus* + *Vampyrodes* as sister taxa, supporting Owen's (1987) hypothesis. Two characters unite these taxa: one unambiguous synapomorphy (fringe of hair on the edge of the uropatagium) and one parallel synapomorphy, which is also present in *Uroderma* (accessory cusps on P4). Lim (1993) found that the sister group to this pair includes *Ectophylla* + *Mesophylla* + *Vampyressa* + *Chiroderma*.

Wetterer et al. (2000) evaluated the phylogenetic relationships among the genera of the family Phyllostomidae using 150 morphological, karyological, and molecular characters. In this analysis, they also found *Platyrrhinus* and *Vampyrodes* to be sister taxa, supported with a bootstrap value of 46. Their ACCTRAN (accelerated transformation optimization) analysis indicated five synapomorphies for this grouping: uropatagial fringe presence, I1 occlusal margin generally straight or slightly rounded, m1 paraconid present, pharyngeal region of tongue completely covered with papillae, cerebral vermis completely covering the longitudinal fissure between inferior colliculi, and inferior colliculi exposed dorsally only along lateral edges of cerebelar vermis. Their DELTRAN (delayed transformation optimization) analysis also identified three of these as synapomorphies: uropatagial fringe presence, M1 hypocone present, and pharyngeal region of tongue completely covered with papillae. In their analysis *Uroderma* was sister to the clade *Platyrrhinus* + *Vampyrodes*, and *Ectophylla* + *Vampyressa* + *Chiroderma* was sister to the clade *Uroderma* + *Platyrrhinus* + *Vampyrodes*.

Baker et al. (2000, 2003) evaluated the phylogenetic relationships of the family Phyllostomidae at the generic level using nuclear and mitochondrial genes. In those analyses they also found *Platyrrhinus* and *Vampyrodes* to be sister taxa. Moreover, *Mesophylla* and *Vampyressa* were found to be the sister of *Platyrrhinus* + *Vampyrodes*.

Materials and Methods

Taxonomic Sample and Outgroup Determination

For this cladistic analysis, the taxonomy of Koopman (1993) was followed with the exception of *P. dorsalis*, *P. lineatus*, and *P. umbratus*. For these species, Velazco and Solari (2003), who recognized three distinct morphs within *P. dorsalis* (two not yet described; they are here denoted *P. dorsalis*, *P. dorsalis* "Norte," and *P. dorsalis* "Centro-Sur"), was followed. They also recognized *P. nigellus* as a valid species and considered *P. umbratus* as a junior synonym of *P. dorsalis*. After the character analysis, two different populations in *P. helleri* and *P. vittatus* were recognized. For the purposes of the analysis herein, they are denoted as *P. helleri* "Eastern," *P. helleri* "Western," *P. vittatus* "Northern," and *P. vittatus* "Southern." A list of all 14 ingroup and 4 outgroup taxa is given in Table 1.

TABLE 1. List of examined taxa.

Ingroup
Playtrrhinus aurarius
Platyrrhinus brachycephalus
Playtrrhinus chocoensis
Platyrrhinus dorsalis
Platyrrhinus dorsalis "Norte"
Platyrrhinus dorsalis "Centro-Sur"
Platyrrhinus helleri "Eastern"
Platyrrhinus helleri "Western"
Platyrrhinus infuscus
Platyrrhinus lineatus
Platyrrhinus nigellus
Platyrrhinus recifinus
Platyrrhinus vittatus "Northern"
Platyrrhinus vittatus "Southern"
Outgroups
Carollia subrufa
Sturnira erythromos
Uroderma magnirostrum
Vampyrodes caraccioli

Only one outgroup is necessary to root a phylogenetic tree (Nixon & Carpenter, 1993), but to establish the polarity of ambiguous characters and to test *Platyrrhinus* monophyly, four taxa were used as outgroups: *Carollia subrufa* (Hahn, 1905), *Sturnira erythromos* (Tschudii, 1844), *Uroderma magnirostrum* Davis, 1968, and *Vampyrodes caraccioli* (Thomas, 1889). Freeman (2000) considered *Carollia* as the most ancestral and least specialized genus in the tribe Stenodermatini. Wetterer et al. (2000) found that *Carollia* + *Rhinophylla* is the sister group of the subfamily Stenodermatinae; they placed *Sturnira* as the most basal taxon in the Stenodermatinae. Owen (1987), Lim (1993), Baker et al. (2000, 2003), and Wetterer et al. (2000) all agreed that *Vampyrodes* was the sister genus of *Platyrrhinus*. With respect to the position of *Uroderma*, Owen (1987) placed it in a clade together with *Ectophylla* and *Artibeus*, Lim (1993) placed *Uroderma* in a clade together with *Artibeus*, and Wetterer et al. (2000) placed

Uroderma as the sister taxon of the clade *Platyrrhinus* + *Vampyrodes*. Baker et al. (2003) placed *Uroderma* as sister to the clade *Mesophylla* + *Ectophylla* + *Platyrrhinus* + *Vampyrodes*.

Sources of Data

Only adult specimens were examined based on Morris (1972), Anthony (1988), and Pacheco and Patterson (1992), and all the specimens belong to scientific collections of museums (skins, skulls, skeletons, and alcohol-preserved specimens). A complete list of the specimens examined is provided in Appendix 1.

A total of 1,314 specimens were examined, belonging to the scientific collections of the following museums; acronyms from museums holding holotypes of *Platyrrhinus* species were also included:

AMNH, American Museum Natural of History, New York, New York, USA; **BMNH,** Natural History Museum, London, England; **EPN,** Escuela Politécnica Nacional, Quito, Ecuador; **FMNH,** Field Museum of Natural History, Chicago, Illinois, USA; **IND-M,** La Unidad de Investigación "Federico Medem"—Inderena, Bogotá, Colombia; **LSUMZ,** Louisiana State University, Museum of Natural Science, Baton Rouge, Louisiana, USA; **MCZ,** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **MSB,** Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA; **MUSM,** Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **MVZ,** Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; **QCAZ,** Pontificia Universidad Católica del Ecuador, Museo de Zoología—Mamíferos, Quito, Ecuador; **ROM,** Royal Ontario Museum, Toronto, Ontario, Canada; **TCWC,** Texas Cooperative Wildlife Collection, Texas A&M Collection, College Station, Texas, USA; **UMMZ,** University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; **UV,** Universidad del Valle, Cali, Colombia; **ZMB,** Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany.

The number of specimens per species examined in this study varied according to their availability in these museum collections; each taxon was represented by at least 12 individuals.

Definition of the Characters and Ordering of Character States

Autapomorphies were included in the phylogenetic analysis for the species of *Platyrrhinus* because they are useful in diagnosis. In addition, relevant characters in the relationships among the outgroups were included to provide resolution. In cases where variation inside the species is present, the character was scored as polymorphic. Simmons and Conway (2001) were followed for the categorization of missing data.

The final data set comprised a total of 60 characters: 17 characters of the pelage and integument, 6 of the skull, 35 dental characters, and 2 characters of the postcranial skeleton (Appendix 2). Fifty-eight percent (35) of the characters were binary, and 42% (25) of the characters were multistate.

Polarity

The "outgroup method" was used to establish the polarity of the character states (Watrous & Wheeler, 1981). On the basis of earlier studies, outgroup species formed the sequence *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes caraccioli. Carollia subrufa* was used to root the tree because it is considered ancestral to the remaining three outgroup species (Freeman, 2000).

Methods of Phylogenetic Analysis

The matrix elaboration and the visualization of the character mapping were performed using MacClade 4.0 (Maddison & Maddison, 2000). The phylogenetic analysis was performed using PAUP version 4.0b6 (Swofford, 2001) on a Macintosh PowerBook G4.

The branch and bound option of PAUP was used to identify the most parsimonious trees with the smallest number of steps and to calculate tree statistics. The analysis was performed using all characters unordered. A strict consensus was performed because more than one parsimonious tree was obtained. To perform the decay analysis (Bremer, 1988), the program TreeRot version 2b (So-

renson, 1999) was used. A branch and bound bootstrap analysis was performed, with 10,000 replications, to evaluate the support of the resulting clades.

Character optimizations were calculated using both the ACCTRAN and DELTRAN. The results of these optimizations are presented in Appendix 3.

Character Descriptions

Pelage and Integument

Character 1—**Facial stripes.** Absent (0); present (1). The facial stripes are present as two lines on each side of the face. The dorsomedial stripe begins at the posterolateral edge of the noseleaf, continues above the eye, and terminates close to the pinna. The ventrolateral stripe begins in the corner of the mouth and runs toward the tragus. The facial stripes are present in all the species of *Platyrrhinus, Vampyrodes caraccioli,* and *Uroderma magnirostrum.* In contrast, the facial stripes are absent in *Carollia subrufa* and *Sturnira erythromos.*

Owen (1987: character 4) uses the facial stripes as part of a multistate character that he termed "Pelage patterns." In this character Owen includes facial stripes, dorsal stripe, shoulders patches, and striping on the wing. I agree with Owen on his facial stripes scoring for the species used in the present analysis. Lim (1993: character 1) and Wetterer et al. (2000: character 6) include facial stripes in their phylogenetic analyses; character states and scoring used in this analysis coincide with theirs.

Character 2—**Brightness of facial stripe.** Dorsomedial and ventrolateral stripes obviously subequal (0); dorsomedial stripe more marked than the ventrolateral stripe (1). In most *Platyrrhinus* species, both facial stripes have the same tonality, either dark or brilliant (e.g., *P. aurarius, P. helleri* "Eastern," *P. nigellus*). In contrast, *P. vittatus* "Northern" and *P. vittatus* "Southern" have a more luminous dorsomedial stripe. *Carollia subrufa* and *Sturnira erythromos* were scored as "—" because they do not have facial stripes. This is the first use of this character in a phylogenetic analysis.

Character 3—**Facial stripe coloration.** Brilliant-white (0); dark (1). The facial stripes are brilliant or white in *P. brachycephalus, P. helleri* "Eastern," *P. helleri* "Western," *P. lineatus, P. recifinus, P. vittatus* "Southern," *Vampyrodes caraccioli,* and *Uroderma magnirostrum.* In contrast, they are dark in *P. aurarius, P. chocoensis, P. dorsalis, P. dorsalis* "Norte," *P. dorsalis* "Centro-Sur," *P. infuscus, P. nigellus,* and *P. vittatus* "Northern." *Carollia subrufa* and *Sturnira erythromos* were scored as "—" because they lack both facial stripes. This is the first use of this character in a phylogenetic analysis.

Character 4—**Basal protuberance where the genal vibrissae are implanted.** Absent (0); present (1). The genal vibrissae are implanted in the cheek, ventral, and/or posterior to the eye. The genal vibrissae are present in all the species of *Platyrrhinus.* These vibrissae are implanted in a basal protuberance in some *Platyrrhinus* (e.g., *P. brachycephalus, P. helleri* "Eastern," *P. lineatus*) (Fig. 3A). In contrast, the genal vibrissae are implanted directly on the cheek in *Carollia subrufa* and some species of *Platyrrhinus* (e.g., *P. aurarius, P. chocoensis*) (Fig. 3B–C). This character has not been used in previous studies.

Character 5—**Number of vibrissae surrounding the margins of the noseleaf in a single array.** Nine vibrissae present (0); eight vibrissae present (1); seven vibrissae present (2); six vibrissae present (3). Some species of *Platyrrhinus* have seven vibrissae surrounding the margins of the noseleaf in a single array (e.g., *P. brachycephalus, P. chocoensis, P. lineatus*) (Fig. 3B). In contrast, six vibrissae are presented to each side of the noseleaf in some *Platyrrhinus* and *Vampyrodes* (e.g., *P. aurarius, P. dorsalis*) (Fig. 3A). *Platyrrhinus helleri* "Eastern" presents intraspecific variation (seven and eight vibrissae present; Fig. 3B–C). *Sturnira erythromos* have nine vibrissae surrounding the margins of the noseleaf.

Character 6—**Number of vibrissae present on the upper lip, ventral to the vibrissae that surround the margins of the noseleaf.** One vibrissa present on each side of the face (0); two vibrissae present (1). In some species of *Platyrrhinus* (e.g., *P. aurarius, P. chocoensis, P. dorsalis*), *Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes,* a single vibrissa is present on the upper lip, ventral to the vibrissae that surround the margins of the noseleaf (Fig. 3A). Only *P. brachycephalus* and *Carollia subrufa* have two vibrissae on the upper lip (Fig. 3B). *Platyrrhinus helleri* "Eastern," *P. infuscus,* and *P. nigellus* present intraspecific variation in this character (one vibrissa and two vibrissae present) (Fig. 3A–B). This character has not been used in any other study.

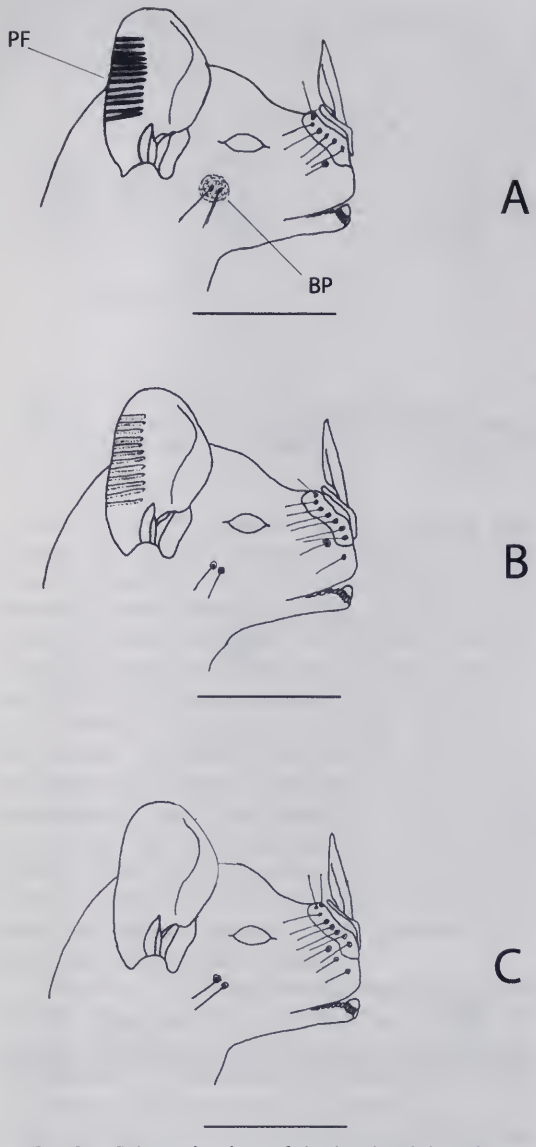

FIG. 3. Schematic view of the heads of three hypothetical bats, showing details of basal protuberance (BP) and pinna folds (PF). Scale bar = 15 mm.

Character 7—**Number of submental vibrissae on each side of the chin.** Absence of submental vibrissae (0); two submental vibrissae present (1); three submental vibrissae present (2); four submental vibrissae present (3); five submental vibrissae present (4). The submental vibrissae are on the chin and lower lip and are usually arranged in two notable parallel longitudinal rows (Pocock, 1914; Brown, 1971). Some *Platyrrhinus* (e.g., *P. aurarius, P. lineatus, P. nigellus*), *Uroderma magnirostrum,* and *Vampyrodes* (Fig. 4C, E) always have four submental vibrissae. *Platyrrhinus dorsalis* "Centro-Sur" has two submental vibrissae (Fig. 4B). *Platyrrhinus brachycephalus* present five submental vibrissae (Fig. 4D). Intraspecific variation was noted (three and four submental vibrissae) in *P. chocoensis* (Fig. 4A, C, E). *Carollia subrufa* lacks submental vibrissae. This character has not been used in previous studies.

Character 8—**Interramal vibrissae.** Absence (0); one interrramal vibrissa present (1); two interramal vibrissae present (2). The interramal vibrissae form a median tuft on the gular region between the two rami of the lower jaws and well behind the mandibular symphysis (Pocock, 1914; Brown, 1971). *Platyrrhinus recifinus, Sturnira erythromos,* and *Uroderma magnirostrum* lack interramal vibrissae (Fig. 4A). An interramal vibrissa is present in some species of *Platyrrhinus* (e.g., *P. brachycephalus, P. lineatus*) and *Vampyrodes* (Fig. 4B–D). Two interramal vibrissae are present in *P. infuscus, P. vittatus* "Northern," *P. helleri* "Western," and *Carollia subrufa* (Fig. 4E). Intraspecific variation is found in *P. vittatus* "Southern" (one and two interramal vibrissae present; Fig. 4B–E). This character was used by Wetterer et al. (2000: character 13).

Character 9—**Inferior border of horseshoe.** Inferior border with no distinct boundary between horseshoe and lip (0); inferior border partially joined to the upper lip (1); inferior border completely free (2). The inferior border of the horseshoe is completely free of the upper lip in some *Platyrrhinus* (e.g., *P. brachycephalus, P. lineatus*), *Uroderma magnirostrum,* and *Vampyrodes* (Fig. 5C). *Platyrrhinus chocoensis, P. dorsalis* "Centro-Sur," and *P. infuscus* have intraspecific variation (inferior border completely free and partially joined (Fig. 5B–C). In *Carollia subrufa* and *Sturnira erythromos,* there is no distinct boundary between horseshoe and the upper lip (Fig. 5A). According to Wetterer et al. (2000: character 25), the inferior border is completely free in all the species of *Platyrrhinus*; however, I do not agree with that assessment.

Character 10—**Parallel folds located in the pinna.** Absent (0); poorly marked but distinguishable (1); well marked (2). *Sturnira erythromos* lacks these folds (Fig. 3C). The folds in the pinna are not very well defined in some species of *Platyrrhinus* (e.g., *P. dorsalis, P. lineatus, P. recifinus*) and *Vampyrodes* (Fig. 3B). In contrast, *P. aurarius, P. chocoensis, P. dorsalis* "Centro-Sur," *P. nigellus, P. vittatus* "Northern," *Carollia subrufa,* and *Uroderma magnirostrum* have well-

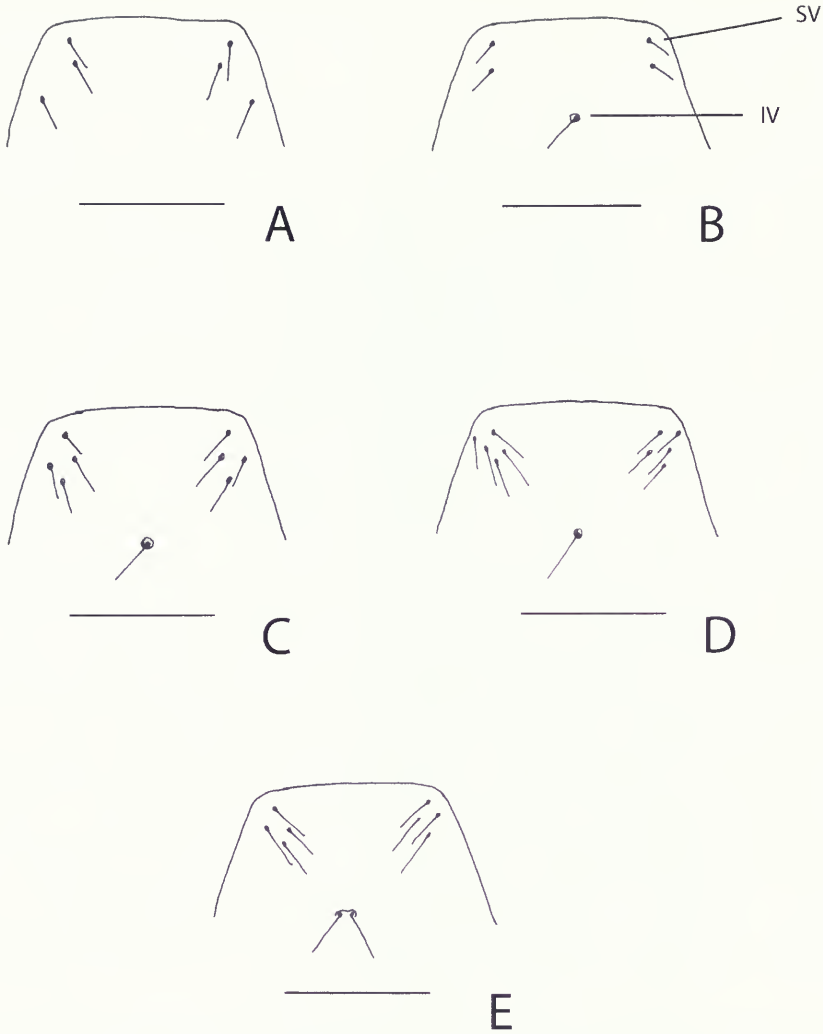

FIG. 4. Ventral view of the chin of five hypothetical bats, showing states of interramal (IV) and submental vibrissae (SV). Scale bar = 5 mm.

marked pinna folds (Fig. 3A). *Platyrrhinus helleri* "Eastern" and *P. infuscus* present intraspecific variation, presenting both states (Fig. 3A–B). This is the first use of this character in a phylogenetic analysis.

Character 11—**Dorsal stripe.** Absent (0); indistinct, thin, and obscured (1); definite but narrow (2); brilliant-white and wide (3). A dorsal midline stripe is absent in *Carollia subrufa* and *Sturnira erythromos.* A narrow dorsal stripe is presented in some species of *Platyrrhinus* (e.g., *P. chocoensis, P. dorsalis*) and *Uroderma magnirostrum. Platyrrhinus lineatus, P. recifinus, P. vittatus* "Northern," *P. vittatus* "Southern," and *Vampyrodes* have the dorsal stripe that is white and wide. In *Platyrrhinus infuscus,* the dorsal stripe is thin and obscure. *Platyrrhinus brachycephalus, P. helleri* "Eastern," and *P. nigellus* all show intraspecific variation in this character, some individuals with a narrow dorsal stripe and others with white and wide stripes. Owen (1987: character 4) used the dorsal stripe as part of a complex multistate character termed "Pelage patterns," in which he included facial stripes, dorsal stripe, and shoulder patches. I agree with Owen (1987) on the scores for dorsal stripe in the species used in the present analysis. Wetterer et al. (2000: character 7) used the dorsal stripe as a character with three states: absent, present, and occasionally present.

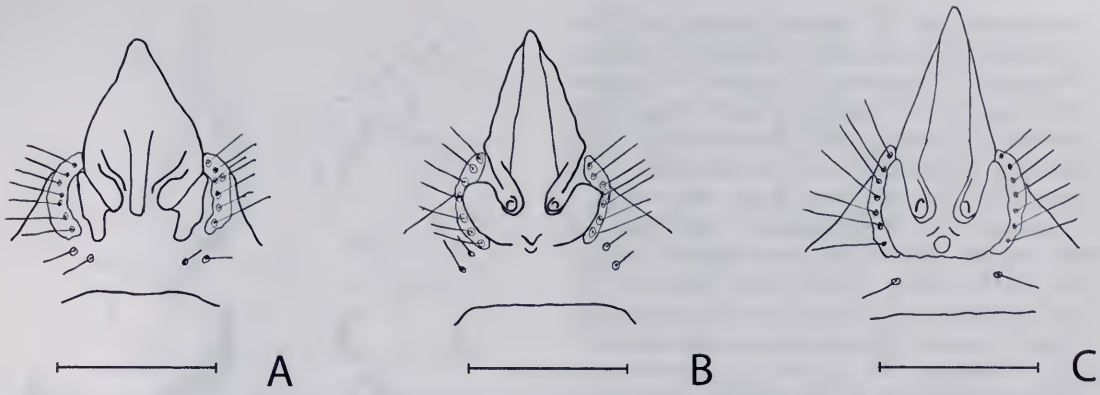

FIG. 5. Frontal view of the noseleaf in (**A**) *Sturnira erythromos* (MUSM 5310); (**B.**) *Platyrrhinus infuscus* (MUSM 9897); (**C**) *P. nigellus* (MUSM 16170). Scale bar = 5 mm.

Character 12—**Length of the dorsal fur.** Long, >8 mm (0); medium, average, 6.30–7.50 mm (1); short, <6.30 mm (2). Dorsal fur is of average length in some species of *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. recifinus*), *Carollia subrufa, Uroderma magnirostrum,* and *Vampyrodes.* In *Platyrrhinus aurarius, P. dorsalis, P. dorsalis* "Norte," *P. nigellus, P. vittatus* "Northern," *P. vittatus* "Southern," and *Sturnira erythromos,* the dorsal fur is long. *Platyrrhinus infuscus* characteristically has short dorsal fur. *Platyrrhinus chocoensis* presents intraspecific variation, in which some individuals have short dorsal fur, while in others it is normal. This character was used by Marques-Aguiar (1994: character 3) in her study of the genus *Artibeus.*

Character 13—**Bands of contrast in the dorsal fur.** Bicolored (0); tricolored (1); tetracolored (2). In most *Platyrrhinus* (e.g., *P. brachycephalus, P. chocoensis, P. dorsalis*), *Carollia subrufa,* and *Uroderma magnirostrum,* the dorsal fur is distinctly tricolored. In contrast, tetracolored dorsal fur is presented in *P. aurarius, P. recifinus,* and *Sturnira erythromos. Vampyrodes* has bicolored dorsal fur. Owen (1987: character 3) and Wetterer et al. (2000: character 5) scored *S. erythromos* as having tricolored dorsal fur; according to my observations, it has tetracolored dorsal fur. Wetterer et al. (2000) scored all *Platyrrhinus* as having bicolored dorsal fur, as did Owen (1987) with the exception of *P. dorsalis* which had tricolored dorsal fur. I agree with Owen's score for *P. dorsalis* but do not agree with the scores of the other *Platyrrhinus* species. Instead, I observed interspecific variation in dorsal fur patterns among the species of *Platyrrhinus.* I agree with Owen (1987) and Wetterer et al. (2000) on the score of *Vampyrodes.*

Character 14—**Bands of contrast in the ventral fur.** Unicolored (0); bicolored (1); tricolored (2); tetracolored (3). A tricolored ventral fur is present in some species of *Platyrrhinus* (e.g., *P. brachycephalus, P. infuscus*), *Carollia subrufa,* and *Vampyrodes.* In contrast, *P. chocoensis, P helleri* "Eastern," *P. vittatus* "Northern," *P. vittatus* "Southern," and *Uroderma magnirostrum* have a bicolored ventral fur. *Platyrrhinus helleri* "Western" presents intraspecific variation because some individuals present a bicolored ventral fur and others a unicolored ventral fur. *Sturnira erythromos* has tetracolored ventral fur. This character has not been used in any other study.

Character 15—**Hair on the dorsum of the feet.** Sparse and short (0); intermediate in density and length (1); dense and long (2). Dense and long hair is present on the dorsal side of the feet in some *Platyrrhinus* (e.g., *P. lineatus, P. vittatus* "Southern") and *Sturnira erythromos.* In *Platyrrhinus aurarius, P. chocoensis, P. dorsalis, P. helleri* "Eastern," and *Vampyrodes,* the hair on the dorsal side of the feet is intermediate in density and length. Only *P. infuscus, P. helleri* "Western," and *Uroderma magnirostrum* have sparse and short hairs on the dorsal side of the feet. *Platyrrhinus brachycephalus* presents intraspecific variation in this character, some individuals with sparse hairs, and others with an intermediate distribution of hair on the dorsal side of the feet. This character has not been used in any other study.

Character 16—**Posterior edge of the uropatagium.** "V" shaped (0); "U" shaped (1). The uropatagium is "U" shaped in some *Platyrrhinus* (e.g., *P. brachycephalus, P. recifinus*), *Carollia subrufa,* and *Sturnira erythromos.* In contrast,

Vampyrodes has "V"-shaped uropatagium. *Platyrrhinus dorsalis*, *P. helleri* "Eastern," *P. helleri* "Western," *P. infuscus*, *P. nigellus*, *P. vittatus* "Northern," and *Uroderma magnirostrum* have intraspecific variation. This character was evaluated only in alcohol-preserved specimens. This character has not been used in any other study.

Character 17—**Distribution of the fringe of hair on the edge of the uropatagium.** Absent (0); usually hairy, occasionally sparsely (1); densely haired (2). A densely haired uropatagium fringe is present in some *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. nigellus*) and *Sturnira erythromos*. In contrast, *P. brachycephalus*, *P. chocoensis*, *P. dorsalis*, *P. infuscus*, *P. vittatus* "Northern," and *Vampyrodes* have a regular or occasionally sparsely haired uropatagium fringe. *Carollia subrufa* and *Uroderma magnirostrum* lack this fringe of hair on the edge of the uropatagium. I agree with Lim (1993: character 13) and Wetterer et al. (2000: character 10) on the score of *Platyrrhinus*, *Carollia*, *Sturnira*, *Uroderma*, and *Vampyrodes*.

Skull

Character 18—**Posterior border of the hard palate.** "U" shaped (0); "V" shaped (1). A "U"-shaped posterior border of the hard palate is present in some species of *Platyrrhinus* (e.g., *P. lineatus*, *P. recifinus*), *Carollia subrufa*, *Sturnira erythromos*, and *Uroderma magnirostrum* (Fig. 6A). In contrast, *P. aurarius*, *P. dorsalis*, and *P. dorsalis* "Norte" have a "V"-shaped posterior border of the hard palate (Fig. 6B). *Platyrrhinus brachycephalus*, *P. chocoensis*, *P. dorsalis* "Centro-Sur," *P. helleri* "Eastern," *P. helleri* "Western," *P. infuscus*, *P. nigellus*, *P. vittatus* "Northern," *P. vittatus* "Southern," and *Vampyrodes* have intraspecific variation for this character, with some individuals possessing the "U"-shaped posterior border of the hard palate and other individuals "V" shaped (Fig. 6A–B). Wetterer et al. (2000: character 45) used this character, but they scored *Platyrrhinus*, *Vampyrodes*, *Uroderma*, and *Sturnira* as "—" because they considered that there was a continuous range of intra- and interspecific variation among the shape of the posterior border, making it not a useful character. According to my observations, I found some species with intraspecific variation. Owen (1987: character 10) used this character, and I do not agree with his scores of *Vampyrodes*; he indicated that *Vampyrodes* only has a "U"-shaped posterior border of the hard palate, but I also found some individuals having a "V"-shaped posterior border of the hard palate. Within *Platyrrhinus*, he did not find intraspecific variation, but according to my observations, *Platyrrhinus* demonstrates intraspecific variation. Lim (1993: character 4) scored *Platyrrhinus*, *Vampyrodes*, and *Sturnira* as having a hard palate extended into interpterygoidal space, but he did not score the shape of the posterior border of

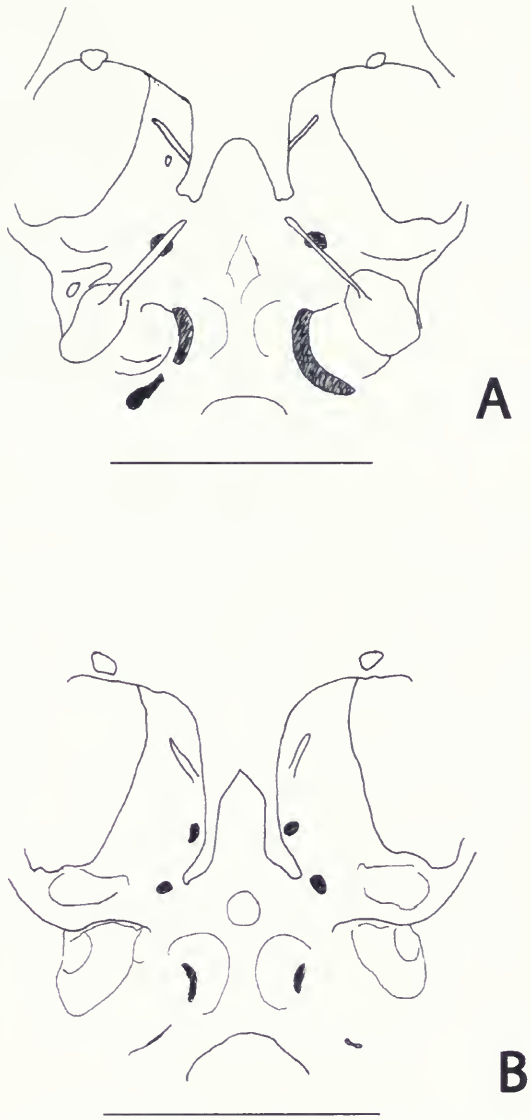

FIG. 6. Ventral view of the basicranium, showing details of the posterior margin of the hard palate: (**A**) *Platyrrhinus brachycephalus* (MUSM 13793); (**B**) *P. helleri* "Western" (MUSM 10725). Scale bar = 8 mm.

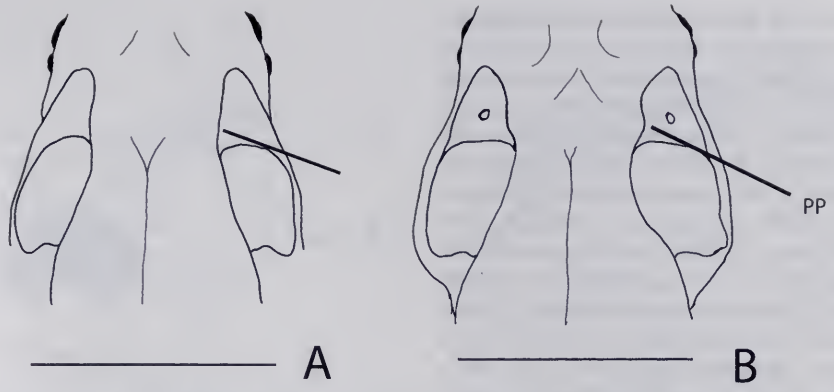

FIG. 7. Dorsal view of two crania, showing details of the postorbital process (PP): (**A**) *Platyrrhinus nigellus* (MUSM 16170); (**B**) *P. infuscus* (MUSM 9897). Scale bar = 12 mm.

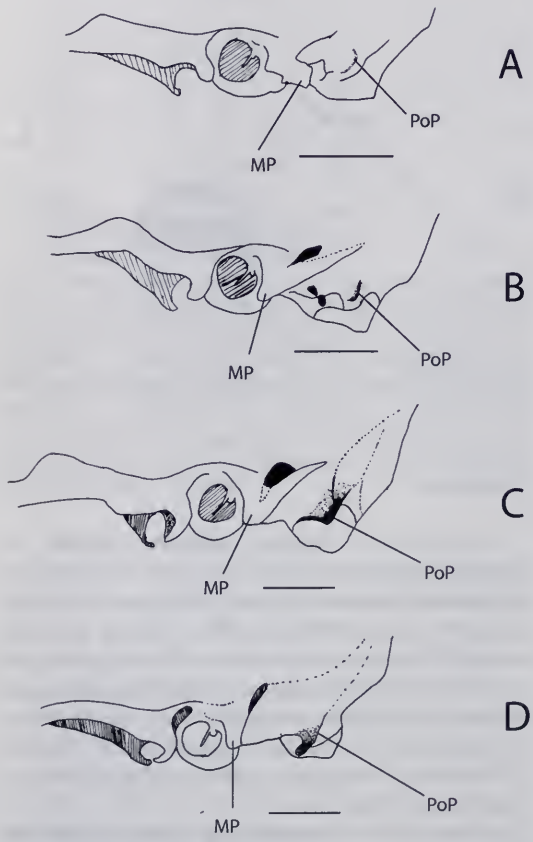

FIG. 8. Lateral view of the temporal region, showing details of the mastoid process (MP) and paraoccipital process (PoP): (**A**) *Platyrrhinus helleri* "Western" (MUSM 10726); (**B**) *P. nigellus* (MUSM 16170); (**C**) *P. vittatus* "Southern" (MUSM 14584); (**D**) *Sturnira erythromos* (MUSM 5260). Scale bar = 2 mm.

the hard palate in these genera. This character was used by Marques-Aguiar (1994: character 21) and Owen (1991: character 23) in their studies of the systematics of the genus *Artibeus* and *Dermanura*, respectively.

Character 19—**Postorbital process.** Absent or poorly developed (0); moderately developed (1); well developed (2). A poorly developed postorbital process is present in some species of *Platyrrhinus* (e.g., *P. chocoensis, P. dorsalis*) and *Sturnira erythromos* (Fig. 7A). In *Platyrrhinus aurarius, P. helleri* "Eastern," *P. infuscus, P. recifinus, P. vittatus* "Northern," *P. vittatus* "Southern," and *Vampyrodes*, the postorbital process is moderately developed (Fig. 7B). *Platyrrhinus lineatus, Carollia subrufa,* and *Uroderma magnirostrum* have a well-developed postorbital process. In *Platyrrhinus dorsalis* "Norte," there is intraspecific variation, with individuals having a poorly developed or moderately developed postorbital process (Fig. 7A–B). This character was used by Marques-Aguiar (1994: character 15) in her study of the genus *Artibeus*.

Character 20—**Paraoccipital process.** Poorly developed, almost imperceptible (0); moderately developed (1); well developed (2). The paraoccipital process appears moderately developed, about half the size of the mastoid process, in some species of *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. nigellus*), *Carollia subrufa, Sturnira erythromos,* and *Vampyrodes* (Fig. 8B). In *Platyrrhinus aurarius, P. infuscus, P. lineatus, P. vittatus* "Southern," and *Uroderma magnirostrum*, the paraoccipital process is well developed, almost the same size as the mastoid process (Fig. 8C–D). *Platyrrhinus brachycephalus* and *P. helleri* "Western" have the paraoccipital process poorly developed,

scarcely a third of the size of the mastoid process (Fig. 8A). Intraspecific variation is present in *P. chocoensis*, with the paraoccipital process poorly to moderately developed (Fig. 8A–B). I do not agree with Owen's (1987: character 12) score for *P. brachycephalus*, *P. helleri*, and *P. nigellus*; he scored them as if they lacked a paraoccipital process. Owen (1987) also scored *P. dorsalis* and *P. infuscus* as having minimal development of the paraoccipital process, but according to personal observations, *P. dorsalis* has a moderately developed process (Fig. 8B), and *P. infuscus* has a well-developed paraoccipital process (Fig. 8C). This character has been used by Marques-Aguiar (1994: character 20), Straney (1980: character J-6), and Owen (1987: character 12) in their phylogenetic analyses of *Artibeus*, Phyllostominae, and *Dermanura*, respectively.

Character 21—**Apophysis in the paraoccipital process.** Present (0); absent (1). All species of *Platyrrhinus*, *Carollia subrufa*, and *Vampyrodes caraccioli* lack an apophysis in the paraoccipital process (Fig. 8A–C). In contrast, *Sturnira erythromos* and *Uroderma magnirostrum* have an apophysis in the paraoccipital process (Fig. 8D). This character has not been used in any other study.

Character 22—**Fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa.** Absent or almost imperceptible (0); shallow (1); deep (2). This fossa is absent or almost imperceptible in some species of *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. lineatus*), *Carollia subrufa*, *Sturnira erythromos*, *Uroderma magnirostrum*, and *Vampyrodes* (Fig. 9A). *Platyrrhinus dorsalis* "Norte," *P. infuscus*, and *P. recifinus* have a shallow fossa (Fig. 9B). *Platyrrhinus aurarius* and *P. dorsalis* have a deep fossa (Fig. 9C). *Platyrrhinus chocoensis* and *P. dorsalis* "Centro-Sur" present intraspecific variation, some individuals have the fossa on the squamosal end of the zygomatic arch absent or almost imperceptible, and others have this fossa shallow. *Platyrrhinus nigellus* also demonstrate intraspecific variation, with a shallow or deep fossa. This character has not been used in any other study.

Character 23—**Posterior clinoid processes.** Absent (0); present (1). This process is located on the posterior face of the *sella turcica* in the sphenoid bone (Stromsten, 1947). *Carollia subrufa*, *Sturnira erythromos*, and *Uroderma magnirostrum* lack these processes (Fig. 10A). In contrast, all the species of *Platyrrhinus* and *Vampyrodes* possess posterior clinoid processes (Fig. 10B).

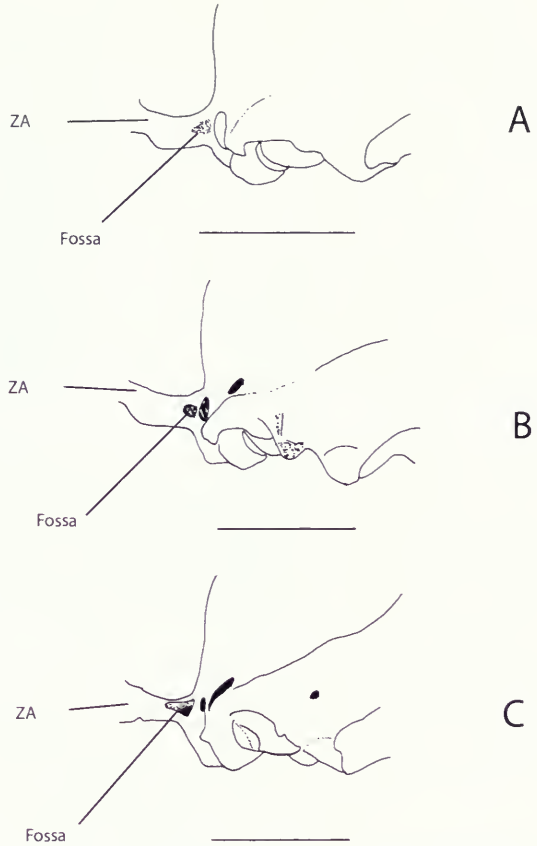

FIG. 9. Posterior view of the temporal region, showing details of zygomatic arch (ZA) and fossa on the squamosal end of the zygomatic arch: (**A**) *Platyrrhinus brachycephalus* (MUSM 13793); (**B**) *P. infuscus* (MUSM 9897); (**C**) *P. dorsalis* (FMNH 128141). Scale bar = 4 mm.

Dentition

Character 24—**Upper median incisors.** In contact (0); without contact (1). The upper median incisors are in contact in some species of *Platyrrhinus* (e.g., *P. chocoensis*, *P. lineatus*), *Carollia subrufa*, *Sturnira erythromos*, and *Vampyrodes*. In contrast, *Uroderma magnirostrum* has the upper median incisors not in contact. *Platyrrhinus brachycephalus*, *P. helleri* "Eastern," *P. helleri* "Western," *P. infuscus*, and *P. recifinus* have intraspecific variation.

Character 25—**Lobulation of the upper lateral incisors.** Monolobed (0); bilobed (1). Monolobed upper lateral incisors are present in some species of *Platyrrhinus* (e.g., *P. chocoensis*, *P. helleri* "Eastern"), *Carollia subrufa*, and *Vampyrodes*. In contrast, *P. dorsalis* "Centro-Sur"

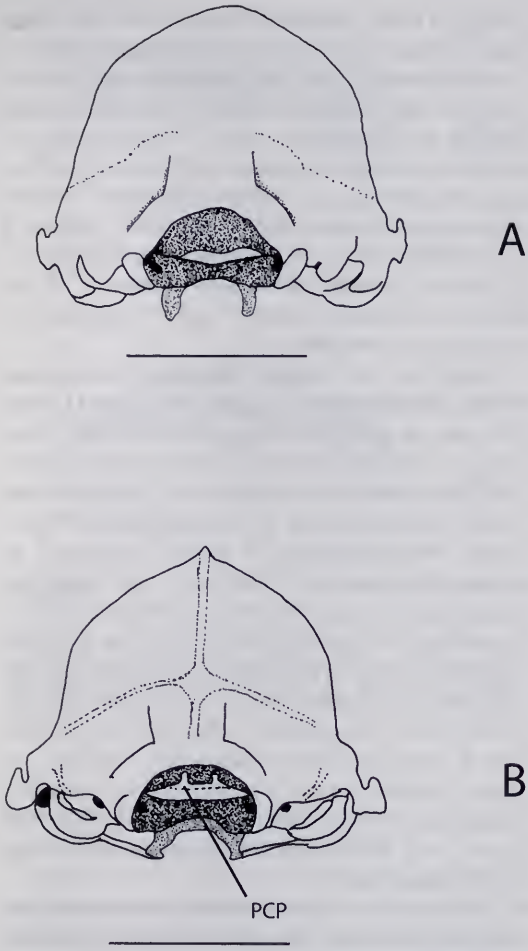

FIG. 10. Detail of the posterior clinoid processes (PCP), in a posterior view of cranium: (**A**) Absence of PCP in *Uroderma magnirostrum* (MUSM 14029); (**B**) Presence of the PCP in *Platyrrhinus infuscus* (MUSM 9897). Scale bar = 8 mm.

and *Uroderma magnirostrum* have bilobed upper lateral incisors. *Platyrrhinus brachycephalus, P. dorsalis* "Norte," *P. helleri* "Western," *P. infuscus, P. lineatus, P. vittatus* "Southern," and *Sturnira erythromos* have intraspecific variation.

Character 26—**Alignment of P3 in the toothrow.** P3 aligned along the axis of the toothrow (0); P3 aligned transversally to the toothrow (1). *Carollia subrufa* and *Sturnira erythromos* have the P3 aligned along the axis of the toothrow (Fig. 11A). In contrast, all the species of *Platyrrhinus, Uroderma magnirostrum,* and *Vampyrodes* have the P3 aligned transversally to the toothrow (Fig. 11B). This character has not been used in any other study.

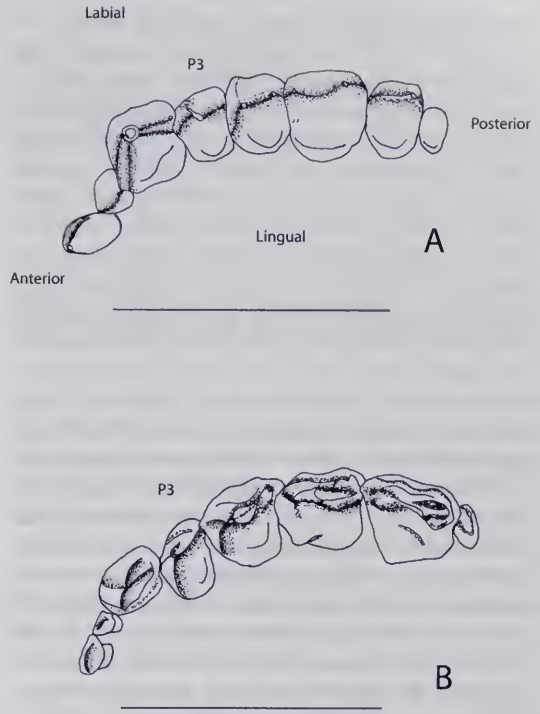

FIG. 11. Occlusal view of the maxillary toothrow: (**A**) *Sturnira erythromos* (MUSM 5310); (**B**) *Platyrrhinus infuscus* (MUSM 9897). Scale bar = 8 mm.

Character 27—**Size of the P3 with regard to P4.** P3 slightly smaller than P4 (0); P3 about half the size of P4 (1). All the species of *Platyrrhinus, Uroderma magnirostrum,* and *Vampyrodes* possess a P3 slightly bigger than half the size of P4. *Carollia subrufa* and *Sturnira erythromos* have a P3 almost the same size as P4. This character has not been used in any other study.

Character 28—**Stylar cusps on the posterior face of P4.** P4 lacking stylar cusps or with one stylar cusp present (0); two stylar cusps present (1). All the species of *Platyrrhinus, Uroderma magnirostrum,* and *Vampyrodes* have two stylar cusps on the posterior face of P4 (Fig. 12). In contrast, *Carollia subrufa* and *Sturnira erythromos* do not possess two stylar cusps on P4, although occasionally they exhibit one stylar cusp. I agree with Lim (1993: character 6) in his scores of *Platyrrhinus* species. I do not agree with Wetterer et al. (2000: character 57) on their scores for *Platyrrhinus* because they indicated that this genus only occasionally has the second stylar cusp. According to my observations, all the individuals of *Platyrrhinus* always have two stylar cusps. They also stated that Lim (1993: character 6) did

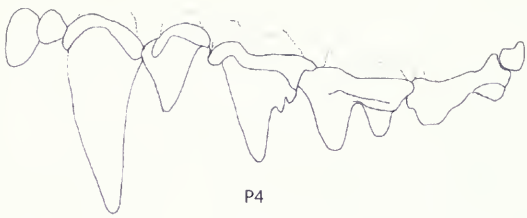

FIG. 12. Lateral view of the maxillary toothrow: *Platyrrhinus infuscus* (MUSM 9897). Scale bar = 8 mm.

not report the presence of the second stylar cusp for *Vampyrodes*, when in fact he did report it.

Character 29—**Sulcus on the posterior face of P4.** Absent (0); present (1). All the species of *Platyrrhinus, Uroderma magnirostrum,* and *Vampyrodes* have a sulcus on the posterior face of P4, starting near the accessory cusps and ending at the tip of P4. In contrast, *Carollia subrufa* and *Sturnira erythromos* lack this sulcus. This character has not been used in any previous study.

Character 30—**Sulcus on the anterior face of P4.** Absent (0); present (1). All the species of *Platyrrhinus* have a sulcus on the anterior face of P4, starting near the cingulum and ending at the tip of P4. In contrast, *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes* lack this sulcus on the anterior face of P4. This character has not been used in any previous study.

Character 31—**Fossa on the hypoconal basin of P4.** Shallow (0); deep (1). The fossa of the hypoconal basin of P4 is deep in some species of *Platyrrhinus* (e.g., *P. recifinus, P. vittatus* "Southern"). In contrast, *P. aurarius, P. chocoensis, P. helleri* "Eastern," *P. lineatus, Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* have a shallow fossa. *Platyrrhinus brachycephalus, P. dorsalis, P. dorsalis* "Norte," *P. dorsalis* "Centro-Sur," *P. helleri* "Western," *P. nigellus,* and *Vampyrodes* have intraspecific variation. This character has not been used by other researchers.

Character 32—**M1 Parastyle.** Absent (0); present (1). The M1 parastyle is present in some species of *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. recifinus*). In contrast, other species of *Playtrrhinus* (e.g., *P. aurarius, P. chocoensis*), *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes* lack the parastyle on M1. *Platyrrhinus lineatus* has intraspecific variation. Straney (1980: character: K 27) used this character in his phylogeny of the Phyllostominae.

Character 33—**M1 Mesostyle.** Absent (0); present (1). The mesostyle on M1 is absent in some species of *Platyrrhinus* (e.g., *P. chocoensis, P. dorsalis*), *Carollia subrufa,* and *Sturnira erythromos.* In contrast, *P. vittatus* "Southern," *Uroderma magnirostrum,* and *Vampyrodes* possess a mesostyle on M1. *Platyrrhinus brachycephalus, P. helleri* "Eastern," *P. helleri* "Western," *P. infuscus, P. dorsalis* "Norte," and *P. nigellus* have intraspecific variation.

Character 34—**Labial cingulum at the base of the M1 metacone.** Absent (0); present (1); stylar cusp on the labial cingulum of the M1 metacone (2). *Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* lack the labial cingulum on the base of the M1 metacone. *Platyrrhinus brachycephalus, P. helleri* "Eastern," *P. helleri* "Western," *P. recifinus,* and *Uroderma magnirostrum* have the labial cingulum without a stylar cusp. In contrast, a stylar cusp on the labial cingulum of the M1 metacone is present in some species of *Platyrrhinus* (e.g., *P. chocoensis, P. infuscus*) and *Vampyrodes. Platyrrhinus lineatus* and *P. nigellus* have intraspecific variation, as some individuals have a stylar cusp on the labial cingulum of the M1 metacone and others lack this stylar cusp. This character has not been used by other researchers.

Character 35—**Sulcus on the posterior face of the M1 paracone.** Absent (0); present (1). All the species of *Platyrrhinus, Uroderma magnirostrum,* and *Vampyrodes* have a sulcus on the posterior face of the M1 paracone. In contrast, *Carollia subrufa* and *Sturnira erythromos* lack this sulcus on M1.

Character 36—**Lingual cingulum on the base of the M1 metacone.** Absent (0); lingual cingulum present at the base of the M1 metacone (1); stylar cusp on the lingual cingulum of the M1 metacone (2). *Carollia subrufa, Sturnira erythromos,* and *Vampyrodes* lack the lingual cingulum on the M1 metacone. A stylar cusp is present on the cingulum of the lingual face of the M1 metacone in some species of *Platyrrhinus* (e.g., *P. infuscus, P. lineatus*). In contrast, *P. helleri* "Eastern," *P. helleri* "Western," *P. recifinus,* and *Uroderma magnirostrum* lack this stylar cusp. *Platyrrhinus brachycephalus, P. chocoensis, P. dorsalis,* and *P. nigellus* have intraspecific variation, as some individuals have a stylar cusp on the lingual cingulum of the M1 metacone and others

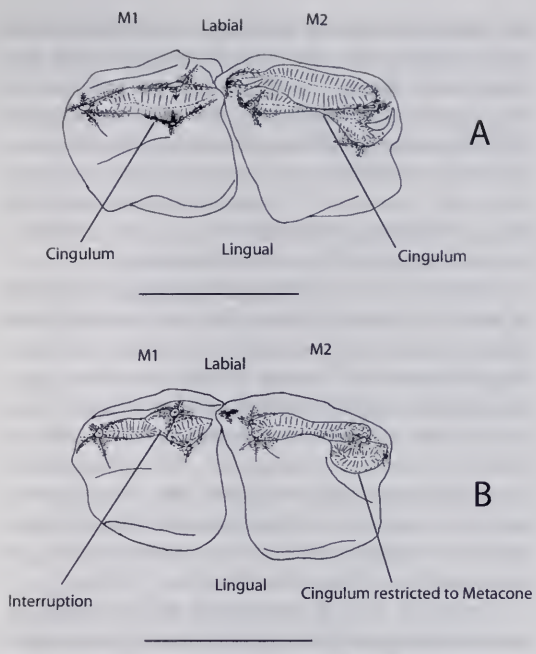

FIG. 13. Occlusal view of M1–M2: (**A**) *Platyrrhinus infuscus* (MUSM 9897); (**B**) *P. dorsalis* "Norte" (MUSM 4946). Scale bar = 2.5 mm.

lack this stylar cusp. This is the first use of this character in a phylogenetic analysis.

Character 37—**Sulcus on the posterior face of the paracone not joined to the cingulum of the lingual face of the metacone on M1.** Absent (0); present (1). The majority of the *Platyrrhinus* species (e.g., *P. aurarius, P. brachycephalus, P. chocoensis*) have this sulcus on the posterior face of the paracone joined to the cingulum of the lingual face of the metacone on M1 (Fig. 13A). In contrast, *P. dorsalis* "Norte" and *Uroderma magnirostrum* have the sulcus on the posterior face of the paracone not joined to the cingulum of the lingual face of the M1 metacone (Fig. 13B). *Carollia subrufa, Sturnira erythromos,* and *Vampyrodes caraccioli* were scored as "—" because they lack the cingulum on the lingual face of the M1 metacone. This character has not been used by other researchers.

Character 38—**M1 metastyle.** Absent (0); present (1). The metastyle on M1 is present in the majority of *Platyrrhinus* species (e.g., *P. dorsalis, P. dorsalis* "Norte"), *Carollia subrufa,* and *Vampyrodes.* In contrast, *Sturnira erythromos* and *Uroderma magnirostrum* lack the metastyle on M1. *Platyrrhinus brachycephalus, P. chocoensis, P. helleri* "Eastern," and *P. helleri* "Western" have intraspecific variation.

Character 39—**M1 protocone.** Well-developed, large (0); moderately developed (1); small and blunt (2). A well-developed M1 protocone is present in *Platyrrhinus brachycephalus.* In contrast, *P. chocoensis, P. dorsalis, P. dorsalis* "Norte," and *P. helleri* "Eastern" possess an M1 protocone that is small and blunt. Some species of *Platyrrhinus* (e.g., *P. aurarius, P. infuscus*), *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes* have a moderately developed protocone on M1. *Platyrrhinus vittatus* "Northern" has intraspecific variation: some individuals have the protocone with a moderate development and others with a well-developed protocone on M1. This character has not been used by other researchers.

Character 40—**M2 parastyle.** Absent (0); present (1). The parastyle on M2 is present in all *Platyrrhinus* species and *Vampyrodes.* In contrast, *Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* lack a parastyle on M2. This character has not been used in any other study.

Character 41—**Labial cingulum of the M2 paracone.** Absent (0); present (1). The labial cingulum on the M2 paracone is present in some species of *Platyrrhinus* (e.g., *P. brachycephalus, P. chocoensis*) and *Vampyrodes.* In contrast, *Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* lack the labial cingulum on the M2 paracone. *Platyrrhinus dorsalis, P. dorsalis* "Norte," and *P. dorsalis* "Centro-Sur" have intraspecific variation. This character has not been used in any other study.

Character 42—**Stylar cusp on the lingual face of the M2 paracone.** Absent (0); present (1). A stylar cusp on the lingual face of the M2 paracone is present in some species of *Platyrrhinus* (e.g., *P. infuscus, P. vittatus* "Southern"). In contrast, other species of *Platyrrhinus* (e.g., *P. aurarius, P. brachycephalus*), *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes* lack this stylar cusp on the lingual face of the M2 paracone. *Platyrrhinus chocoensis* and *P. dorsalis* have intraspecific variation. This character has not been used in any other study.

Character 43—**M2 metastyle.** Absent (0); present (1). A metastyle on M2 is present in some species of *Platyrrhinus* (e.g., *P. brachycephalus, P. chocoensis*) and *Uroderma magnirostrum.* In contrast, *P. vittatus* "Southern," *Carollia subrufa, Sturnira erythromos,* and *Vampyrodes* lack a metastyle on M2. *Platyrrhinus nigellus* has intraspe-

cific variation. This character has not been used in any other study.

Character 44—**Stylar cusp on the lingual face of the M2 metacone.** Absent (0); present (1). A stylar cusp on the lingual face of the M2 metacone is present in some species of *Platyrrhinus* (e.g., *P. infuscus, P. vittatus* "Southern") and *Vampyrodes.* In contrast, other species of *Platyrrhinus* (e.g., *P. aurarius, P. chocoensis*), *Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* lack a stylar cusp on the lingual face of the M2 metacone. *Platyrrhinus dorsalis* "Norte," *P. dorsalis* "Centro-Sur," and *P. lineatus* have intraspecific variation. This character has not been used in any other study.

Character 45—**Lingual cingulum of the M2 metacone.** Absent (0); lingual cingulum of the M2 metacone restricted to the metacone (1); lingual cingulum of the M2 metacone continuous to the paracone (2). *Carollia subrufa, Sturnira erythromos,* and *Vampyrodes* lack the lingual cingulum of the M2 metacone. The lingual cingulum of the M2 metacone is continuous to the paracone in *Platyrrhinus chocoensis, P. dorsalis,* and *P. recifinus* (Fig. 13A). In contrast, the lingual cingulum of the M2 metacone is restricted to the metacone in some species of *Platyrrhinus* (e.g., *P. brachycephalus, P. vittatus* "Southern") and *Uroderma magnirostrum* (Fig. 13B). *Platyrrhinus helleri* "Western," *P. infuscus, P. lineatus,* and *P. nigellus* have intraspecific variation in this character: some individuals have the lingual cingulum of the M2 metacone restricted to the metacone, whereas others have lingual cingulum of the M2 metacone continuous to the paracone. This character has not been used by other researchers.

Character 46—**M2 hypoconal basin.** Developed (0); rudimentary or small (1). A developed hypoconal basin on M2 is present in all the species of *Platyrrhinus* and *Sturnira erythromos.* In contrast, in *Carollia subrufa, Uroderma magnirostrum,* and *Vampyrodes,* the M2 hypoconal basin is rudimentary or small.

Character 47—**Two sulci on the lingual face of the main cone of p4.** Absent (0); present (1). Two sulci on the lingual face of the main cone of p4 are present in all the *Platyrrhinus* species, *Uroderma magnirostrum,* and *Vampyrodes.* These sulci originate at the base of the main cone and continue to the tip of the main cone. In contrast, *Carollia subrufa* and *Sturnira erythromos* lack these sulci on p4. This character has not been used in any other study.

Character 48—**Cones on the posterior face of p4 (one lingual and the other one labial).** Two cones present (0); one cone present on either the labial or the lingual face (1); no cones present (2). Two cones on the posterior face of p4 are present in all the species of *Platyrrhinus* and *Vampyrodes. Sturnira erythromos* and *Uroderma magnirostrum* have only one cone. *Carollia subrufa* lack both cones on the posterior face of p4. This character has not been used by other researchers.

Character 49—**Labial and lingual cingulum of p4.** Both cingula absent (0); only one cingulum present, either the lingual or the labial (1); both cingula present (2). Both cingula on p4 are present in the majority of *Platyrrhinus* species (e.g., *P. dorsalis, P. vittatus* "Southern"). In *Platyrrhinus aurarius, P. chocoensis, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes,* only one cingulum is present on p4. *Carollia subrufa* lack cingula on p4. This character has not been used by other researchers.

Character 50—**Stylid cusps on the anterior or anterolingual face of the main cone of p4.** Absent (0); one stylid cusp present (1); two stylid cusps present (2). Two stylid cusps on the anterior face of the main cone of p4 are present in *Platyrrhinus brachycephalus.* In *Platyrrhinus vittatus* "Northern" and *Vampyrodes,* one and two stylid cusps, respectively, are present on the anterolingual face. *Platyrrhinus helleri* "Eastern" has a single stylar cusp on the anterior face of p4. In contrast, other *Platyrrhinus* species (e.g., *P. aurarius, P. chocoensis*), *Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* lack stylid cusps on the anterior face of the main cone of p4. This is the first use of this character in a phylogenetic study.

Character 51—**Stylid cusp on the posterior face of the main cone of p4.** Absent (0); present (1). One or two stylid cusps are present on the posterior face of the main cone of p4 in some species of *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. helleri* "Western"). In contrast, other species of *Platyrrhinus* (e.g., *P. aurarius, P. chocoensis*), *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes* lack stylid cusps on the posterior face of the main cone of p4. This character has not been used by other researchers.

Character 52—**m1 paraconid.** Present (0); absent (1). Most *Platyrrhinus* species (e.g., *P. aurarius, P. chocoensis*), *Carollia subrufa, Uroderma magnirostrum,* and *Vampyrodes* lack a paraconid on m1. In contrast, *Sturnira erythromos* has a paraconid on m1. *Platyrrhinus nigellus* has intraspecific variation. Wetterer et al. (2000: char-

acter 68) used this character in their phylogeny of the Phyllostomidae, but I do not agree on their score for *Platyrrhinus*. They scored it as a polymorphism (with the paraconid occasionally present). However, my observations indicate that the majority of *Platyrrhinus* lack the paraconid on m1, as does *Vampyrodes*.

Character 53—**m1 cingulum.** Absent (0); only the labial cingulum present (1); both labial and lingual cingula present (2). Both cingula on m1 are present in all the species of *Platyrrhinus*. In contrast, *Carollia subrufa* and *Sturnira erythromos* lack both cingula on m1. *Uroderma magnirostrum* and *Vampyrodes* have only the labial cingulum. This character has not been used in any other study.

Character 54—**Stylid cusps on the anterior face of the m1 protoconid.** Absent (0); present (1). A stylid cusp on the anterior face of the m1 protoconid is present in all species of *Platyrrhinus*. In contrast, *Carollia subrufa, Sturnira erythromos, Uroderma magnirostrum,* and *Vampyrodes* lack this stylid cusp on the anterior face of the m1 protoconid. This character has not been used in any other study.

Character 55—**m1 metaconid.** Well developed (0); poorly developed (1); absent (2). A well-developed m1 metaconid is present in *Platyrrhinus infuscus, P. lineatus,* and *Sturnira erythromos*. However, other species of *Platyrrhinus* (e.g., *P. aurarius, P. recifinus*), *Uroderma magnirostrum,* and *Vampyrodes* lack a metaconid on m1. *Platyrrhinus dorsalis* "Norte," *P. vittatus* "Northern," *P. vittatus* "Southern," and *Carollia subrufa* have a poorly developed m1 metaconid. *Platyrrhinus nigellus* has intraspecific variation, with some specimens lacking the m1 metaconid and others with it poorly developed. I do not agree with the score of present that Wetterer et al. (2000: character 69) assigned to *Vampyrodes* because, according to my observations, *Vampyrodes* lacks a metaconid on m1.

Character 56—**m2 hypoconid.** Present (0); absent (1). The m2 hypoconid is present in *Carollia subrufa* and *Sturnira erythromos*. In contrast, the majority of the species of *Platyrrhinus* (e.g., *P. brachycephalus, P. nigellus*), *Uroderma magnirostrum,* and *Vampyrodes* lack the hypoconid on m2. *Platyrrhinus helleri* "Eastern" has intraspecific variation. This character has not been used in other studies.

Character 57—**Stylid cusp between the metaconid and protoconid on m2.** Absent (0); present (1). A stylid cusp between the metaconid and protoconid on m2 is present in some species of *Platyrrhinus* (e.g., *P. brachycephalus, P. vittatus* "Southern") and *Vampyrodes*. In contrast, *P. chocoensis, P. infuscus, P. recifinus, Carollia subrufa, Sturnira erythromos,* and *Uroderma magnirostrum* lack this stylid cusp between the metaconid and protoconid on m2. This character has not been used in any other study.

Character 58—**Cingula on m2.** Both cingula labial and lingual absent (0); labial cingulum present (1); both cingula present (2). Both cingula on m2 are present in the majority of species of *Platyrrhinus* (e.g., *P. brachycephalus, P. infuscus*) and *Uroderma magnirostrum*. In contrast, *Vampyrodes* has only the labial cingulum, and *Carollia subrufa* and *Sturnira erythromos* lack both cingula on m2. *Platyrrhinus helleri* "Western" has intraspecific variation, with some individuals with both cingula and others with only the labial cingulum. This character has not been used by other researchers.

Postcranial Skeleton

Character 59—**Third and fifth metacarpal arrangement.** Length of M III > M V (0); length of M III = M V (1); length of M III < M V (2). *Platyrrhinus aurarius, P. dorsalis* "Norte," *P. lineatus, P. nigellus, P. vittatus* "Northern," *Sturnira erythromos,* and *Vampyrodes* have the third metacarpal shorter that the fifth metacarpal. In *Platyrrhinus helleri* "Eastern," *P. helleri* "Western," *P. recifinus,* and *Uroderma magnirostrum,* the third metacarpal is longer than the fifth metacarpal. The third metacarpal is subequal to the fifth in *P. vittatus* "Southern." *Platyrrhinus chocoensis, P. dorsalis, P. dorsalis* "Centro-Sur," and *P. infuscus* exhibit intraspecific variation: the third metacarpal can be subequal to or shorter than the fifth metacarpal. *Platyrrhinus brachycephalus* and *Carollia subrufa* also have intraspecific variation: the third metacarpal can be subequal to or longer than the fifth metacarpal. Wetterer et al. (2000: character 84) used this character in their phylogeny of the Phyllostomidae; they indicated that in all species of *Platyrrhinus,* the third metacarpal was subequal in length to the fifth metacarpal. Simmons (1996: character 8) used this character in her phylogeny of the genus *Micronycteris*.

Character 60—**Insertion of the posterior edge of the plagiopatagium.** Onto the ankle region (0); onto the first metatarsal (1). The pos-

terior edge of the plagiopatagium inserts at the first metatarsal in all the species of *Platyrrhinus* (e.g., *P. helleri* "Eastern," *P. recifinus*), *Uroderma magnirostrum*, and *Vampyrodes*. The posterior edge of the plagiopatagium inserts at the ankle region in *Carollia subrufa* and *Sturnira erythromos*. Owen (1987: character 6) and Wetterer et al. (2000: character 84) used this character, and I agree with the scores assigned to *Platyrrhinus* and the outgroup. Marques-Aguiar (1994: character 7) used this character in her phylogeny of the genus *Artibeus*, as did Straney (1980: characters G 9–13) in his phylogeny of the subfamily Phyllostominae.

Results

Parsimony analysis of the data resulted in two most parsimonious trees of 162 steps each (CI = 0.54; CI excluding uninformative characters = 0.52; RI = 0.58). A strict consensus of these trees with the bootstrap and decay values is shown in Figure 14. Monophyly of *Platyrrhinus* was supported with bootstrap and decay values of 84% and 3%, respectively.

Two main clades were observed within *Platyrrhinus*. One is comprised of the smaller species + *P. lineatus* and *P. recifinus* and is supported weakly by a bootstrap value of 33% and a decay value of 1. In this clade, the basal species *P. lineatus* and *P. recifinus* were unresolved, whereas the clade formed by *P. helleri* "Eastern" + *P. brachycephalus* + *P. helleri* "Western" was supported by a bootstrap value of 72% and a decay value of 1. The clade formed by *P. brachycephalus* + *P. helleri* "Western" also was supported by a bootstrap value of 72% and a decay value of 1. The second main clade comprised of the remaining nine species of *Platyrrhinus* was completely resolved and was supported by a bootstrap value of 43% and a decay value of 2. *Platyrrhinus chocoensis*, *P. dorsalis*, and *P. aurarius* occupied the three most basal branches, followed by *P. nigellus* + *P. dorsalis* "Centro-Sur," *P. dorsalis* "Norte," *P. infuscus*, *P. vittatus* "Northern," and *P. vittatus* "Southern."

There was strong support (bootstrap = 98% and decay = 6) for *Vampyrodes caraccioli* as sister taxon of *Platyrrhinus*. The analysis also supported (bootstrap = 100% and decay = 10) *Uroderma magnirostrum* as sister taxa of the clade comprised of *Platyrrhinus* + *Vampyrodes*. The most basal branches of the tree were occupied by *Carollia subrufa* (subfamily Carolliinae) and *Sturnira erythromos* (most basal genus of the Stenodermatinae).

Discussion and Conclusions

The present phylogenetic analysis strongly supports *Platyrrhinus* monophyly but only weakly supports the interspecific relationships (Fig. 14). Owen's (1987) phylogenetic hypothesis also supported *Platyrrhinus* monophyly but did not include all the species, nor did it provide support values. Three synapomorphies are described for the first time for *Platyrrhinus*: sulcus on the anterior face of the P4, both labial and lingual cingula present on the m1, and stylid cusps present on the anterior face of the m1 protoconid.

Two main divisions of *Platyrrhinus* were evident in both analyses. However, they were weakly supported, so I do not suggest recognizing them as separate subgenera. The first clade includes all the smaller species of *Platyrrhinus* (*P. brachycephalus* + *P. helleri* "Eastern" + *P. helleri* "Western"), *P. lineatus*, and *P. recifinus* and is supported by six characters: poorly marked but distinguishable pinna folds (character 10), dense and long hair on the dorsum of the feet (15), a densely haired uropatagium edge (17), M1 parastyle present (32), labial cingulum at the base of the M1 metacone present (34), and both labial and lingual cingula present on p4 (49). The present hypothesis strongly contradicts with Owen's interspecific phylogenetic hypothesis. Owen's (1987) preferred hypothesis placed *P. brachycephalus* and *P. helleri* (the only "small" species of *Platyrrhinus* recognized at that time) in different clades. In the present study, *P. brachycephalus* and the two forms of *P. helleri* were placed in the same clade.

The second clade, containing the nine larger species of *Platyrrhinus*, is supported by seven synapomorphies: dark facial stripes (character 3), absence of the basal protuberance where the genal vibrissae are implanted (4), folds in the pinna well marked (10), dorsal stripe definite but narrow (11), posterior border of the hard palate "V"-shaped (18), postorbital process absent or poorly developed (19), and M1 protocone small and blunt (39).

The present analysis supports the hypothesis of Velazco and Solari (2003), recognizing *P.*

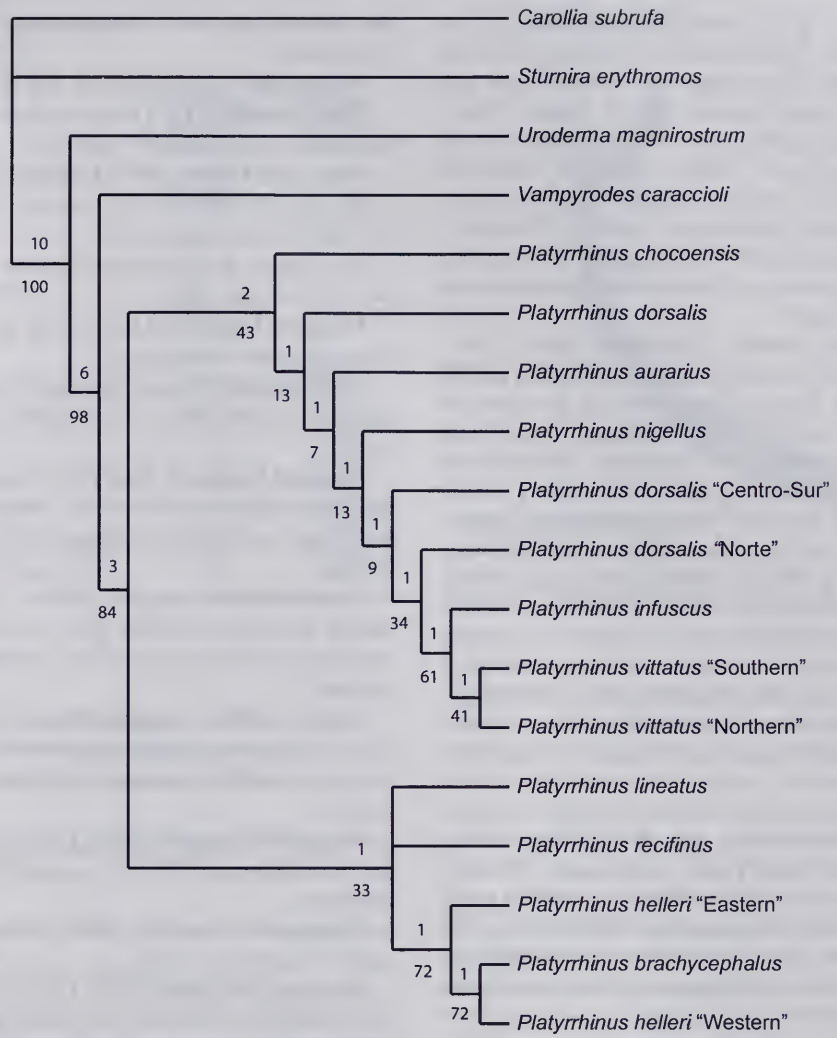

FIG. 14. Strict consensus tree of the analysis with the characters unordered. Decay values are given above each branch; bootstrap values are below.

dorsalis as a complex of three different species (two not yet described). The analysis placed *P. dorsalis* close to *P. chocoensis,* which also is a species that occurs on the western slope of the Andes. *Platyrrhinus dorsalis* "Norte" and *P. dorsalis* "Centro-Sur" (the two undescribed species) were placed closer to *P. nigellus* and *P. infuscus,* species that are distributed on the eastern slope of the Andes. No differences were found between the paratypes of *P. umbratus* and the specimens of *P. dorsalis.* Therefore, I treat *P. umbratus* as a junior synonym of *P. dorsalis. Platyrrhinus dorsalis* "Norte" and *P. dorsalis* "Centro-Sur" exhibit several autopomorphies that differentiate them from *P. dorsalis* and each other. Consequently, these two taxa are named and described here. *Platyrrhinus lineatus* and *P. nigellus* demonstrate clear morphological differences and are located in different clades, supporting their validity as species.

The branches representing *P. helleri* "Eastern" and *P. helleri* "Western" have sufficient distinguishing characteristics to be considered different species. The distribution of *P. helleri* "Eastern" is the widest of the genus, comprising most of Central and South America and encompassing

type localities of *P. helleri* (Peters, 1866), *P. zarhinus* (Allen, 1891), and *P. zarhinus incarum* (Thomas, 1912). Comparisons between the descriptions of these species and *P. helleri* "Eastern" suggest that *P. helleri* is the appropriate binomial name for *P. helleri* "Eastern," with *P. zarhinus* and *P. zarhinus incarum* representing junior synonyms. *Platyrrhinus helleri* "Western," which is found in the Chocó region in Colombia and Ecuador, does not have a name available and is described here.

Platyrrhinus vittatus "Northern" and *P. vittatus* "Southern" are the largest forms in this genus. *Platyrrhinus vittatus* "Northern" is restricted to the lowlands in Costa Rica, Panama, Atlantic and Pacific Colombia, and Venezuela. *Platyrrhinus vittatus* "Southern" is distributed mainly in the highlands of Ecuador, Peru, and Bolivia. The holotype of *P. vittatus* is from Puerto Cabello, Venezuela, and is distinguishable both qualitatively and morphometrically from *P. vittatus* "Southern." *Platyrrhinus vittatus* "Southern" is larger than *P. vittatus* "Northern" and has qualitative morphological and morphometric differences. *Platyrrhinus vittatus* "Southern" is a taxon without an available name and therefore is described here.

Like previous phylogenetic hypotheses for the family Phyllostomidae that placed *Platyrrhinus* and the monotypic genus *Vampyrodes* as sister taxa (Baker et al., 2000, 2003; Lim, 1993; Owen, 1987 [only discrete characters]; Smith, 1976; Van Den Bussche, 1992; Wetterer et al., 2000), the present study places *Vampyrodes* as a sister taxa of *Platyrrhinus*.

Taxonomic Diagnoses of the *Platyrrhinus* Species

A taxonomic diagnosis for 14 species of *Platyrrhinus* used in the phylogenetic analysis is presented. This includes descriptions of four new species. The diagnoses are based on the ACCTRAN and DELTRAN optimizations of the data. Unambigously derived conditions are in italics. States with ambiguous optimizations are not italicized. All observations are based on adult individuals, external and craniodental measurements are in millimeters, and body mass (weight) is in grams. The first five measurements listed here were obtained from skin tags or field notes made by the collector of each specimen; the other dimensions were measured with a digital caliper to the nearest 0.01 mm. Measurements are defined as follows:

Weight (W): Body mass in grams.

Total length (TL): Distance from the snout to the tip of the last caudal vertebra.

Hind foot length (HL): Distance from the anterior edge of the base of the calcar to the tip of the claw of the longest toe.

Ear length (E): Distance from the notch to the fleshy tip of the pinna.

Forearm length (FA): Distance from the olecranon process to the carpals.

Tibia length (Tibia): Distance from the proximal end of the tibia to the posterior base of the calcar.

Greatest length of skull (GLS): Distance from the most posterior point of the occiput to the anteriormost point of the premaxilla (excluding incisors).

Condiloincisive length (CIL): Distance between the posterior-most point of the occipital condyles and the anterior-most point on the upper incisors.

Condilocanine length (CCL): Distance between the posterior-most point of the occipital condyles and the anterior-most point on the upper canines.

Postorbital breadth (PB): Least breadth across the frontals posterior to the postorbital processes or bulges.

Zygomatic breadth (ZB): Greatest breadth across zygomatic arches.

Braincase breadth (BB): Greatest breadth of the braincase, excluding the mastoid and paraoccipital processes.

Mastoid breadth (MB): Greatest breadth across the mastoid region.

Maxillary toothrow length (MTRL): From the anterior-most edge of the canine crown to the posterior-most edge of the crown of M3.

Breadth across molars (BAM): Greatest breadth across the outer edges of the crowns of the upper molars.

Measurements of male and females were combined in species comparisons because no differences in size were apparent between males and females in any species of *Platyrrhinus*. Velazco and Solari (2003) evaluated sexual dimorphism in the Peruvian populations of *P. dorsalis* "Norte," *P. dorsalis* "Centro-Sur," and *P. nigellus* and concluded that these three species did not demonstrate significant sexual dimorphism.

TABLE 2. Measurements of the type series of *Platyrrhinus albericoi*.

	Holotype MUSM 19149	Paratype FMNH 170145
Sex	Female	Female (pregnant)
Weight	55	68
Total length	100	100
Hind foot length	16	15
Ear length	25	24
Forearm length	63	62
Tibia length	23.93	23.71
Greatest length of skull	32.84	32.51
Condyloincisive length	32.63	31.63
Condylocanine length	31.89	30.82
Postorbital beadth	7.65	7.39
Zygomatic breadth	20.85	20.68
Braincase breadth	13.38	13.58
Mastoid breadth	15.85	16.12
Maxillary toothrow length	13.89	13.44
Breadth across molars	15.23	15.57

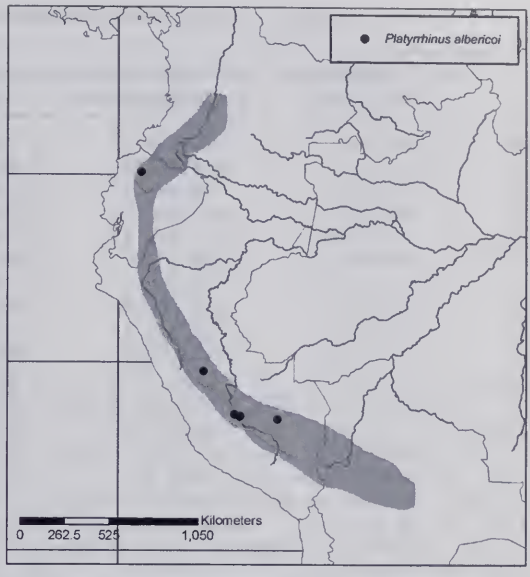

FIG. 15. Distributional map of *Platyrrhinus albericoi*.

Systematics

Family Phyllostomidae Gray, 1825
Subfamily Phyllostominae Gray, 1825
Genus *Platyrrhinus* Saussure, 1866

Platyrrhinus albericoi, new species. Figures 1, 16 (bottom)

Vampyrops vittatus Gardner and Carter, 1972b: 74–75 (part)
Vampyrops vittatus Koopman, 1978: 11
Vampyrops vittatus Swanepoel and Genoways, 1979: 66, 104 (part)
Vampyrops vittatus Barquez and Olrog, 1980: 53–54
Vampyrops vittatus Anderson et al., 1982: 7–8
Vampyrops vittatus Anderson, 1985: 7
Vampyrops vittatus Alberico, 1990: 349 (part)
Platyrrhinus vittatus Anderson, 1993: 8, 24, 69
Platyrrhinus vittatus Anderson, 1997: 36, 244, 589 (part)
Platyrrhinus vittatus Albuja, 1999: 134–135 (part)
Platyrrhinus vittatus Emmons et al., 2001: 255
Platyrrhinus vittatus Romo, 2001: 258
Platyrrhinus vittatus Solari et al., 2001: 112, 263
Platyrrhinus vittatus Salazar-Bravo et al., 2003: 15
Platyrrhinus vittatus "Southern" (this paper)

TYPE MATERIAL—The holotype, MUSM 19149, is an adult female collected by Sergio Solari (original field number SS 2067) on 14 April 2001 at San Pedro, Paucartambo-Pilcopata road, 1480 m in elevation, Province of Paucartambo, Department of Cuzco, Peru, approximately 13°0′1′S, 71°32′46′W. The type locality is in the Cultural Zone of the Manu Biosphere Reserve. The skin, skull, and alcohol preserved carcass were in good condition. Frozen tissues are deposited at the Field Museum of Natural History (FMNH 172107).

The paratype is an adult female (FMNH 170145) from Suecia, km 138.5 Carretera Shintuya, Province of Paucartambo, Department of Cuzco, Peru. The holotype and paratype as well as other specimens from the known distributional range are listed in Appendix 1. Dimensions of each specimen of the type series of *Platyrrhinus albericoi* are provided in Table 2.

DISTRIBUTION—*Platyrrhinus albericoi* is currently known from the Eastern slope of the Andes in Ecuador, Peru, and Bolivia. Currently, the northern limit of its distribution is the Province of Pichincha (Ecuador), and the southern limit is the Department of Cochabamba (Bolivia). However, this taxon is expected to occur in southern Colombia (Fig. 15). The elevational range comprise from 1480 to 2500 m.

ETYMOLOGY—The specific epithet is chosen to honor Michael Alberico, who devoted his scientific career to the study of Colombian mammals.

DIAGNOSIS—Size large (FA = 62–63 mm; CIL = 31.6–32.6 mm; W = 55–68 g); facial stripes brilliant-white; *folds in the pinna poorly marked but distinguishable*; *fringe of hair on the edge of the uropatagium dense*; *paraoccipital process well developed*; M1 mesostyle present; M2 me-

TABLE 3. Selected measurements[a,b] of members of the genus *Platyrrhinus*.

	Platyrrhinus aurarius	*Platyrrhinus brachycephalus*	*Platyrrhinus chocoensis*	*Platyrrhinus dorsalis*	*Platyrrhinus helleri*
W	30.5 ± 0.7	13.6 ± 2.8	30.5 ± 2.1	—	14.5 ± 2.7
	30–31 (2)	10–20 (20)	29–32 (2)		11–19 (10)
TL	78.5 ± 4.9	58.3 ± 3.8	76.5 ± 2.1	75.5 ± 6.4	57.7 ± 3.9
	75–82 (2)	52–68 (33)	75–78 (2)	71–80 (2)	52–65 (15)
HL	15.0 ± 0.8	11.0 ± 1.0	14.5 ± 0.7	13.2 ± 0.7	10.5 ± 0.9
	14–17 (12)	9–13 (37)	14–15 (2)	12–15 (11)	8–12 (21)
E	20.7 ± 0.6	16.3 ± 1.2	19.0 ± 1.4	18.8 ± 0.7	15.7 ± 1.4
	20–22 (12)	13–19 (33)	18–20 (2)	18–20 (11)	12–17 (14)
FA	52.7 ± 1.1	37.6 ± 1.8	48.5 ± 0.7	48.9 ± 1.3	37.8 ± 1.5
	51–54 (12)	33–42 (37)	48–49 (2)	46–50 (11)	35–40 (21)
Tibia	21.30 ± 0.76	15.36 ± 0.93	19.65 ± 1.72	20.32 ± 1.34	15.04 ± 0.69
	20.00–22.00 (12)	13.18–17.60 (33)	18.43–20.86 (2)	17.39–21.88 (11)	13.60–16.00 (21)
GLS	27.23 ± 0.38	20.44 ± 0.50	27.33–0.49	26.42 ± 0.47	21.21 ± 0.75
	26.53–27.87 (12)	19.50–21.53 (47)	26.77–27.69 (3)	25.46–27.40 (13)	19.04–22.50 (67)
CIL	26.18 ± 0.39	19.08 ± 0.53	25.59 ± 0.84	25.06 ± 0.48	19.95 ± 0.80
	25.62–27.01 (12)	18.30–20.26 (47)	24.64–26.22 (3)	24.33–25.75 (13)	18.03–21.28 (66)
CCL	25.55 ± 0.36	18.64 ± 0.50	25.18 ± 0.76	24.59 ± 0.48	19.49 ± 0.79
	25.12–26.35 (12)	17.75–19.86 (47)	24.33–25.80 (3)	23.82–26.43 (13)	17.65–20.80 (67)
PB	6.65 ± 0.12	5.39 ± 0.22	6.55 ± 0.22	6.32 ± 0.12	5.44 ± 0.15
	6.39–6.83 (12)	4.92–6.15 (48)	6.33–6.77 (3)	6.13–6.59 (13)	5.17–5.88 (67)
ZB	16.89 ± 0.33	12.29 ± 0.55	16.91 ± 0.34	16.13 ± 0.67	12.56 ± 0.49
	16.38–17.57 (9)	11.46–13.64 (38)	16.57–17.26 (3)	14.88–17.10 (12)	11.49–13.54 (55)
BB	11.85 ± 0.19	9.31 ± 0.30	11.82 ± 0.08	11.52 ± 0.33	9.38 ± 0.27
	11.55–12.28 (12)	8.76–9.94 (47)	11.74–11.89 (3)	10.74–11.93 (13)	8.62–9.89 (66)
MB	14.01 ± 0.34	10.66 ± 0.32	13.75 ± 0.43	13.34 ± 0.33	10.88 ± 0.38
	13.42–14.58 (12)	10.04–11.44 (47)	13.26–14.06 (3)	12.76 –13.91 (13)	10.04–11.61 (66)
MTRL	11.07 ± 0.26	7.37 ± 0.27 (41)	10.94 ± 0.29	10.68 ± 0.33	7.88 ± 0.40
	10.71–11.55 (12)	6.82–7.94 (41)	10.70–11.25 (3)	10.17–11.34 (13)	6.96–8.59 (63)
BAM	12.45 ± 0.33	8.75 ± 0.37	11.55 ± 0.12	11.49 ± 0.49	9.02 ± 0.45
	11.88–12.90 (12)	8.11–9.72 (48)	11.45–11.69 (3)	10.88–12.60 (13)	8.14–9.80 (65)

tastyle absent; length of the third metacarpal subequal to the fifth metacarpal.

DESCRIPTION—The largest known species of *Platyrrhinus* (FA = 62–63 mm; GLS = 32.5–32.8 mm; Tables 2–3). Dorsal fur dark brown, ventral fur light brown, dorsal and ventral hair tricolored; dorsomedial facial stripes more marked than the ventrolateral; dorsal hairs > 8 mm long on the back; narrow dorsal stripe brighter than the facial ones; folds in the pinna poorly marked but distinguishable; six vibrissae surrounding the margins of the noseleaf in a single array; four submental vibrissae present; one or two interramal vibrissae present; noseleaf longer than wide, inferior border of the horseshoe completely free of the upper lip; dense and long hair on the dorsum of the feet; "U"-shaped posterior edge of the uropatagium with a densely haired fringe, uropatagium extends along the midline 4.5–7 mm long; insertion of the posterior edge of the plagiopatagium onto the first metatarsal; third metacarpal subequeal in length with fifth metacarpal.

Almost imperceptible fossa on the squamosal end of the zygomatic arch; postorbital process moderately developed; paraoccipital process well developed; upper median incisors convergent and in contact; sulcus on the posterior face of the upper canines; two stylar cusps present on the posterior face of the P4; stylar cusp present on the cingulum of the lingual face of the M1 metacone; M1 metastyle and mesostyle present; M1 protocone moderately developed; stylar cusp present on the lingual face of the M2 paracone; M2 metastyle absent; M2 parastyle present; stylar cusp present on the lingual face of the M2 metacone; lingual cingulum of the M2 metacone restricted to the metacone; two sulci present on the lingual face of the main cone of p4; both labial and lingual cingula present on p4; stylid cusps absent on the anterior or anterolingual face of the main cone of p4; m1 paraconid absent; stylid cusp present on the anterior face of the m1 protoconid; poorly developed m1 metaconid; m2 hypoconid absent; stylid cusp between the metaconid and protoconid

TABLE 3. Continued.

	Platyrrhinus infuscus	*Platyrrhinus lineatus*	*Platyrrhinus nigellus*	*Platyrrhinus recifinus*	*Platyrrhinus vittatus*
W	44.5 ± 5.1	21.9 ± 3.1	21.6 ± 3.1	17.7 ± 0.8	62.3 ± 2.5
	36–59 (23)	18–28 (20)	19–30 (13)	17–19 (6)	60–65 (3)
TL	88.4 ± 6.4	70.1 ± 4.7	65.9 ± 3.3	91.3 ± 1.5	92.6 ± 7.3
	77–105 (36)	60–78 (22)	60–74 (32)	89–93 (6)	83–100 (5)
HL	15.5 ± 0.9	12.3 ± 0.9	12.1 ± 0.9	12.2 ± 0.7	14.9 ± 1.5
	14–18 (57)	10–1 (28)	10–15 (33)	11–13 (6)	13–17 (7)
E	22.4 ± 1.1	19.4 ± 1.4	18.5 ± 1.1	19.2 ± 0.7	24.0 ± 1.0
	20–24 (36)	15–2 (22)	16–21 (31)	18–20 (6)	23–25 (5)
FA	57.9 ± 1.6	47.1 ± 0.8	43.0 ± 1.6	42.5 ± 0.5	59.8 ± 1.2
	54–62 (52)	46–48 (22)	40–47 (33)	42–43 (6)	57–61 (7)
Tibia	23.75 ± 1.13	19.51 ± 0.82	16.94 ± 0.73	16.28 ± 0.76	21.74 ± 0.90
	20.80–26.00 (49)	18.12–21.00 (20)	15.62–18.46 (30)	15.20–17.50 (6)	20.43–22.82 (7)
GLS	29.74 ± 0.73	24.01 ± 0.46	24.43 ± 0.51	23.32 ± 0.29	30.57 ± 0.82
	27.96–31.22 (63)	23.08–24.94 (29)	23.51–25.88 (35)	23.03–23.76 (6)	28.90–31.39 (7)
CIL	28.32 ± 0.65	22.52 ± 0.39	23.04 ± 0.54	22.26 ± 0.26	29.63 ± 1.09
	26.39–29.89 (61)	21.98–23.45 (24)	21.94–24.50 (34)	21.99–22.61 (6)	28.12–31.29 (8)
CCL	27.70 ± 0.63	21.89 ± 0.39	22.56 ± 0.54	21.73 ± 0.21	28.91 ± 1.03
	25.93–29.01 (63)	21.36–22.79 (24)	21.57–23.98 (35)	21.55–22.06 (6)	27.48–30.41 (8)
PB	6.88 ± 0.20	6.31 ± 0.18	6.12 ± 0.17	5.74 ± 0.21	7.49 ± 0.24
	6.32–7.34 (65)	5.98–6.61 (30)	5.61–6.41 (36)	5.46–6.10 (6)	7.23–7.89 (8)
ZB	18.39 ± 0.48	14.42 ± 0.35	14.30 ± 0.35	14.20 ± 0.33	19.07 ± 0.43
	17.42–19.33 (60)	13.80–15.28 (26)	13.45–15.48 (35)	13.55–14.45 (6)	18.41–19.67 (8)
BB	12.69 ± 0.28	10.77 ± 0.24	10.72 ± 0.19	10.44 ± 0.21	13.17 ± 0.26
	11.96–13.35 (62)	10.77–11.25 (29)	10.37–11.20 (36)	10.18–10.80 (6)	12.81–13.50 (8)
MB	15.15 ± 0.38	12.22 ± 0.33	12.32 ± 0.32	11.94 ± 0.30	15.43 ± 0.38
	14.16–15.97 (63)	11.76–12.89 (25)	11.66–13.18 (35)	11.57–12.41 (6)	14.68–15.96 (7)
MTRL	12.17 ± 0.28	8.91 ± 0.19	9.54 ± 0.30	8.96 ± 0.26	12.72 ± 0.45
	11.53–12.79 (63)	8.57–9.30 (30)	8.96–10.16 (31)	8.62–9.39 (6)	12.02–13.30 (7)
BAM	13.79 ± 0.39	10.13 ± 0.21	10.55 ± 0.29	10.41 ± 0.30	14.43 ± 0.57
	12.88–14.52 (63)	9.62–10.83 (31)	10.04–11.09 (36)	9.90–10.71 (6)	13.59–15.37 (8)

[a] Weight is in grams, all other measurements are in millimeters.
[b] Summary statistics (mean and standard deviation [above], observed range and sample size [below]) of measurements for each species (see Appendix 1 for a list of the specimens measured).

of m2 present; both labial and lingual cingula present on m2.

COMPARISONS—*Platyrrhinus albericoi* is found sympatrically with *P. dorsalis* "Norte," *P. dorsalis* "Centro-Sur," and *P. nigellus*. *Platyrrhinus albericoi* is easily distinguishable from these three species by its larger forearm length and greatest length of skull: *P. albericoi* (FA = 62–63 mm; GLS = 32.5–32.8 mm), *P. dorsalis* "Centro-Sur" (FA = 45–51 mm; GLS = 25.0–26.8 mm), and *P. nigellus* (FA = 40–47 mm; GLS = 23.5–25.9 mm). *Platyrrhinus albericoi* has been traditionally confused with *P. vittatus*, so subsequent comparisons are restricted to these two large species.

Externally, *Platyrrhinus albericoi* can be distinguished from *P. vittatus* by darker dorsal fur and brighter and wider facial stripes in *P. albericoi*. Moreover, folds in the pinna are poorly marked but distinguishable in *P. albericoi*, whereas in *P. vittatus* the folds in the pinna are well marked. The dorsal stripe is white and narrow in *P. albericoi*, whereas in *P. vittatus* the dorsal stripe is white and wide. The posterior edge of the uropatagium always is "U" shaped in *P. albericoi*, whereas it can be "U" or "V" shaped in *P. vittatus*. A densely haired uropatagium fringe is present in *P. albericoi*, whereas the uropatagium fringe is usually hairy, occasionally sparsely in *P. vittatus*. The third metacarpal is greater in length than the fifth metacarpal in *P. albericoi* but is subequal in length in *P. vittatus*.

Cranially, *Platyrrhinus albericoi* and *P. vittatus* are very similar. The only apparent differences are that the cranium of *P. albericoi* is more robust than that of *P. vittatus*, and the paraoccipital process is better developed in *P. albericoi*.

Dentally, *Platyrrhinus albericoi and P. vittatus* differ as follows: M1 mesostyle present in *P. albericoi* and absent in *P. vittatus*; moderately developed M1 protocone in *P. albericoi*, whereas in

P. vittatus the protocone on M1 tends to be better developed; M2 metastyle absent in *P. albericoi* and present in *P. vittatus*; stylid cusps absent on the anterior or anterolingual face of the main cone of p4 in *P. albericoi,* whereas one stylid cusp on the anterolingual face of the main cone of p4 is present in *P. vittatus* (Fig. 16).

Platyrrhinus aurarius (Handley and Ferris, 1972)

Vampyrops aurarius Handley and Ferris, 1972. Type locality: km 125, 85 km SSE El Dorado, State of Bolivar, Venezuela.

HOLOTYPE—*Vampyrops aurarius* USNM 387163, an adult male preserved as skin and skull, was collected by Merlin D. Tuttle and Arden L. Tuttle on 18 May 1966 at km 125, 85 km SSE El Dorado, State of Bolivar, Venezuela, elevation 1000 m.

DISTRIBUTION—Endemic to the Guianan Shield (southern Venezuela, Guyana, and Suriname), from 140 to 1250 m (Fig. 17).

DIAGNOSIS—Size medium (FA = 51–54 mm; CIL = 25.6–27.0 mm; W = 30–31 g; Table 3); *dorsal fur tetracolored*; *postorbital process moderately developed*; *paraoccipital process well developed*; only the labial cingulum present on p4.

Platyrrhinus brachycephalus (Rouk and Carter, 1972)

Vampyrops brachycephalus Rouk and Carter, 1972. Type locality: 3 mi S Tingo Maria, Department of Huánuco, Peru.
Vampyrops latus Handley and Ferris, 1972. Type locality: San Juan, Province of Oxapampa, Department of Pasco, Peru (USNM 364408).
Vampyrops latus saccharus Handley and Ferris, 1972. Type locality: Manacal, 5 km S and 25 km E Carúpano, State of Sucre, Venezuela (USNM 408411).

HOLOTYPE—*Vampyrops brachycephalus* TCWC 12193, adult male preserved as skin and skull, was collected by D. C. Carter (original field number 5513) on 28 August 1964 at 3 mi S Tingo Maria, Department of Huánuco, Peru, elevation 2400 ft (731 m).

DISTRIBUTION—Known from the Amazon Basin (Brazil, Bolivia, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela) and the mountain forests in Ecuador and Peru, from 90 to 1295 m (Fig. 17).

Diagnosis—Size small (FA = 33–42 mm; CIL = 18.3–20.3 mm; W = 10–20 g) (Table 3); *one vibrissa present on the upper lip, ventral to the vibissae that surround the margin of the noseleaf*; *five submental vibrissae present on each side of the chin*; ventral fur tricolored; *fringe of hair on the edge of the uropatagium usually hairy, occasionally sparsely*; *a well-developed M1 protocone*; *two stylid cusps present on the anterior face of the main cone of p4.*

Platyrrhinus chocoensis Alberico and Velasco, 1991

Platyrrhinus chocoensis Alberico and Velasco, 1991. Type locality: Quebrada El Platinero, 12 km W Istmina (by road), Department of Chocó, Colombia.

HOLOTYPE—*Platyrrhinus chocoensis* UV 3817, adult male preserved as skin and skull, was collected by M. S. Alberico (original field number, MSA 1316) on 16 April 1984 at Quebrada El Platinero, 12 km W Istmina (by road), Department of Chocó, Colombia, elevation 100 m.

DISTRIBUTION—Found in the lowlands of the Chocó biogeographic region of Colombia, to northwestern Ecuador, from 35 to 305 m (Fig. 18).

DIAGNOSIS—Size medium (FA = 48–49 mm; CIL = 24.6–26.2 mm; W = 29–32 g; Table 3); *ventral fur bicolored*; M1 protocone small and blunt; only the labial cingulum present on the p4; *stylid cusp between the metaconid and protoconid of the m2 present.*

Platyrrhinus dorsalis (Thomas, 1900)

Vampyrops dorsalis Thomas, 1900. Type locality: Paramba, Province of Imbabura, Ecuador.
Vampyrops umbratus Lyon, 1902. Type locality: San Miguel, Department of La Guajira, Colombia (MCZ B8180).
Vampyrops oratus Thomas, 1914. Type locality: "Galifari" Picacho de Galipán, Cerro del Avila, Distrito Federal, Venezuela (BMNH 14.7.27.1).
Vampyrops aquilus Handley and Ferris, 1972. Type locality: On the head of the Río Pucro, Cerro Malí, Province of Darién, Panama (USNM 338025).

HOLOTYPE—*Vampyrops dorsalis* BMNH 99.12.5.1, juvenile male preserved as skin and skull, was collected by R. Miketta (original field number 61) on 14 April 1899 at Paramba, Province of Imbabura, Ecuador, elevation 1100 m.

DISTRIBUTION—From southern Panama, along both slopes of the Andes in Colombia, and only the western slope in Ecuador, and northern Venezuela, from 230 to 2012 m (Fig. 18).

DIAGNOSIS—Size medium (FA = 46–50 mm; CIL = 24.3–25.7 mm; Table 3); folds in the pinna

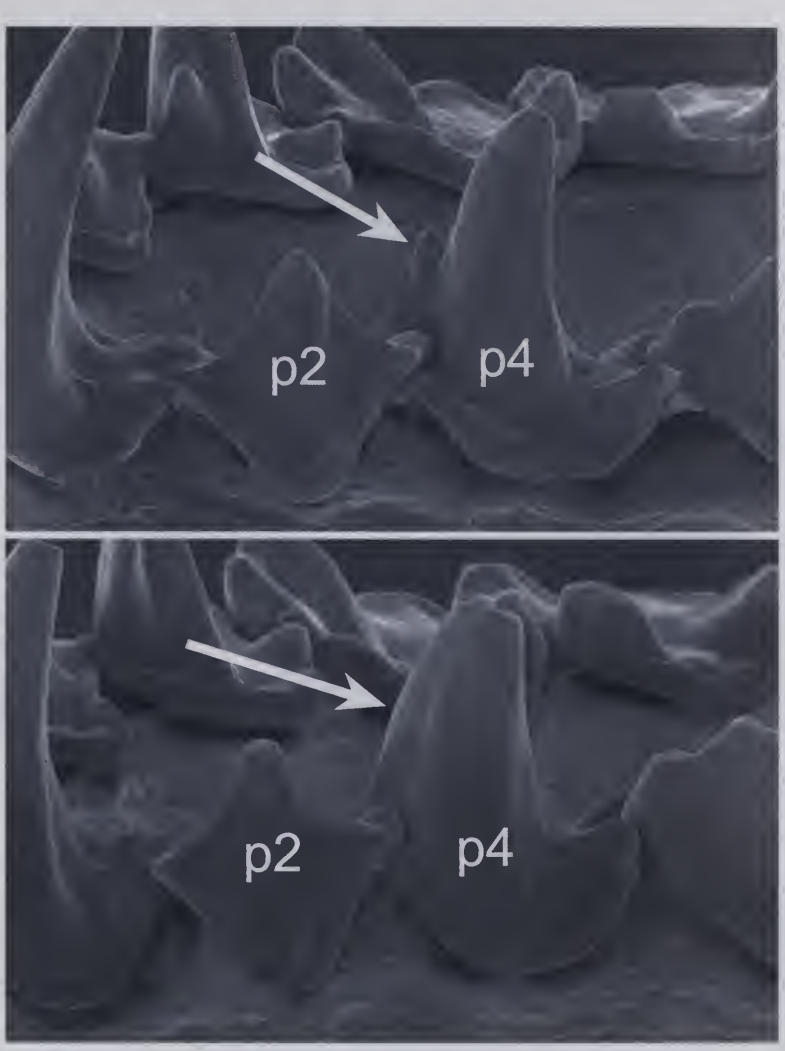

FIG. 16. Labial views of the left p2 and p4 illustrating taxonomic differences in the presence or absence of accessory cusps on the anterolingual face of the main cone of p4. (**Top**) *Platyrrhinus vittatus* (LSUMZ 25465) with one accessory cusp (arrow). (**Bottom**) *Platyrrhinus albericoi* (FMNH 170145) without accessory cusp (arrow).

absent; M1 protocone small and blunt; only the labial cingulum present on p4; *stylar cusp present on the lingual face of the M2 metacone*; both labial and lingual cingula present on p4.

Platyrrhinus helleri (Peters, 1866)

Vampyrops helleri Peters, 1866. Type locality: Mexico.
Vampyrops zarhinus Allen, 1891. Type locality: Obispo, Canal Zone, Panama (MCZ 3211).
Vampyrops zarhinus incarum Thomas, 1912. Type locality: Pozuzo, Department of Pasco, Peru (BMNH 12.1.15.1).

SYNTYPE—*Vampyrops helleri* ZMB 3276, adult, preserved as skin with the skull not removed, was collected by Heller in 1850 in Mexico.

DISTRIBUTION—From Mexico (Oaxaca and Veracruz) to Peru, Bolivia, and Amazonian Brazil, plus Trinidad and Tobago, from 160 to 1295 m (Fig. 19).

DIAGNOSIS—Size small (FA = 35–40 mm; CIL = 18.0–21.3 mm; W = 11–19 g; Table 3); ventral fur bicolored; hair on the dorsum of the feet intermediate in density and length; *M1 protocone small and blunt*; *one stylid cusp present on the anterior face of the main cone of p4.*

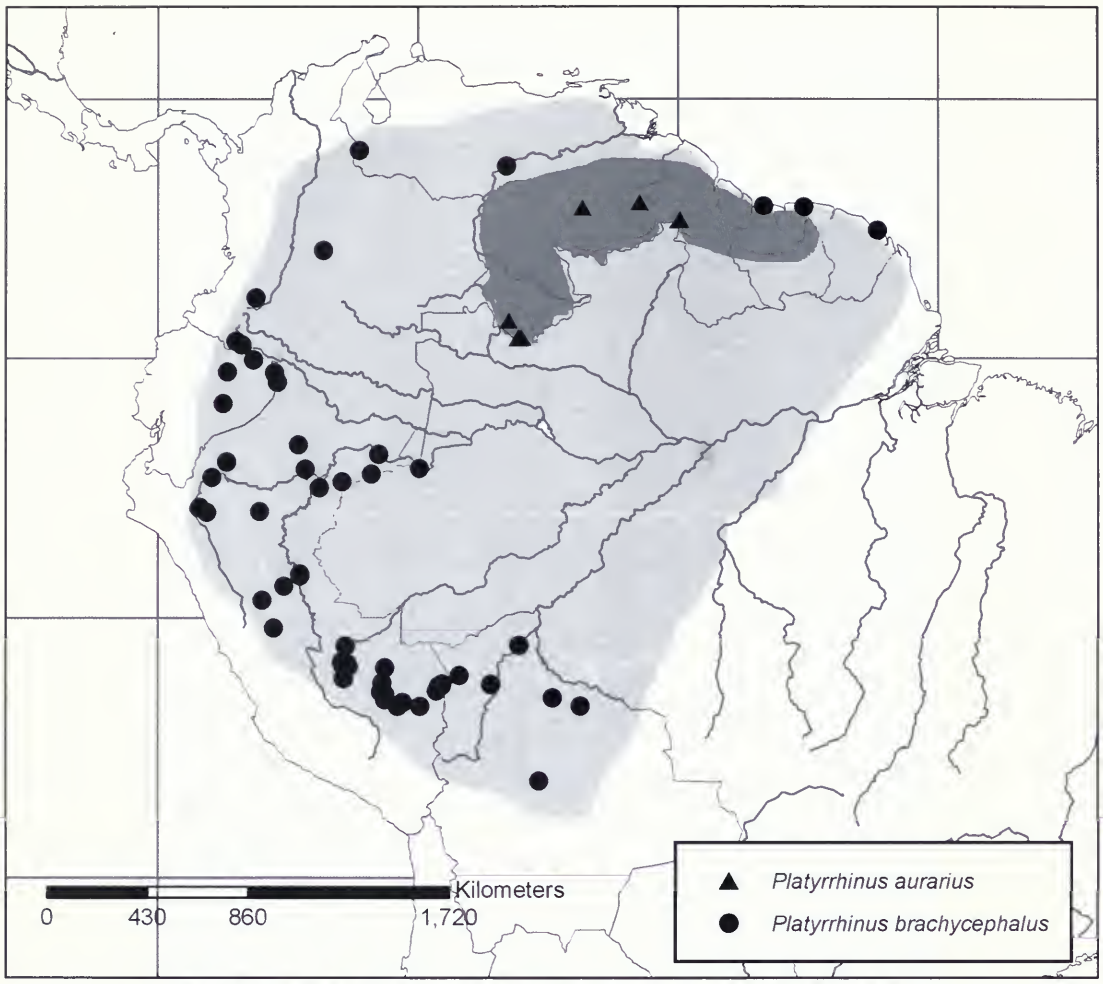

FIG. 17. Distributional map of *Platyrrhinus aurarius* and *P. brachycephalus*.

Platyrrhinus infuscus (Peters, 1880)

Vampyrops infuscus Peters, 1880. Type locality: Gruta de Ninabamba, Hacienda Ninabamba, Province of Hualgayoc, Department of Cajamarca, Peru.
Vampyrops fumosus Miller, 1902. Type locality: Huitanaã, upper Purus River, State of Amazonas, Brazil (USNM 105530).
Vampyrops intermedius Marinkelle, 1970. Type locality: Mina de Upin, near Restrepo, Department of Meta, Colombia (Universidad de los Andes, Colombia 14885).

HOLOTYPE—The holotype collected by L. Taczanowski from Gruta de Ninabamba, Hacienda Ninabamba, Province of Hualgayoc, Department of Cajamarca, Peru, and deposited in the Warsaw Museum (Polska Akademia Nauk, Instytut Zoologiczny) was apparently destroyed by fire, perhaps as early as 1936 (Gardner & Carter, 1972b). In 1972, Gardner and Carter designated a neotype: TCWC 12199, adult male, preserved as skin and skull, collected by D. C. Carter (original field number 5477) on 26 August 1964 at 2 mi N Tingo Maria, Province of Leoncio Prado, Department of Huánuco, Peru, elevation 2000 ft (610 m).

DISTRIBUTION—Colombia to Peru, Bolivia, and NW Brazil, from 183 to 1900 m (Fig. 20).

DIAGNOSIS—Size large (FA = 54–62 mm; CIL = 26.4–29.9 mm; W = 36–59 g; Table 3); *dorsal stripe indistinct, thin and obscured; dorsal fur short, <6.30 mm; sparse and short hair on the dorsum of the feet*; uropatagium fringe usually hairy, occasionally sparsely; paraoccipital process well developed; *M1 parastyle present; m1 meta-*

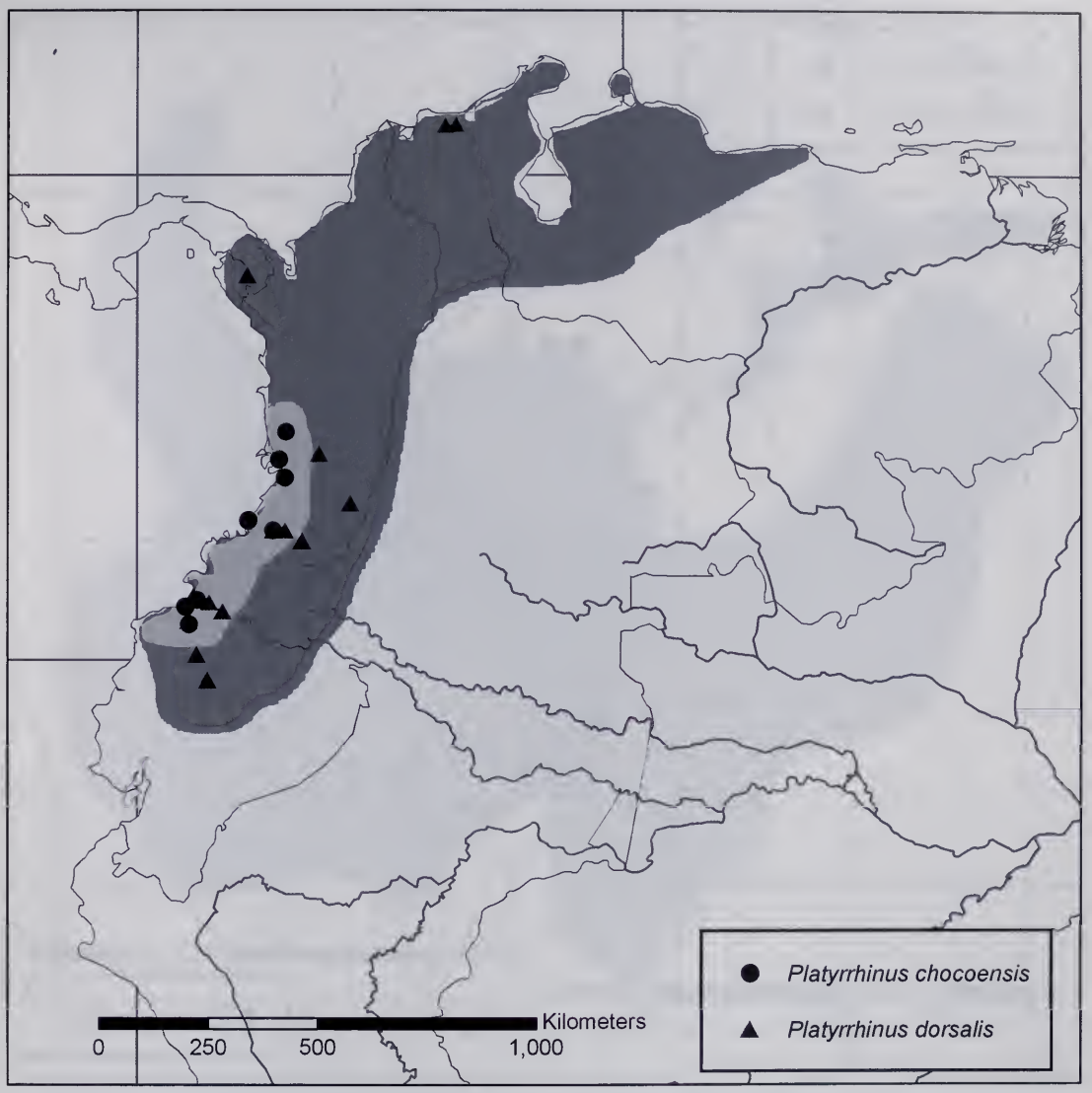

FIG. 18. Distributional map of *Platyrrhinus chocoensis* and *P. dorsalis*.

conid developed; stylid cusp absent between the metaconid and protoconid of m2.

Platyrrhinus ismaeli, new species Figure 21, 23 (top)

cf. *Vampyrops aurarius* Lemke et al., 1982: 230–231
Vampyrops sp. C Alberico, 1990: 349–352
Platyrrhinus dorsalis Pacheco and Patterson, 1991: 101, 104, 111, 112, 113, 114, 121
Platyrrhinus dorsalis Albuja, 1999: 135–136 (part)
Platyrrhinus "dorsalis norte" Solari et al., 2001: 263
Platyrrhinus dorsalis "Norte" Velazco and Solari, 2003
Platyrrhinus dorsalis "Norte" (this paper)

TYPE MATERIAL—The holotype, MUSM 4946, is an adult collected by Bruce D. Patterson (original field number BDP 2484) on 2 May 1987 at 19 km E of Balsas, 1945 m (6380 ft) in elevation, Province of Chachapoyas, Department of Amazonas, Peru. The skin, skull, and skeleton were in good condition. Frozen tissues are deposited at the Field Museum of Natural History (FMNH 129138).

Paratypes include five adult specimens: one female (FMNH 129134) and one male (FMNH 129136) from the type locality; and two females (FMNH 129139, 129146) and one male (FMNH

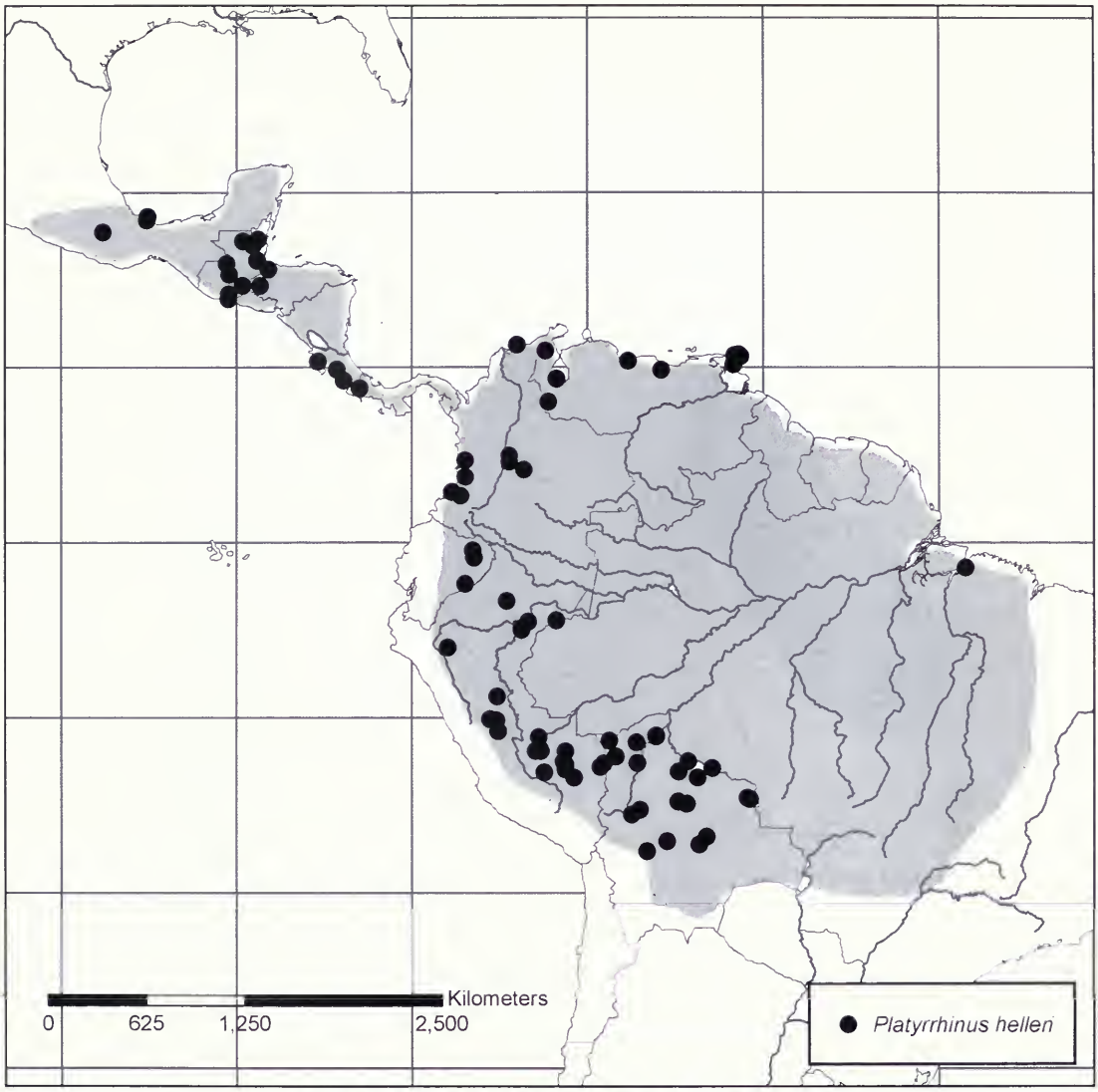

FIG. 19. Distributional map of *Platyrrhinus helleri*.

129143) from Hacienda Limón, W of Balsas, Province of Celendin, Department of Cajamarca, Peru. The holotype and paratypes along with other specimens from the known distributional range are listed in Appendix 1. Measurements of each specimen of the type series of *Platyrrhinus ismaeli* are provided in Table 4.

DISTRIBUTION—*Platyrrhinus ismaeli* (Fig. 21) is currently known from both slopes of the Andes in Colombia, Ecuador, and Peru. The northern limit of the distribution is the Department of Huila (Colombia), and the southern limit is the Department of San Martin (Peru). The elevation is from 1230 to 2950 m (Fig. 22).

ETYMOLOGY—*Platyrrhinus ismaeli* is named in honor of Ismael Ceballos Bendezú, an internationally well-known naturalist from Cuzco, Peru, in recognition of his important contributions to the study of Peruvian bats.

DIAGNOSIS—Size medium (FA = 50–56 mm; CIL = 26.6–28.2 mm; W = 30–51 g); *folds in the pinna absent*; sulcus on the posterior face of the paracone not joined to the cingulum of the lingual face of the metacone on M1; m1 metaconid poorly developed.

DESCRIPTION—A medium-sized species of *Platyrrhinus* (FA = 50–56 mm; GLS = 27.8–30.1 mm) with dark brown dorsal fur, grayish ventral

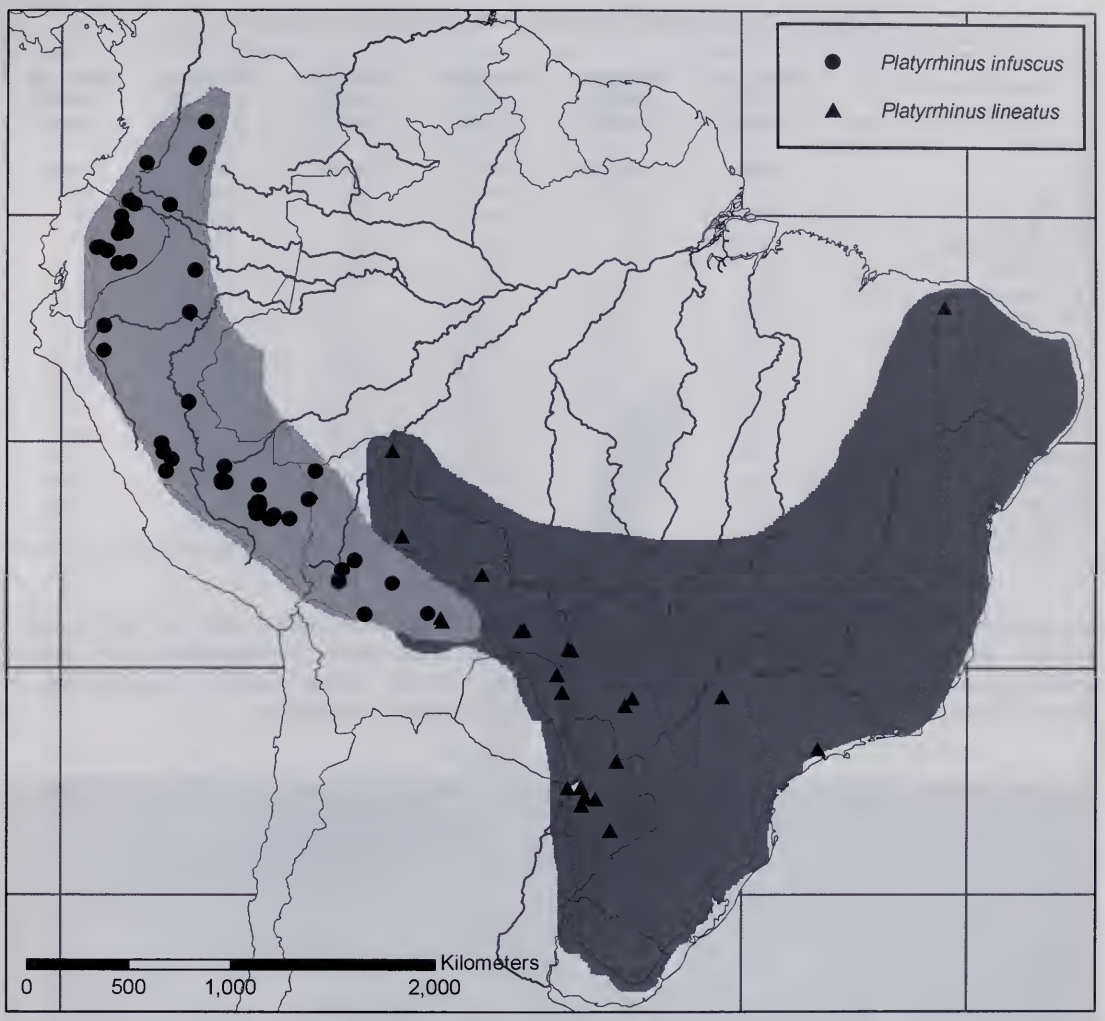

FIG. 20. Distributional map of *Platyrrhinus infuscus* and *P. lineatus*.

fur, and tricolored dorsal and ventral hair. Dorsomedial and ventrolateral facial stripes obviously subequal and darkish, dorsal hairs 8–10 mm long on the back; narrow dorsal stripe brighter than the facial ones; folds in the pinna poorly marked but distinguishable; six vibrissae surrounding the margins of the noseleaf in a single array; four submental vibrissae present; one interramal vibrissa present; noseleaf longer than wide, inferior border of the horseshoe completely free of the upper lip; dense and long hair on the dorsum of the feet; "U"-shaped posterior edge of the uropatagium with a densely haired fringe, uropatagium extends along the midline 4.5–7 mm long; insertion of the posterior edge of the plagiopatagium onto the first metatarsal; third metacarpal shorter than fifth metacarpal; fossa on the squamosal end of the zygomatic arch shallow; upper median incisors convergent and in contact; sulcus present on the posterior face of the upper canines; two stylar cusps present on the posterior face of P4; labial cingulum present at the base of the metacone of M1; stylar cusp present on the cingulum of the lingual face of the M1 metacone; sulcus on the posterior face of the paracone not joined to the cingulum of the lingual face of the metacone on M1; M1 metastyle present; M1 protocone small and blunt; stylar cusp present on the lingual face of the M2 paracone; M2 metastyle present; two sulci present on the lingual face of the main cone of p4; m1 paraconid absent; m1 entoconid present; stylid cusp present on the anterior face of the m1 pro-

TABLE 4. Measurements of the type series of *Platyrrhinus ismaeli*.

	Holotype MUSM 4946	Paratype FMNH 129134	Paratype FMNH 129136	Paratype FMNH 129139	Paratype FMNH 129143	Paratype FMNH 129146
Sex	Male	Female	Male	Female	Male	Female
Weight	35	40	38	35	30	31
Total length	84	82	87	82	83	79
Hind foot length	18	13	18	15	16	17
Ear length	20	21	22	20	21	21
Forearm length	52	53	54	54	52	56
Tibia length	21.68	19.52	21.68	21.27	20.56	21.31
Greatest length of skull	27.94	27.77	28.15	28.14	28.47	28.17
Condyloincisive length	27.10	26.57	27.47	27.06	26.83	26.62
Condylocanine length	26.22	26.07	26.88	26.49	26.14	26.06
Postorbital breadth	6.46	6.27	6.57	6.43	6.36	6.65
Zygomatic breadth	17.13	16.93	18.21	17.31	17.33	16.41
Braincase breadth	12.00	11.57	12.29	12.03	12.02	11.70
Mastoid breadth	13.99	13.63	14.72	14.04	13.98	14.06
Maxillary toothrow length	11.35	11.43	11.66	11.75	11.33	11.48
Breadth across molars	12.63	12.65	12.81	13.08	12.45	12.41

toconid; poorly developed m1 metaconid; m2 hypoconid absent; stylid cusp present between the metaconid and protoconid of m2; both labial and lingual cingula present on m2. Velazco (2001) and Velazco and Solari (2003) did not find secondary sexual dimorphism in populations of *P. ismaeli* from Peru in either qualitative morphologic or morphometric characters.

FIG. 21. Frontal view of *Platyrrhinus ismaeli*; adult male photographed at Hacienda Limón, Cajamarca, Peru, by B. D. Patterson.

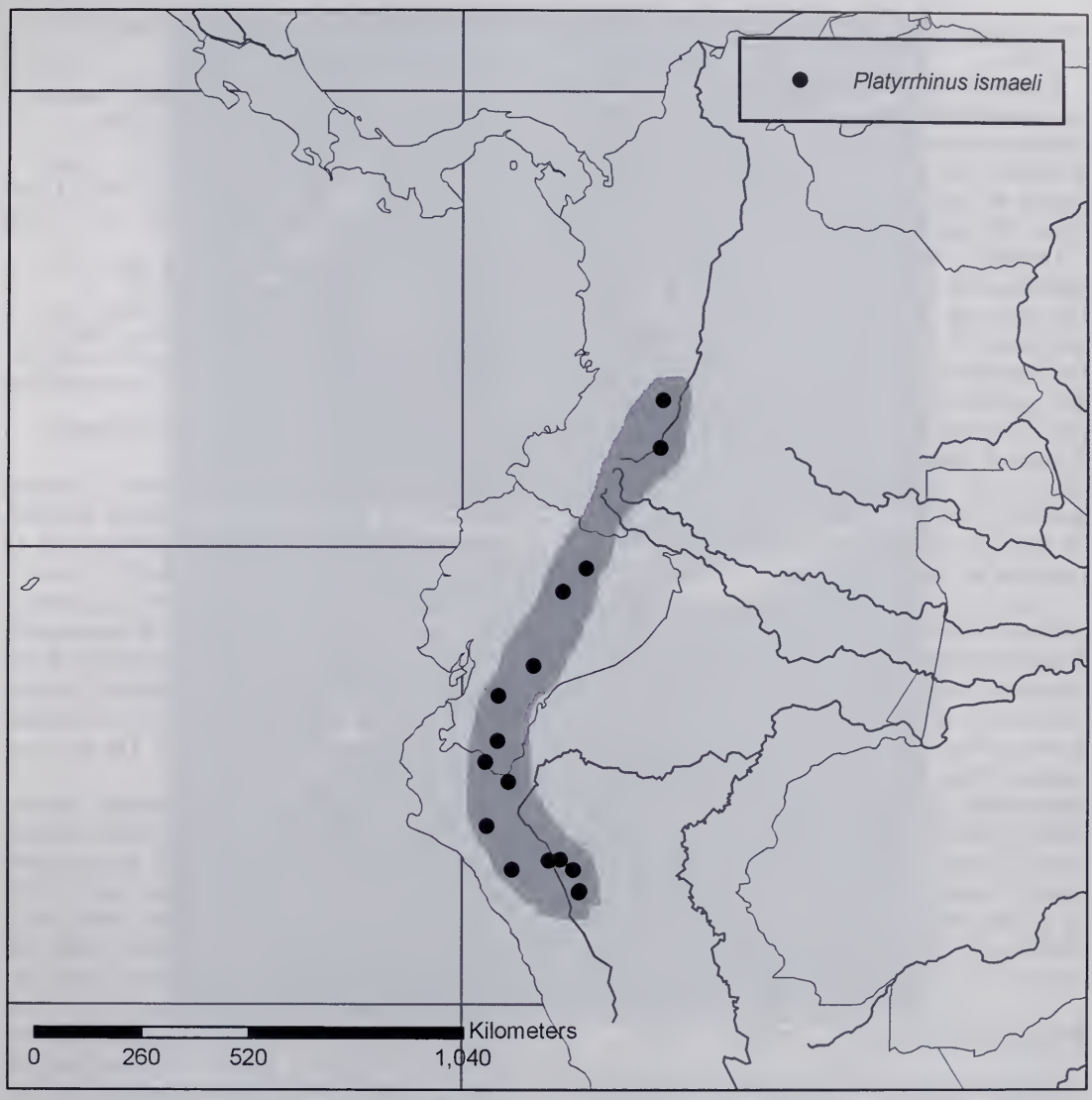

FIG. 22. Distributional map of *Platyrrhinus ismaeli.*

COMPARISONS—In several localities *Platyrrhinus ismaeli* is found sympatrically with *P. albericoi* and *P. nigellus,* and it occurs with *P. dorsalis* in one locality at El Parque Nacional Natural de la Cueva de Los Guacharos, Department of Huila, in Colombia. *Platyrrhinus ismaeli* is easily distinguished from *P. albericoi* and *P. nigellus* by its forearm length and greatest length of skull: *P. albericoi* (FA = 62–63 mm; GLS = 32.5–32.8 mm) and *P. nigellus* (FA = 40–47 mm; GLS = 23.5–25.9 mm; Tables 2–4). It differs from *P. dorsalis* in its GLS, condiloincisive length, condilocanine length, and maxillary toothrow length (Tables 3–4). *Platyrrhinus ismaeli* has traditionally been confused with *P. dorsalis,* so subsequent comparisons are restricted to these two species.

Externally, *Platyrrhinus ismaeli* can be distinguished from *P. dorsalis* by two characters. *Platyrrhinus ismaeli* has dense and long hair on the dorsal side of the feet, whereas the hair in the dorsum of the feet is sparsely distributed and with some long hairs in *P. dorsalis.* The hairs on the edge of the uropatagium are densely haired and longer than 2.1 mm in *P. ismaeli,* whereas *P. dorsalis* presents a regular or occasionally sparsely

haired uropatagium fringe, with hairs shorter than 1.5 mm.

Cranially, *Platyrrhinus ismaeli* and *P. dorsalis* are very similar. *Platyrrhinus ismaeli* has a more robust cranium with a wider rostrum. Moreover, *P. ismaeli* has a shallow fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, whereas *P. dorsalis* has a deep fossa.

Dentally, *Platyrrhinus ismaeli* and *P. dorsalis* exhibit some differences. Whereas in *P. ismaeli* the sulcus on the posterior face of the paracone not joined to the cingulum of the lingual face of the metacone on M1, this discontinuity is absent in *P. dorsalis* (Fig. 23). The lingual cingulum of the M2 metacone is restricted to the metacone in *P. ismaeli,* whereas in *P. dorsalis* the lingual cingulum of the M2 metacone continuous to the M2 paracone. Finally, a poorly developed metaconid on m1 is present in *P. ismaeli,* whereas *P. dorsalis* lacks the m1 metaconid.

Comments—In his systematic review of *Platyrrhinus* from the northwestern South America, Alberico (1990) identified *Platyrrhinus* sp. C as a potentially new species from Colombia. *Platyrrhinus* sp. C (FA = 50.9–53.2 mm) was collected at several localities in the Cueva de los Guacharos National Park near the headwaters of the Magdalena River at midelevations (ca. 1500 m) in Colombia. *Platyrrhinus ismaeli* has been collected at Cueva de los Guacharos National Park, and the range of variation of the FA size in *Platyrrhinus* sp. C falls within the range of *P. ismaeli* (FA = 50–56 mm). Therefore, it is likely that *Platyrrhinus* sp. C is conspecific with *P. ismaeli.*

Platyrrhinus lineatus (É. Geoffroy, 1810)

Phyllostoma lineatum É. Geoffroy St.-Hilaire, 1810. Type locality: Asunción, Paraguay.
Vampyrops lineatus sacrillus Thomas,1924. Type locality: Rio Doce, State of Espírito Santo, Brazil (BMNH 23.12.12.9).

Holotype—*Phyllostoma lineatum* MNHN 953, adult, preserved as skin and skull, was collected by Felix de Azara in Asunción, Paraguay.

Distribution—Lowlands from eastern and southeastern Brazil, northern Uruguay, northeastern Argentina, Paraguay, and Bolivia, from 122 to 971 m (Fig. 20).

Diagnosis—Size medium (FA = 46–48 mm; CIL = 22.0–23.4 mm; W = 18–28 g; Table 3); dense and long hair on the dorsum of the feet; postorbital process well developed; *paraoccipital process well developed*; *m1 metaconid developed.*

Platyrrhinus masu, new species. Figure 24

Vampyrops dorsalis Sanborn, 1951: 10
Vampyrops dorsalis Barquez and Orlog, 1980: 54
Vampyrops dorsalis Anderson et al., 1982: 7
Vampyrops dorsalis Anderson, 1985: 7
Platyrrhinus dorsalis Anderson, 1993: 8, 23, 69
Platyrrhinus dorsalis Anderson et al., 1993: 14, 24
Platyrrhinus dorsalis Anderson, 1997: 36, 37, 239, 240 (part)
Platyrrhinus dorsalis Emmons et al., 2001: 255
Platyrrhinus dorsalis Romo, 2001: 258
Platyrrhinus cf. *dorsalis* Solari et al., 2001: 112
Platyrrhinus "dorsalis sur" Solari et al., 2001: 263
Platyrrhinus dorsalis Salazar-Bravo et al., 2003: 15
Platyrrhinus dorsalis "Centro-Sur" Velazco and Solari (2003)
Platyrrhinus dorsalis "Centro-Sur" (this paper)

Type Material—The holotype, FMNH 123917, is an adult female collected by David E. Willard (original field number DEW 425) on 18 October 1981 at Consuelo, km 165, 17 km by road west of Pilcopata, Province of Paucartambo, Department of Cuzco, Peru, approximately 13°07′59′S, 71°15′W. The type locality is in the Cultural Zone of the Manu Biosphere Reserve. The holotype is a specimen preserved in alcohol with the skull removed and cleaned. The skull and body were in good condition.

Paratypes include six adult specimens: one female (FMNH 172100) from San Pedro, Paucartambo-Pilcopata road, Province of Paucartambo, Department of Cuzco, Peru; one male (MVZ 166595) from Kiteni, Río Urubamba, Province of La Convención, Department of Cuzco, Peru; two females (MUSM 14562, 14566) from Campamento Llactahuaman, Kimbiri, Province of La Convención, Department of Cuzco, Peru; and two males (MUSM 18265, 18266) from Cordillera de Carpish, Chinchao, Province of Huánuco, Department of Huánuco, Peru. The holotype, paratypes, and other specimens from the known distributional range are listed in Appendix 1. Measurements of each specimen of the type series of *Platyrrhinus masu* are provided in Table 5.

Distribution—*Platyrrhinus masu* (Fig. 24) is currently known from the eastern slope of the Andes in Bolivia and Peru. The northern limit of the distribution is the Department of Huánuco (Peru) and the southern limit is the Department of La Paz (Bolivia). The elevational range extends from 650 to 3350 m (Fig. 25).

Etymology—From the Quechua word "masu," meaning bat. Most of the collection localities of *Platyrrhinus masu* have Quechua as the main language.

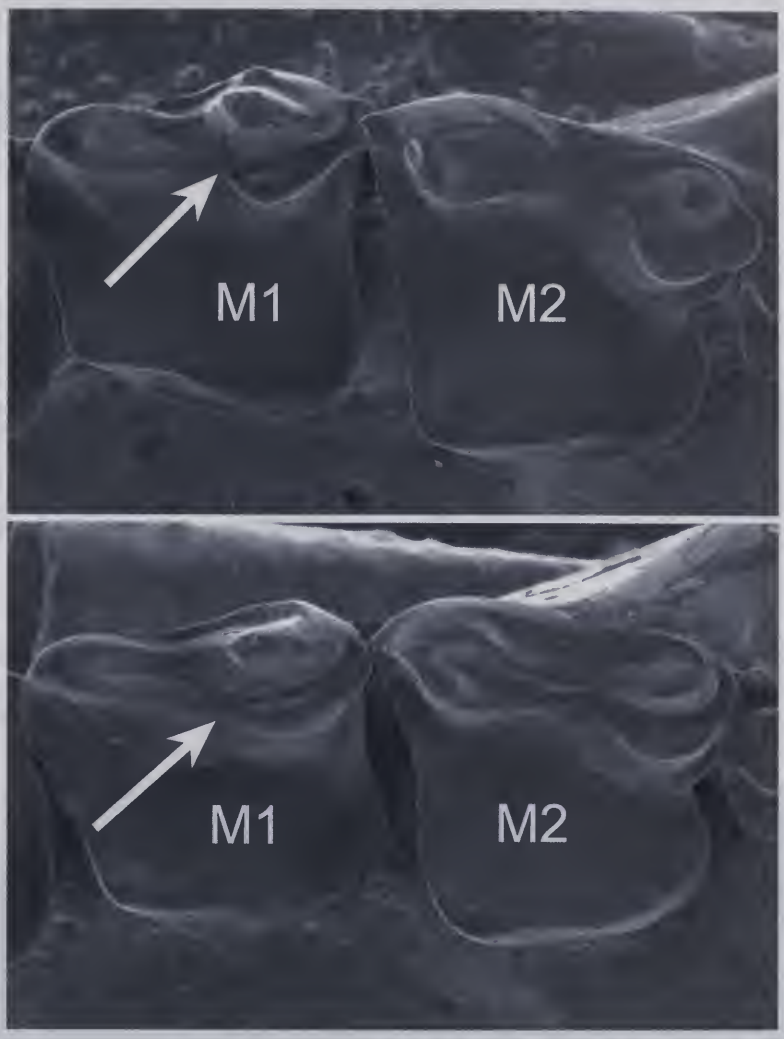

FIG. 23. Occlusal views of the left M1 and M2 illustrating taxonomic differences in the presence or absence of a connection between the sulcus on the posterior face of the paracone on M1 and the cingulum of the lingual face of the metacone on M1. (**Top**) *Platyrrhinus ismaeli* (MUSM 4946) not connected (arrow). (**Bottom**) *Platyrrhinus dorsalis* (FMNH 128141) connected (arrow).

DIAGNOSIS—Size medium (FA = 45–51 mm; CIL = 24.0–25.5 mm; W = 23–33 g; Table 6); two submental vibrissae on each side of the chin; dorsal stripe brilliant-white and wide; dorsal hairs on the back 6.3–7.5 mm; upper lateral incisors bilobed.

DESCRIPTION—A medium-sized species of *Platyrrhinus* (FA = 45–51 mm; GLS = 25.0–26.8 mm; Table 6). Dorsal fur dark brown, ventral fur grayish, dorsal and ventral hair tricolored; dorsomedial and ventrolateral facial stripes obviously subequal and darker; dorsal hairs 6.3–7.5 mm long on the back; narrow dorsal stripe brighter that the facial ones, starting at the end of the dorsomedial facial stripes and ending on the rump; dorsal stripe definite but narrow; folds in the pinna well marked; six vibrissae surrounding the margins of the noseleaf in a single array; two submental vibrissae present on each side of the chin; one interramal vibrissae present; noseleaf longer than wide; dense and long hair on the dorsum of the feet; "U"-shaped posterior edge of the uropatagium with a densely haired fringe, uropatagium extends along the midline 4.5–7 mm long; insertion of the posterior edge of the plagiopatagium onto the first metatarsal; third metacarpal

TABLE 5. Measurements of the type series of *Platyrrhinus masu*.

	Holotype FMNH 123917	Paratype FMNH 172100	Paratype MVZ 166595	Paratype MUSM 14562	Paratype MUSM 14566	Paratype MUSM 18265	Paratype MUSM 18266
Sex	Female	Female	Male	Female	Female	Male	Male
Weight	—	28	30	26	28	28	33
Total length	73	75	82	75	70	73	77
Hind foot length	12	14	15	14	13	13	14
Ear length	18	18	18	19	20	17	19
Forearm length	47	50	48	50	50	49	51
Tibia length	19.58	19.03	20.41	19.13	19.28	20.15	19.63
Greatest length of skull	26.03	26.42	26.14	26.70	26.84	26.53	26.41
Condyloincisive length	24.87	24.77	25.52	25.40	25.13	25.35	25.51
Condylocanine length	24.39	24.19	24.87	24.69	24.54	24.87	25.04
Postorbital breadth	6.19	6.50	6.57	6.30	6.39	6.14	6.10
Zygomatic breadth	16.02	16.52	16.11	16.78	15.93	16.31	16.96
Braincase breadth	11.33	11.62	11.93	11.74	11.56	11.70	11.76
Mastoid breadth	13.19	13.09	13.71	13.60	13.50	13.81	13.91
Maxillary toothrow length	10.37	10.33	10.53	10.69	10.59	10.96	11.11
Breadth across molars	11.82	12.11	11.55	12.58	12.02	12.17	12.78

shorter than or subequal to fifth metacarpal; postorbital process absent or poorly developed; zygomatic arches slightly divergent; paraoccipital process well developed; upper median incisors convergent and in contact; upper lateral incisors bilobed; sulcus present on the posterior face of the upper canines; two stylar cusps present on the posterior face of P4; labial cingulum present at

FIG. 24. Frontal view of *Platyrrhinus masu* (FMNH 174760); adult male photographed at La Esperanza in the Cultural zone of the Manu Biosphere Reserve, Cuzco, Peru, by B. D. Patterson.

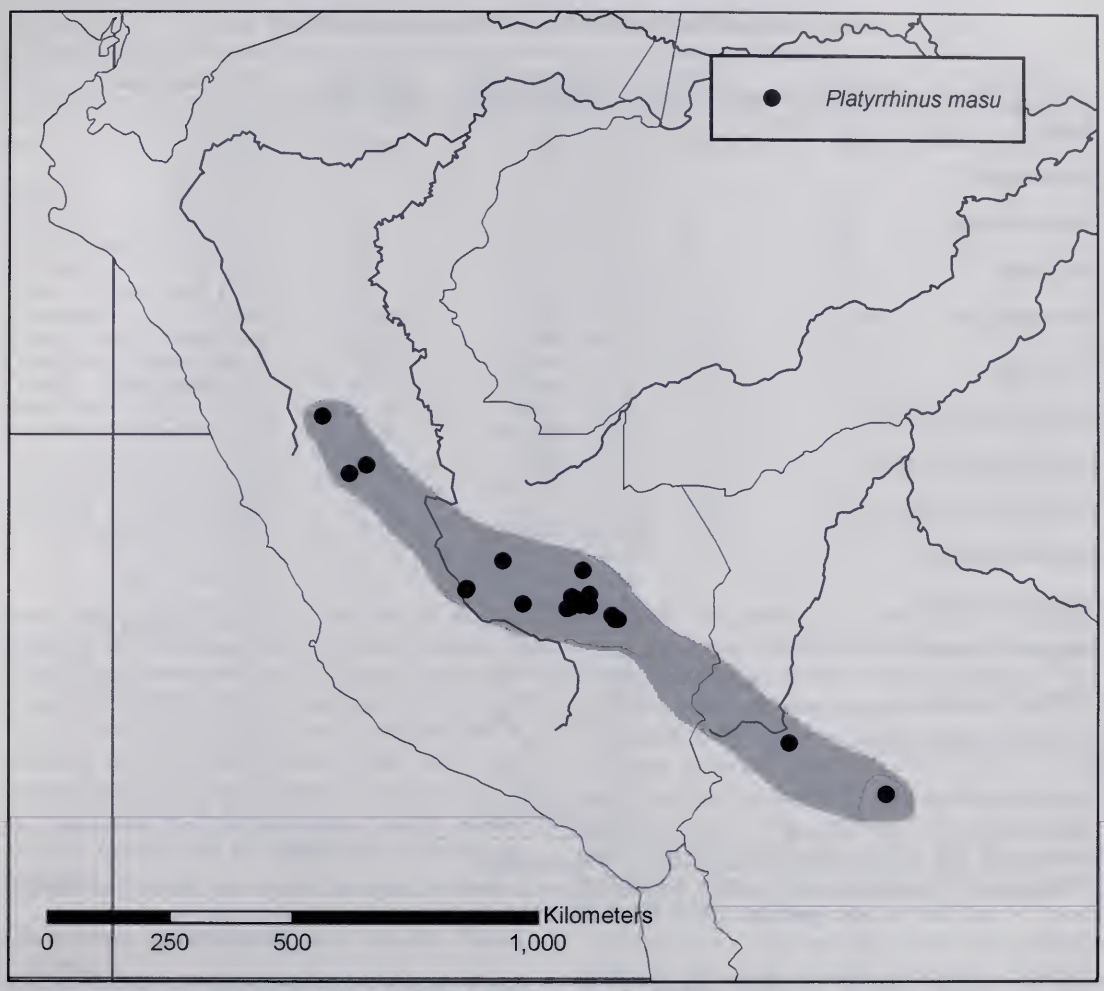

FIG. 25. Distributional map of *Platyrrhinus masu*.

the base of the metacone on M1; sulcus present on the posterior face of the M1 paracone; stylar cusp present on the cingulum of the lingual and labial face of the M1 metacone; M1 metastyle present; moderately developed M1 protocone; stylar cusp present on the lingual face of the M2 paracone; M2 metastyle present; lingual cingulum of the M2 metacone restricted to the metacone; M2 hypoconal basin developed; two sulci present on the lingual face of the main cone of p4; two cones present on the posterior face of p4; both labial and lingual cingula present on p4; both labial and lingual cingula present on m2; m1 paraconid absent; m1 entoconid present; stylid cusp on the anterior face of the m1 protoconid; m1 metaconid absent; m2 hypoconid present; stylid cusp present between the metaconid and protoconid of m2; both labial and lingual cingula present on m2. Velazco (2001) and Velazco and Solari (2003) did not find secondary sexual dimorphism in either qualitative morphologic or morphometric characters.

COMPARISONS—*Platyrrhinus masu* is found sympatrically with *P. albericoi* and *P. nigellus* in several localities. Morphometrically, *P. masu* is easily distinguished from *P. albericoi,* but there is overlap in some measurements of *masu* and *nigellus*: *P. albericoi* (FA = 62–63 mm; CIL = 31.6–32.6 mm; W = 55–68 g), *P. nigellus* (FA = 40–47 mm; CIL = 21.9–24.5 mm; W = 19–30 g), and *P. masu* (FA = 45–51 mm; CIL = 23.0–25.5 mm; W = 23–33 g). *Platyrrhinus masu* has been traditionally confused with *P. dorsalis*; however, it also exhibits overlap of measurements

TABLE 6. Selected measurements[a,b] of *Platyrrhinus ismaeli* and *P. masu*.

	Platyrrhinus ismaeli	*Platyrrhinus masu*
Weight	37.1 ± 5.2 30–51 (19)	27.0 ± 2.7 23–33 (21)
Total length	86.7 ± 5.3 78–98 (20)	74.3 ± 3.2 70–82 (25)
Hind foot length	15.5 ± 1.6 13–18 (20)	13.6 ± 0.9 12–16 (26)
Ear length	21.2 ± 0.7 20–22 (19)	19.2 ± 1.4 16–21 (25)
Forearm length	52.7 ± 1.4 50–56 (20)	48.4 ± 1.5 45–51 (26)
Tibia length	21.97 ± 0.87 18.34–21.96 (20)	19.44 ± 0.80 17.35–20.86 (26)
Greatest length of skull	28.53 ± 0.56 27.77–30.08 (20)	26.02 ± 0.53 24.96–26.84 (26)
Condyloincisive length	27.19 ± 0.43 26.57–28.33 (20)	24.87 ± 0.44 23.98–25.52 (26)
Condylocanine length	26.57 ± 0.44 26.06–27.59 (20)	24.36 ± 0.41 23.45–25.04 (26)
Postorbital breadth	6.48 ± 0.20 6.17–6.86 (20)	6.33 ± 0.18 5.99–6.61 (26)
Zygomatic breadth	17.21 ± 0.49 16.25–18.21 (20)	16.13 ± 0.34 15.62–16.96 (25)
Braincase breadth	11.97 ± 0.23 11.57–12.29 (20)	11.54 ± 0.21 11.19–11.93 (26)
Mastoid breadth	14.07 ± 0.30 13.43–14.72 (20)	13.46 ± 0.22 13.09–13.91 (26)
Maxillary toothrow length	11.84 ± 0.34 11.33–12.48 (20)	10.57 ± 0.22 10.17–11.11 (25)
Breadth across molars	13.08 ± 0.46 12.40–13.83 (20)	12.05 ± 0.28 11.55–12.78 (25)

[a] Weight is in grams, all other measurements are in millimeters.
[b] Summary statistics (mean and standard deviation [above], observed range and sample size [below]) of measurements for each species (see Appendix 1 for a list of the specimens measured).

with *P. ismaeli* and *P. nigellus* (Tables 3, 6). Therefore, comparisons will focus on differentiation of these four species.

Externally, *Platyrrhinus masu* can be distinguished from these species by three submental vibrissae on each side of the chin in *P. masu*, whereas *P. dorsalis*, *P. ismaeli*, and *P. nigellus* have four submental vibrissae on each side of the chin; inferior border of the noseleaf partially joined to the upper lip in some individuals and completely free in others in *P. masu*, whereas in *P. dorsalis*, *P. ismaeli*, and *P. nigellus*, the inferior border of the noseleaf is completely free in all individuals; parallel folds in the pinna well marked in *P. masu* and *P. nigellus*, whereas in *P. dorsalis* and *P. ismaeli*, the parallel folds are poorly marked but distinguishable; dorsal stripe white and wide in *P. masu* and *P. nigellus*, whereas in *P. dorsalis* and *P. ismaeli*, the dorsal stripe is definite but narrow; dorsal fur length 6.3–7.5 mm in *P. masu*, whereas *P. dorsalis*, *P. ismaeli*, and *P. nigellus* have the dorsal fur length >8 mm; dense and long hair on the dorsum of the feet in *P. ismaeli*, *P. masu*, and *P. nigellus*, whereas *P. dorsalis* has the hair on the dorsum of the feet intermediate in density and length; and fringe of hair on the edge of the uropatagium densely haired in *P. ismaeli*, *P. masu*, and *P. nigellus*, whereas *P. dorsalis* has the uropatagium fringe usually hairy, occasionally sparsely.

Dentally, *Platyrrhinus masu* can be distinguished from these species by the following characters: upper lateral incisors bilobed in *P. masu*, whereas *P. dorsalis* and *P. nigellus* have the upper lateral incisors monolobed; *P. dorsalis*, *P. masu*, and *P. nigellus* present the sulcus on the posterior face of the paracone of M1 joined to the cingulum of the lingual face of the metacone on M1, whereas *P. ismaeli* present these two structures not joined; M1 protocone moderately developed in *P. masu* and *P. nigellus*, whereas *P. dorsalis* and *P. ismaeli* have the M1 protocone small and blunt;

TABLE 7. Measurements of the type species of *Platyrrhinus matapalensis*.

	Holotype FNH 81079	Paratype FMNH 81080	Paratype FMNH 81081	Paratype MUSM 10725	Paratype MUSM 10726
Sex	Male	Male	Male	Male	Female (pregnant)
Weight	—	—	—	16	20
Total length	58	58	56	65	65
Hind foot length	13	13	13	10	12
Ear length	17	17	17	16	19
Forearm length	39	37	39	37	38
Tibia length	17.34	15.50	17.09	14.69	14.43
Greatest length of skull	22.04	22.00	21.46	22.24	21.07
Condyloincisive length	20.77	20.92	20.22	21.34	20.12
Condylocanine length	20.30	20.40	19.82	20.82	19.65
Postorbital breadth	5.43	5.54	5.40	5.67	5.47
Zygomatic breadth	12.99	13.06	—	—	12.57
Braincase breadth	9.41	9.49	9.47	9.75	9.35
Mastoid breadth	10.99	11.31	10.54	11.11	10.61
Maxillary toothrow length	8.31	8.54	8.22	8.56	8.13
Breadth across molar	9.14	9.46	9.06	9.39	9.01

stylar cusp present on the lingual face of the M2 paracone in *P. ismaeli* and *P. masu,* whereas in *P. nigellus,* that stylar cusp is lacking; lingual cingulum of the M2 metacone restricted to the metacone in *P. ismaeli* and *P. masu,* whereas in *P. dorsalis,* the lingual cingulum of the M2 metacone continues to the paracone; and lack of the m1 metaconid in *P. dorsalis* and *P. masu,* whereas in *P. ismaeli,* the m1 metaconid is poorly developed.

Platyrrhinus matapalensis new species. Figure 27 (top)

Vampyrops helleri Sanborn, 1955: 412 (part)
Vampyrops helleri Tuttle, 1970: 73 (part)
Vampyrops helleri Koopman, 1978: 12 (part)
Platyrrhinus helleri Rodriguez, 1998: 73
Platyrrhinus helleri Albuja, 1999: 139–140 (part)
Platyrrhinus helleri "Western" (this paper)

TYPE MATERIAL—The holotype, FMNH 81079, is an adult male collected by Celestino Kalinowski (original field number 1524) on 3 July 1954 at Matapalo, 54 m in elevation, Province of Zarumilla, Department of Tumbes, Peru, approximately 3°40′59′S, 80°12′W. The skin and skull were in good condition.

Paratypes include four adult specimens: two males (FMNH 81080, 81081) from the type locality; and one female (MUSM 10726) and one male (MUSM 10725) from Quebrada Naranjal-Campo Verde, Z.R. Tumbes, 620–680 m in elevation, Province of Zarumilla, Department of Tumbes, Peru. All these specimens are adult and are listed in Appendix 1 with other specimens from the known distributional range. Measurements of each specimen of the type series of *Platyrrhinus matapalensis* are provided in Table 7.

DISTRIBUTION—*Platyrrhinus matapalensis* is currently known from the western slope of the Andes in Ecuador and Peru. The northern limit of the distribution is the province of Esmeraldas (Ecuador) and the southern limit is the Department of Tumbes (Peru). The elevational range extends from 54 to 680 m (Fig. 26).

ETYMOLOGY—The specific name *matapalensis* refers to the type locality Matapalo (Tumbes, Peru), where the taxon was first collected.

DIAGNOSIS—Size small (FA = 37–39 mm; CIL = 20.1–21.3 mm; W = 16–20 g); two interramal vibrissae; *dorsal stripe definite but narrow*; *ventral fur bicolored, occasionally unicolored*; *dense and long hair on the dorsum of the feet.*

DESCRIPTION—A small-sized species of *Platyrrhinus* (FA = 37–39 mm; GLS = 21.1–22.2 mm). Dorsal fur light brown, ventral fur brownish, dorsal hair tricolored, ventral hair bicolored in some individuals and in others unicolored; dorsomedial and ventrolateral facial stripes obviously subequal and brighter, dorsal hairs 6.3–7.5 mm long on the back; narrow dorsal stripe with the same coloration as the facial ones; folds in the pinna poorly marked but distinguishable; seven vibrissae surrounding the margins of the noseleaf in a single array; four submental vibrissae present; two interramal vibrissae present; noseleaf longer than wide, inferior border of the horseshoe completely

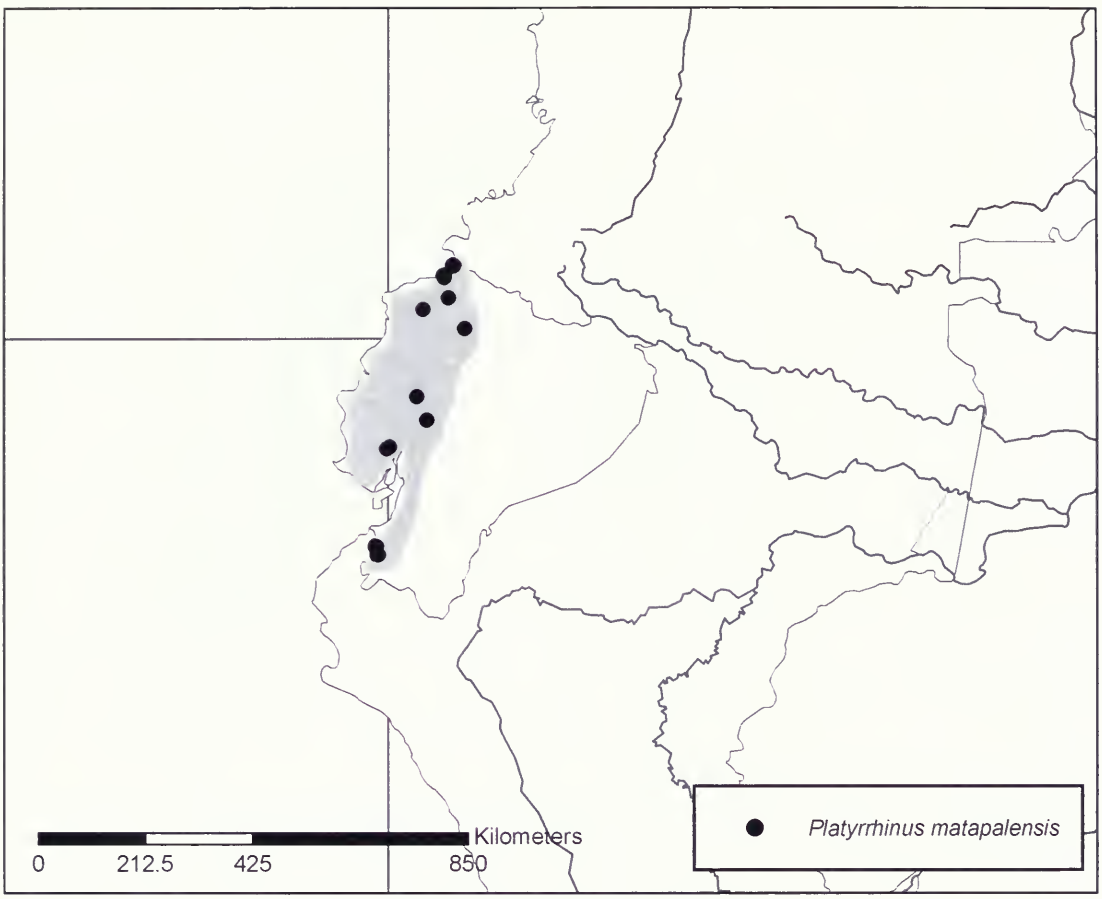

FIG. 26. Distributional map of *Platyrrhinus matapalensis*.

free of the upper lip; hairs on the dorsum of the feet sparse and short; "U" or "V" shaped posterior edge of the uropatagium with a fringe densely haired, uropatagium extends along the midline <4.5 mm long; insertion of the posterior edge of the plagiopatagium onto the first metatarsal; fifth metacarpal shorter than third metacarpal; postorbital and paraoccipital processes poorly developed; fossa on the squamosal end of the zygomatic arch almost imperceptible; sulcus present on the posterior face of the upper canines; two stylar cusps present on the posterior face of P4; both labial and lingual cingulum present at the base of the metacone of M1; sulcus on the posterior face of the paracone joined to the cingulum of the lingual face of the M1 metacone; M1 parastyle present; M1 metastyle occasionally present; M1 protocone moderately developed; stylar cusp absent on the lingual face of the M2 paracone; labial cingulum of the M2 paracone present; M2 metastyle present; stylar cusp absent on the lingual face of the M2 paracone; both labial and lingual cingula present on p4; stylid cusps absent on the anterior or anterolingual face of the main cone of p4; stylid cusp present on the posterior face of the main cone of p4; m1 paraconid absent; m1 metaconid absent; m2 hypoconid absent; stylid cusp between the metaconid and protoconid of m2 present; both labial and lingual cingula present on m2, but occasionally only the labial cingulum is present.

COMPARISONS—*Platyrrhinus matapalensis* is found sympatrically with *P. chocoensis* and *P. dorsalis*. Morphometrically, *P. matapalensis* is easily distinguished from both as follows: *P. chocoensis* (FA = 48–49 mm; CIL = 24.6–26.2 mm; W = 29–32 g), *P. dorsalis* (FA = 46–50 mm; CIL = 24.3–25.7 mm), and *P. matapalensis* (FA = 37–39 mm; CIL = 20.1–21.3 mm; W = 16–20 g). *Platyrrhinus matapalensis* has been confused with *P. helleri* (Sanborn, 1955; Tuttle, 1970;

Koopman, 1978); however, *P. matapalensis* could also be mistaken for *P. brachycephalus* because there is overlap in the measurements (Table 3, 7). Therefore, the comparisons focus on *P. matapalensis, P. brachycephalus,* and *P. helleri* because these are the smaller species in the genus and are subject to potential confusion.

Externally, *Platyrrhinus matapalensis* can be distinguished from the other two species by the following: one vibrissa present on the upper lip of *P. matapalensis,* ventral to the vibrissae that surround the margins of the noseleaf in, whereas *P. brachycephalus* has two vibrissae on the upper lip; four submental vibrissae on each side of the chin in *P. helleri* and *P. matapalensis,* whereas *P. brachycephalus* has five submental vibrissae on each side of the chin; two interramal vibrissae present in *P. matapalensis,* whereas *P. brachycephalus* and *P. helleri* have one interramal vibrissa; ventral fur unicolored or bicolored in *P. matapalensis,* whereas *P. brachycephalus* has the ventral fur tricolored and *P. helleri* bicolored; sparse and short hair on the dorsum of the feet in *P. matapalensis,* whereas in *P. helleri,* the hair on the dorsum of the feet is intermediate in density and length; and fringe of hair on the edge of the uropatagium densely haired in *P. helleri* and *P. matapalensis,* whereas *P. brachycephalus* has the fringe of hair on the edge of the uropatagium usually hairy, occasionally sparsely.

Cranially, *Platyrrhinus matapalensis* can be distinguished from the other two species by the following characters: a poorly developed postorbital process in *P. brachycephalus* and *P. matapalensis,* whereas in *P. helleri,* the postorbital process is moderately developed; and paraoccipital process almost imperceptible in *P. brachycephalus* and *P. matapalensis,* whereas in *P. helleri,* the paraoccipital process is moderately developed.

Dentally, *Platyrrhinus matapalensis* can be distinguished from the other two species by the following: M1 protocone moderately developed in *P. matapalensis,* whereas in *P. brachycephalus,* the M1 protocone is well developed, and in *P. helleri,* the M1 protocone is small and blunt, and lack of stylid cusps on the anterior face of the main cone of p4 in *P. matapalensis,* whereas *P. brachycephalus* has two stylid cusps on the anterior face of the main cone of p4, and *P. helleri* has only one stylid cusp (Fig. 27).

Platyrrhinus nigellus (Gardner and Carter, 1972)

Vampyrops nigellus Gardner and Carter, 1972a. Type locality: Huanhuachayo, Department of Ayacucho, Peru.

HOLOTYPE—*Vampyrops nigellus* LSUMZ 16415, adult male, preserved as skin and skull, was collected by A. L. Gardner (original field number ALG 11684) on 6 May 1971 at Huanhuachayo, Department of Ayacucho, Peru, elevation 1660 m.

DISTRIBUTION—Along the Andes from western Venezuela south to Colombia, Ecuador, Peru, and Bolivia, from 620 to 2757 m (Fig. 28).

DIAGNOSIS—Size medium (FA = 40–47 mm; CIL = 21.9–24.5 mm; W = 19–30 g; Table 3); facial stripes darker; absence of a basal protuberance, where the genal vibrissae are implanted; postorbital process moderately developed; paraoccipital process moderately developed; a deep fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa; m1 metaconid poorly developed.

Platyrrhinus recifinus (Thomas, 1901)

Vampyrops recifinus Thomas, 1901. Type locality: Recife, State of Pernambuco, Brazil.

HOLOTYPE—*Vampyrops recifinus* BMNH 81.2.16.4, adult male, preserved in alcohol with the skull removed and cleaned, was collected by W. A. Forbes at Recife, State of Pernambuco, Brazil.

DISTRIBUTION—Eastern Brazil, elevation 200 m (Fig. 28).

DIAGNOSIS—Size small to medium (FA = 42–43 mm; CIL = 22.0–22.6 mm; W = 17–19 g; Table 3); *interramal vibrissae absent*; *dorsal fur tetracolored*; dense and long hair on the dorsum of the feet; *an almost imperceptible fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa*; *a deep fossa on the hypoconal basin of P4*; *stylid cusp absent between the metaconid and the protoconid of m2.*

Platyrrhinus vittatus (Peters, 1860)

Artibeus vittatus Peters, 1860. Type locality: Puerto Cabello, State of Carabobo, Venezuela.

HOLOTYPE—*Artibeus vittatus* ZMB 568, adult male, preserved in alcohol with the skull removed and cleaned, was collected by von Appun at Puerto Cabello, State of Carabobo, Venezuela.

DISTRIBUTION—Costa Rica, Panama, western and northern Colombia, and northern Venezuela, from 640 to 1400 m (Fig. 28).

DIAGNOSIS—Size large (FA = 57–61 mm; CIL = 28.1–31.3 mm; W = 60–65 g; Table 3); *par-*

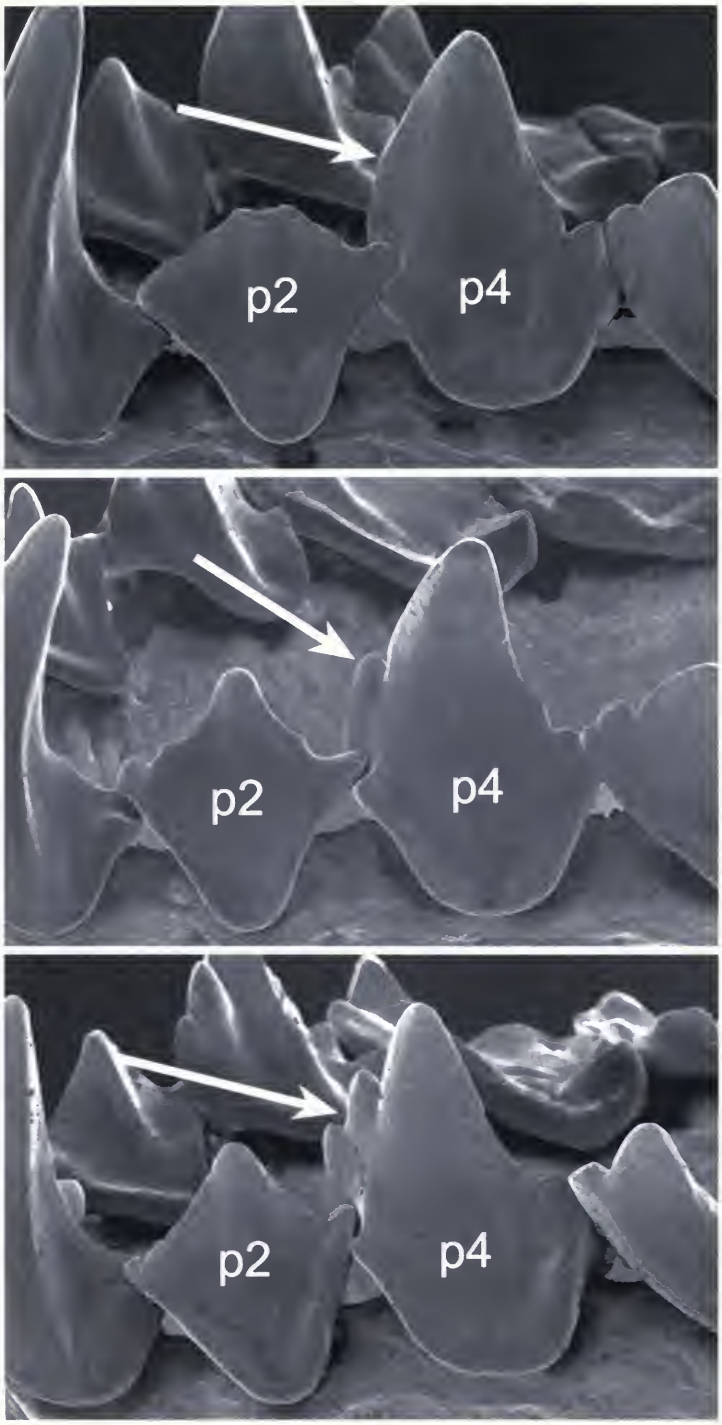

FIG. 27. Labial views of the left p2 and p4 illustrating taxonomic differences in the number of stylid cusps on the anterior face of the main cone of p4. (**Top**) *Platyrrhinus matapalensis* (FMNH 81079) lack stylid cusps (arrow). (**Center**) *Platyrrhinus helleri* (FMNH 127127) with one stylid cusp present (arrow). (**Bottom**) *Platyrrhinus brachycephalus* (FMNH 139584) with two stylid cusps present (arrow).

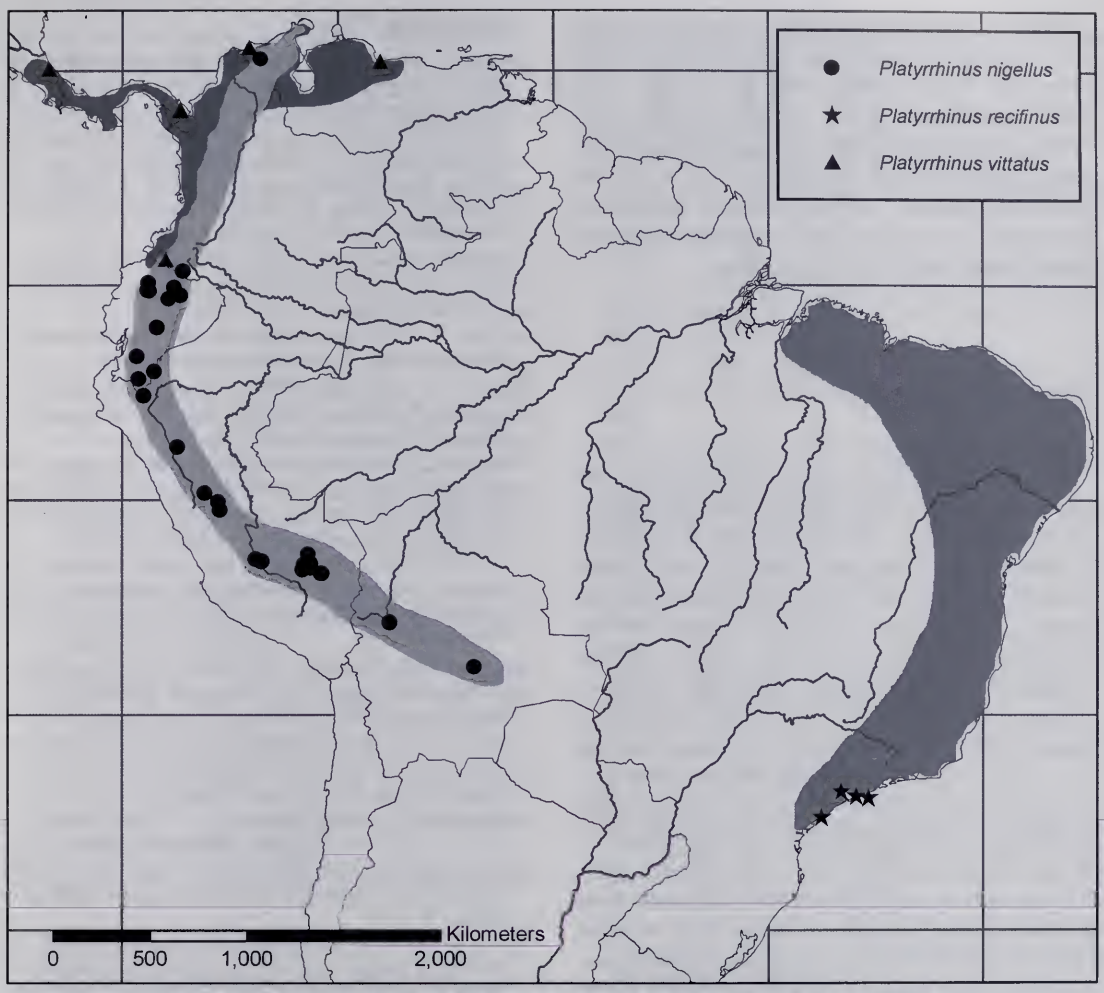

FIG. 28. Distributional map of *Platyrrhinus nigellus, P. recifinus,* and *P. vittatus.*

allel folds in the pinna well marked; dorsal stripe brilliant-white and wide; *fringe of hair on the edge of the uropatagium usually hairy, occasionally sparsely*; *paraoccipital process moderately developed*; one stylid cusp present on the anterolingual face of the main cone of p4. In older individuals (AMNH 15100–15101, 34232; ZMB 568 [Holotype]) with a moderate degree of tooth wear, this stylid cusp appears as a nub on the anterolingual face of the main cone.

COMMENTS—In his systematic review of *Platyrrhinus* from northwestern South America, Alberico (1990) identified *Platyrrhinus* sp. B as a potentially new species from Colombia. *Platyrrhinus* sp. B (FA = 56.9–59.4 mm) was collected only at the northern end of the Andes in Colombia, in the Department of Antioquia at 500 m; this taxon shows the same range of variation in FA size as *P. vittatus* (sensu this paper) and was found within the geographic range of *P. vittatus.* Some populations of *P. vittatus* (sensu Alberico, 1990) belong to *P. albericoi,* suggesting that *Platyrrhinus* sp. B is conspecific with *P. vittatus.*

From the three potentially new species identified by Alberico (1990), two are conspecific with *Platyrrhinus ismaeli* and *P. vittatus*; the third probably constitutes a new species. *Platyrrhinus* sp. A (FA = 53.0–57.0 mm) is found along the western base of the western Andes of Colombia from the department of Chocó, south almost to the Department of Nariño, from 230 to 1000 m in elevation. Based on both geographical range and FA size, this taxon does not overlap with any of the other 14 *Platyrrhinus* taxa.

Commonly, between 8 and 10 nominal species are recognized for *Platyrrhinus* (Alberico, 1990; Ferrell & Wilson, 1991; Jones & Carter, 1976, 1979; Koopman, 1993, 1994; Nowak, 1999; Owen, 1987; Swanepoel & Genoways, 1979). Based on the results obtained in this work, the genus *Platyrrhinus* contains at least 14 species. Therefore, it currently ranks as the most speciose genus in the family Phyllostomidae.

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Appendix 1: Specimens Examined

The following list includes all specimens examined in this study, with their respective localities. See Materials and Methods for abbreviations. Individuals or series marked with an asterisk were used in the elaboration of the Tables 2 to 7.

Platyrrhinus albericoi: **Ecuador:** Pichincha, Nanegal, Gavilán de Orongo (QCAZ 1979, 2003); **Peru:** Ayacucho, Yuraccyacu (MUSM 993); Cuzco, La Convención, Kimbiri, Camp. Wayrapata (MUSM 14599); Cuzco, La Convención, Kimbiri, Camp. Llactahuaman (FMNH 177477, MUSM 14583–14584, 14586, 14588–14589); Cuzco, Paucartambo, San Pedro (MUSM 19149*); Cuzco, Paucartambo, Suecia, km 138.5 Carretera Shintuya (FMNH 170145*); Cuzco, Paucartambo, Pillahuata (FMNH 172108); Pasco, Oxapampa, Pozuzo, Palmira (MUSM 10973).

Platyrrhinus aurarius: **Guyana:** Potaro-Siparuni, Mount Ayanganna, Toe Slope Camp (ROM 114679*); Potaro-Siparuni, Mount Ayanganna, First Plateau Camp (ROM 114702*); **Venezuela:** Amazonas, Cerro de la Neblina, Base del Pico Maguire (FMNH 137294–137298*, 137299–137303, 137304–137307*, 137308–137311); Amazonas, Cerro de la Neblina, Left Bank del Río Baria (FMNH 137312, 137313*); Amazonas, 3½ km W Pico Zuloaga (AMNH 261225–261229); Bolívar, Cerro Guaiquinima (AMNH 235339–235342); Bolívar, La Escalera (AMNH 265572–265584).

Platyrrhinus brachycephalus: **Bolivia:** Cochabamba, 4 km SE Villa Tunari (UMMZ 126755); El Beni, Itenez, Buenavista (FMNH 115012*); El Beni, Mamore, San Joaquin (FMNH 96092*, 115016–115018*); El Beni, Vaca Diez, La Esperanza (FMNH 115003*, 115005*); La Paz, Santa Ana de Madidi (AMNH 262353); Pando, Santa Rosa (AMNH 262520); **Brazil:** Amazonas, Tabatinga (AMNH 170623); **Colombia:** Arauca, Río Arauca (FMNH 92302–92303, 92326*, 92327); Meta, La Macarena Parque, Refugio (FMNH 58739*); Meta, Villavicencio (AMNH 207872–207873, 207875); Meta, Villavicencio, Finca El Buque (FMNH 121261*); Putumayo, Estación de Bombeo, Guamues (FMNH 113657); Putumayo, San Antonio, Río Guamues (FMNH 114018–114020); **Ecuador:** Napo, Marian (FMNH 124990*); Napo, San José (AMNH 64033); Napo, San Jose de Payamino (FMNH 124991–124992*); Napo, Zancudo (FMNH 124985–124986*); Orellana, Cantón Aguarico, Pozo Exploratorio PCSA-2 (EPN 985199, 985201); Pastaza, Sarayacu (AMNH 67649); **French Guiana:** Cayenne (FMNH 21745–21746); **Peru:** Amazonas, Condorcanqui, Santa Rosa de Nieva (MUSM 12789); Amazonas, San Juan (Bagua Grande) (MUSM 1010); Cuzco, La Convención, Camisea, Armihuari (MUSM 13770, 13774–13775, 13778–13779, 13786, 13808); Cuzco, La Convención, Camisea, Cashiriari (MUSM 13788–13790, 13821, 13833); Cuzco, La Convención, Kiteni (MUSM 1012; UMMZ 160637); Cuzco, La Convención, Camisea, Konkariari (MUSM 14788); Cuzco, La Convención, Camisea, Pagoreni (MUSM 13791–13792); Cuzco, La Convención, Camisea, San Martín (MUSM 13793–13794, 13844); Cuzco, La Convención, Camisea, Segakiato (MUSM 14793); Cuzco, Paucartambo, Consuelo, km 165, 17 km by road W Pilcopata (FMNH 123920*, 123923*); Cuzco, Quispicanchi, Collpa de San Lorenzo (FMNH 93580*, 93582–93585*); Cuzco, Quispicanchi, Huajyumbe (FMNH 84381*); Huánuco, Leoncio Prado, Tingo Maria, Río Azul (FMNH 98008*); Loreto, Alto Amazonas, Río Morona, Quebrada Pushaga (FMNH 89091*); Loreto, Alto Amazonas, Yurimaguas (FMNH 19651*); Loreto, Quebrada Sucusari, Camp. Explornapo (MUSM 6750); Loreto, Requena, Jenaro Herrera (MUSM 5927); Loreto, Loreto, Río Samiria, Base Atun (FMNH 122874–122876*, 122878*); Loreto, Loreto, Río Tigre, 1 km above Río Tigrillo (FMNH 122880*); Loreto, Mariscal Ramon Castilla, Río Amazonas, mouth of Río Peruate (FMNH 89096*); Loreto, Mariscal Ramon Castilla, Río Yavari Mirim, Quebrada Esperanza (FMNH 89095*); Loreto, Maynas, Río Nanay, Santa Luisa (FMNH 87074*); Madre de Dios, Albergue Río Madre de Dios, 12 km E Puerto Maldonado (MUSM 1013); Madre de Dios, Manu, Alto Río Madre de Dios, Haci-

enda Amazonia (FMNH 139639*, FMNH 125930*, 125938*; MUSM 8850); Madre de Dios, Hacienda Erika, Río Alto Madre de Dios, opposite Salvación (UMMZ 160636, 160638); Madre de Dios, Reserva Cuzco Amazónico, 15 km NE Puerto Maldonado (MUSM 6268–6270, 7150); Madre de Dios, Manu, Pakitza (MUSM 6769, 12558, 12560, 12562, 12564); Madre de Dios, Manu, Río Palotoa (MUSM 9844); Madre de Dios, Manu, Río Palotoa, left bank, 12 km upstream from mouth (FMNH 139581*, 139584–139585*, 139587*); Madre de Dios, Río Tambopata (MUSM 191); Madre de Dios, Río Tambopata, Explorer's Inn (MUSM 1002, 1006–1007); Pasco, Oxapampa, Huancabamba, Comunidad Nativa Castillo (MUSM 394–396, 398, 400, 430, 496–499); Puno, Carabaya, Coasa, mouth of Quebrada Ursulinda with the Río Candamo (MUSM 15882); Ucayali, Coronel Portillo, Pucallpa (FMNH 64316–64317*); Ucayali, Coronel Portillo, Yarinacocha (FMNH 98009*); Ucayali, Padre Abad, B. N. von Humboldt (MUSM 8527); **Suriname:** Nickerie, Wageningen (UMMZ 175688); Paramaribo, Peu Et Contant (UMMZ 175768); **Venezuela:** Tachira, San Juan de Colon (FMNH 21117*).

Platyrrhinus chocoensis: **Colombia:** Cauca, Alto Micay, Betania (FMNH 113745*, 113822–113823, 113825–113927, 113830–113832); Cauca, Quebrada Guangui (AMNH 235774–235779); Chocó, Quebrada Docordo (AMNH 233186–233187); Valle del Cauca, Concesión Bajo Calima, Cuartel BV83 (FMNH 140696–140697*); Valle del Cauca, Zabaletas (FMNH 85838; UMMZ 169039–169040, 169048); **Ecuador:** Esmeraldas, Borbón, Río Cayapas, Community of Zapote (QCAZ 2063); Esmeraldas, Borbón, Río Cayapas, Community of Viruela (QCAZ 2175); Esmeraldas, San Lorenzo, Estación La Chiquita (QCAZ 2375, 2378, 3281–2382); Esmeraldas, 3 km S San Miguel (EPN 84361).

Platyrrhinus dorsalis: **Colombia:** Cauca, Alto Micay, Betania (FMNH 113372, 113380, 113385, 113394–113396, 113821*, 113824*, 113828–113829*, 113831*, 113833–113835*); Cauca, Charguayaco (FMNH 113538–113539*); Cauca, Popayán (FMNH 90327*); Huila, Las Cuevas Parque, Upper Cabana (FMNH 58740*); La Guajira, San Antonio (MCZ B-8300); Magdalena, Palomino (MCZ B-8301); Valle del Cauca, El Silencio (UMMZ 169038); **Ecuador:** Carchi, Pailón, NW Parroquia de Chical (EPN 871732, 871748, 871778, 871843–871848, 871868); Carchi, Parroquia Tobar Donoso, El Pailón (EPN 871747, 871765); Esmeraldas, Borbón, Río Cayapas, Río Chimbocal, Comuna Corriente Grande (QCAZ 2157); Esmeraldas, Eloy Alfaro, Pichiyacu, Río Cayapas, upstream Borbón (QCAZ 1468); Pichincha, Nanegal (QCAZ 1975); Pichincha, Tambillo, 25 km S Quito (EPN 7465, 7467); **Panama:** Darien, Parque Nacional Darien, Rancho Frio (FMNH 128141*).

Platyrrhinus helleri: **Belize:** Cayo district, Banana Bank (FMNH 58264*); Cayo district, Banana Bank Ranch (FMNH 58265–58268*); Cayo district, Macaw Bank (FMNH 106804*); Toledo district, Columbia Forest Preserve, Forestry Camp (FMNH 58270*); Toledo district, Columbia Forest Preserve, Mahogany Plant, N Forestry Camp (FMNH 58269*); Toledo district, Forest Home (FMNH 128073*); **Bolivia:** Beni, 6 km W Casarabe (AMNH 255919, 255921–255922, 255927); Beni, Gral. José Ballivián, Serrania Pilon, 27 km N Río Quiquibey by road to San Borja (AMNH 261058, 261062, 261064–261069, 261071–261074); Beni, Itenes, Buenavista (FMNH 115001*, 115009–115011*, 115012, 115013*); Beni, Mamore, San Joaquín (FMNH 96092, 115002, 115006, 115007–115008*, 115016–115018, 115019*); Beni, opposite Costa Marques, Brazil (AMNH 209502); Beni, Puerto Almacén (AMNH 255909, 255912); Beni, Vaca Diez, La Esperanza (FMNH 115003–115005, 115014*); Cochabamba, 3 km SW Villa Tunari (AMNH 244629–244630); Cochabamba, 50 km NW Villa Tunari (UMMZ 126754, 126756); La Paz, Santa Ana de Madidi (AMNH 261628–261631, 261634–261639, 261642–261647, 262351, 262354–262355); La Paz, Sararia, 2 hr (river) NW Puerto Linares (UMMZ 126757–126758); Pando, La Cruz (AMNH 262507); Pando, Las Piedras (AMNH 262514); Pando, Río Nareuda (AMNH 248880, 249062); Pando, Santa Rosa (AMNH 262518, 262522–262523); Pando, W Bank Río Beni, opposite Hamburgo (AMNH 262510) ; Santa Cruz, 23 km S Camp Los Fierros, Parque Nacional Noel Kempff Mercado (AMNH 264068–264070); Santa Cruz, 4.5 km N Buen Retiro (AMNH 260228); Santa Cruz, Camp Los Fierros (AMNH 263616); Santa Cruz, Estancia Cachuela Esperanza (AMNH 260219–260221, 260223–260224, 260226–260227); Santa Cruz, San Rafael de Amboro (AMNH 261663, 262350); **Brazil:** Pará, Belém, Mocambo/Embrapa (FMNH 126601*, 126602, 126603*, 126604–126605, 126606*); Rondônia, Pedras Negras (AMNH 209517); **Colombia:** Cauca, Alto Micay, Betania (FMNH 113321, 113330, 113344, 113348,

113883–113884, 113885*, 113886, 113887–113889*, 114023–114026); Cauca, Quebrada Guangui (AMNH 235780–235788); Cauca, Río Saija, Quebrada Huanqui (FMNH 104841, 104843); Chocó, Quebrada Docordo (AMNH 233188); Cundinamarca, Mesitas de Colegio (AMNH 207863, 207871); Cundinamarca, Sasaima (FMNH 49156*); Magdalena, Cacagualito (FMNH 13202*); Meta, Villavicencio (FMNH 121262*); Valle del Cauca, Río Zabaletas (UMMZ 168982–168984, 168987, 168993–168995, 168999); **Costa Rica:** Alajuela, Guayabo (FMNH 18045–18046*); Guanacaste, Guanacaste 2 km S, 12 km E Bolson (FMNH 123152); Puntarenas, 2 km S San Vito, Finca Las Cruces (FMNH 123153); Puntarenas, Dominical (UMMZ 112024, 112031); **Ecuador:** Napo, Estación La Selva, 85 km SE Coca (QCAZ 2518–2519); Napo, Orellana, Comuna Indillana, mouth of Río Indillana and Río Napo, P. N. Yasuní (QCAZ 969); Pastaza, Río Cushueme, Cushueme, 150 km SE Puyo (FMNH 104753, 104759); **Guatemala:** Alta Vera Paz, Los Rápidos (AMNH 214242); Peten, Tikal National Park (FMNH 58584*); Santa Rosa, Avellana (AMNH 243774, 243923); Santa Rosa, 13 km N Avellana, Finca Camalote (AMNH 243775); Santa Rosa, 2 km ESE Ixpaco (AMNH 244337); Santa Rosa, 5 km N Avellana, Chiquihuitan (AMNH 245325); **Honduras:** Cortes, Santo Domingo, aprox. 5.5 km ESE Cuyamel (AMNH 265119–265120); Lempira, Tepusuna (FMNH 47615–47616*); **Mexico:** Oaxaca, Tutla (FMNH 51856*); Veracruz, Tuxtla Mts (FMNH 127127–127130*); Veracruz, Tuxtla Mts, 0.5 km E cerro Balzapote (FMNH 127115–127120*, 127125–127126*, 127131–127132*, 127134–127136*); Veracruz, Tuxtla Mts, 0.5 km W cerro Balzapote (FMNH 127121–127124*); **Panama:** Darién, Cana (LSUMZ 25485–25486*); **Peru:** Amazonas, Bongara, Río Utcubamba, between Churuja and Pedro Ruiz (FMNH 129149–129150*; MUSM 4950–4952); Amazonas, Luya, Río Utcubamba, 11 km by road NW Pedro Ruiz (FMNH 129152–129153*); Cuzco, La Convención, Camisea, Armihuari (MUSM 13799, 13803, 13807); Cuzco, La Convención, Camisea, Cashiriari (MUSM 13811, 13824–13825); Cuzco, La Convención, Camisea, Las Malvinas (MUSM 14794); Cuzco, La Convención, San Martín (MUSM 13846–13847, 13849); Cuzco, Quispicanchi, Collpa de San Lorenzo (FMNH 93586–93587*); Junín, Alto Yurinaqui (MUSM 1009); Loreto, Mariscal Ramon Castilla, Río Yavari Mirim, Quebrada Esperanza (FMNH 89094*); Loreto, Maynas, Río Nanay, Santa Luisa (FMNH 87080*); Loreto, Requena, Jenaro Herrera (MUSM 871, 4217, 5526, 5598, 5928); Loreto, Requena, Jenaro Herrera, 1.4 km N Centro de Investigación Jenaro Herrera (MUSM 5500); Loreto, Río Yarapa, Albergue Yacumana, SE Iquitos (MUSM 9434); Madre de Dios, Albergue, Río Madre de Dios, 12 km E Puerto Maldonado (MUSM 1008); Madre de Dios, Manu, Aguas Calientes, Río Alto Madre de Dios, 1 km below Shintuya (UMMZ 160635); Madre de Dios, Manu, Hacienda Amazonia (FMNH 125951*, 139631*; MUSM 8855, 9863–9864); Madre de Dios, Manu, Pakitza (MUSM 6768, 12555–12557, 12559, 12563, 12565–12575); Madre de Dios, Manu, Río Palotoa (MUSM 9884); Madre de Dios, Manu, Río Palotoa, left bank, 12 km upstream from mouth (FMNH 139648*); Madre de Dios, Río Tambopata, Explorer's Inn (MUSM 1003); Pasco, Oxapampa, Pozuzo (MUSM 10942, 10946); Pasco, Villa América (MUSM 1005); Ucayali, Padre Abad, Bosque Nacional Alexander von Humboldt (MUSM 8633–8636, 8528–8531); **Trinidad and Tobago:** Saint George, Arima Valley (AMNH 149624); Saint George, Chaguaramas, U.S. Naval Station (AMNH 183164); Saint George, Maracas Valley, Water Fall road (AMNH 176283); Saint George, Port of Spain, Saint Clair, 2 Scott (AMNH 176284); Saint George, 4 mi by road N Arima (AMNH 246222–246224); Saint Patrick, Point Fortin (AMNH 183858–183859); **Venezuela:** Aragua, Rancho Grande (AMNH 144386); Guarico, 8 km N 13 km W San José de Guaribe (AMNH 247644); Tachira, San Juan de Colón (FMNH 20539–20540*); Zulia, 9 km N Rio Catatumbo (AMNH 244039); Zulia, Puerto Delicias (AMNH 244038).

Platyrrhinus infuscus: **Bolivia:** Beni, Gral. José Ballivián, Serranía Pilón, 27 km by road N Río Quiribay (AMNH 261076); Cochabamba, 4 km SE Villa Tunari (UMMZ 126761); La Paz, 6.6 km downstream Canavari, Valle del Río Coroico (AMNH 246621); La Paz, Serrania Bellavista, 35 km N Canavari (AMNH 246622–246623); Pando, Río Nareuda (AMNH 248882–248883); Santa Cruz, 3 km N and 13.5 km W San Rafael de Amboro, Río Saguayo (AMNH 261623); Santa Cruz, San Rafael de Amboro (AMNH 261664); **Colombia:** Meta, La Macarena Parque, Camp. Izawa (FMNH 58741*, 58745*); Meta, La Macarena Parque, Cano, Refugio Cabana (FMNH 58742–58743*, 58744); Meta, La Macarena Parque, Cano Cabana, Cabana Duda (FMNH 58746*); Meta, La Macarena Parque, Refugio (FMNH

58747*); Meta, Villavicencio, Villavicencio (FMNH 51733*); Meta, Villavicencio, Small Cano (FMNH 58748); Putumayo, Estación de Bombeo, Guamues (FMNH 113699, 113752, 113898); Putumayo, San Antonio, Río Guamues (FMNH 113413, 113415, 113417, 113899–113900, 114128–114129); Putumayo, Río Mecaya (FMNH 71525, 72123*); **Ecuador:** Napo, Loreto, P. N. Napo-Galeras, W side, line 28 (QCAZ 1533–1534); Napo, Loreto, P. N. Napo-Galeras, W side, line 30 (QCAZ 1406–1407); Napo, Río Cotapino, Oriente (FMNH 47587*); Napo, Río Suno (AMNH 67929); Napo, San José (AMNH 67907–67912, 67918–67919, 67922, 67925–67926); Napo, San José de Payamino (FMNH 124989*); Pastaza, Montalvo, (FMNH 41429*); Pastaza, Río Copotaza (FMNH 53503*); Pastaza, Río Pindo Yaco (FMNH 43137–43139*); Sucumbíos, Gonzalo Pizarro, Los Cedros, Bosque, 10 km S Lumbaquí (QCAZ 521–523); Tungurahua, Baños, Oriente (FMNH 47588*); Tungurahua, Palmera (AMNH 67658–67664); **Peru:** Amazonas, 43 km NE Chiriaco (MUSM 143); Amazonas, Luya, Río Utcubamba, 15 km by road NW Pedro Ruiz (FMNH 129158–129159*, 129161*; MUSM 4953–4954); Cuzco, La Convención, Camisea, Armihuari (MUSM 13850); Cuzco, La Convención, Camisea, Pagoreni (MUSM 13858–13859); Cuzco, La Convención, Camisea, San Martín (MUSM 13862); Cuzco, La Convención Camisea, Segakiato (MUSM 14798); Cuzco, Paucartambo, Consuelo, km 165, 17 km by road W Pilcopata (FMNH 123931–123932*; MUSM 9923–9924); Cuzco, Paucartambo, Tono, 5 km S Río Tono and 18 km W Patria (MUSM 9950); Cuzco, Quispicanchi, Collpa de San Lorenzo (FMNH 93545*); Cuzco, Quispicanchi, Hacienda Cadena (FMNH 68447*, 68449*, 78691–78692*, 78694*); Cuzco, Quispicanchi, Huajyumbe (FMNH 68450–68454*, 75153–75154*, 78693*, 84406*); Cuzco, Quispicanchi, San Juan Grande (FMNH 75155–75156*); Junín, Alto Yurinaqui (MUSM 994); Junin, Chanchamayo, Tarma, Vitoc Valley (FMNH 51525*); Loreto, Mouth of Río Curaray (AMNH 71696–71701, 71708); Loreto, Loreto, Río Tigre, 1 km above Río Tigrillo (FMNH 122902*); Madre de Dios, Hacienda Erika, Río Alto Madre de Dios opposite Salvación (UMMZ 160628–160629); Madre de Dios, Manu, Río Alto Madre de Dios, Hacienda Amazonia (FMNH 125990*, 126010*, 126019*, 139663–139665*, 139674*, 139676*, 139685*, 139695–139696*, 139700–139702*, 139710*; MUSM 994, 9847, 9897, 9902–9904, 9910, 9928); Madre de Dios, Manu, Aguas Calientes, Río Alto Madre de Dios, 1 km below Shintuya (UMMZ 160630–160632); Madre de Dios, Manu, Cerro de Pantiacolla (FMNH 122134*, 139737*, 139739–139742*, 139745*, 139748–139749*; MUSM 9918, 9920–9921); Madre de Dios, Manu, Itahuania (FMNH 84405*); Madre de Dios, Manu, Pakitza (MUSM 12576); Madre de Dios, Reserva Cuzco Amazónico, 15 km NE Puerto Maldonado (MUSM 6272–6273); Pasco, Oxapampa, Pozuzo (MUSM 10960, 10969); Pasco, Oxapampa, Pozuzo, Palmira (MUSM 10941, 10947); Puno, Carabaya, Coasa, mouth of Quebrada Ursulinda with Río Candamo (MUSM 15824); Ucayali, Affluent of Mamanchita (MUSM 370).

Platyrrhinus ismaeli: **Colombia:** Huila, Las Cuevas Parque, Cueva India (FMNH 58733–58735*, 58737–58738*); Huila, Cuevas de los Guacharos National Park, 225 m W Upper Cabaña (IND 1993*); Huila, Cuevas de los Guacharos National Park, Entrance to Indian Cave (IND 2244*); Huila, Cueva de Los Guacharos National Park, on top Guacharos Cave (IND 2308*); Huila, Cuevas de los Guacharos National Park, Upper Bridge on Río Suaza (FMNH 58732*, 58736*); **Ecuador:** Azuay, Hacienda Sector de Challtapac, close to Río Girón (QCAZ 2237); Loja, Loja, San Pedro de Vilcabamba, 3 km N Vilcabamba (QCAZ 1171–1174, 1177, 1180); Morona Santiago, San José Alto, Cantón Paute, Río San Vicente (EPN 912940); Napo, Loreto, P. N. Napo-Galeras, W side, line 28 (QCAZ 1291); Napo, San Rafael Cascada (FMNH 124988*); **Peru:** Amazonas, 19 km E Balsas (FMNH 129133–129134*, 129136–129137*; MUSM 4944–4945, 4946*); Cajamarca, 12 km SSW by road to San Miguel (MUSM 4949); Cajamarca, Celendin, Hacienda Limón, W Balsas (FMNH 129139*, 129143*, 129145–129146*; MUSM 4947–4948); Cajamarca, San Ignacio (MUSM 12884–12889); Lambayeque, Ferreñafe, Bosque Chiñama (MUSM 925–926); Piura, Ayabaca, ca. 44 km ESE by road from Ayabaca, ladera Cerro Mayordomo (MUSM 996–998); San Martín, Huallaga (MUSM 16167–16169); San Martín, La Playa, 28 km NE Pataz (MUSM 7283); San Martín, Las Palmas, 32 km NE Pataz (MUSM 7285–7293); San Martín, Las Papayas (MUSM 7294).

Platyrrhinus lineatus: **Bolivia:** Beni, Río Mamoré (AMNH 210805–210807, 210809); Beni, Río Tijamuchi (AMNH 262352); Santa Cruz, 4 km N and 1 km W Santiago de Chiquitos (AMNH 260231); Santa Cruz, 12 km S and 8 km E Santa

Cruz (AMNH 255931–255932); Santa Cruz, Cercado, Cercado (FMNH 50990*); Santa Cruz, Chiquitos, Santiago (FMNH 105844–105862*, 105899–105908, 105909*, 105910–105913); Santa Cruz, Chiquitos, 3 km S and 3 km W Santiago de Chiquitos (AMNH 261042–261052, 261054–261056); Santa Cruz, Roboré (AMNH 260232–260233); Santa Cruz, Santa Rosa de la Roca (AMNH 263618); **Brazil:** Bahia, Município de Valença, Guaibim (MVZ 185601); Ceará, Serra de Ibiapaba (FMNH 19516); Espírito Santo, Município de Santa Teresa, Estação Biológica Santa Lúcia (MVZ 185602); Mato Grosso do Sul, Belvedere de Urucum de Corumbá (AMNH 37019–37021); Mato Grosso do Sul, Maracajú (AMNH 134923–134926); Mato Grosso do Sul, Rio Vacaria, Fazenda Capão Bonito (FMNH 47963–47966, 47968–47977, 47980, 47983–47994, 48008); Mato Grosso do Sul, Urucum (AMNH 36993–37002, 37004–37005, 37007–37018, 39017–39019, 39026–39029; FMNH 26775, 26777–26781*, 26783–26784*, 30032–30048); Paraíba, João Pessoa, Mata do Buraquinho (MVZ 185596); Pernambuco, Município de Tamandaré, Coqueiral just outside S border Ibama headquarters at Tamandaré (MVZ 185598); Rio de Janeiro, Município Duas Barras, Town Duas Barras, Garden at house of Mario & Tereza Habib (MVZ 185603); São Paulo, São Paulo, (AMNH 207091); São Paulo, Valparaíso (FMNH 41645*); **Paraguay:** Alto Paraguay, Fuerte Olimpo (FMNH 145258*); Alto Paraguay, W Bank Río Paraguay, Estancia Puerto Ramos, 5 km SSE Bahía Negra (AMNH 265411–265413); Canendiyu, Igatimi, (AMNH 234285); Central, Asunción, District Catedral (AMNH 205183–205185); Central, Asunción, Recoleta (AMNH 248311–248325, 248503; UMMZ 124321–124332, 125422–125443, 125876–125877, 125879–125901, 133734); Guairá, villarrica (AMNH 148662–148666); Itapúa, Trinidad (AMNH 36523); La Cordillera, 1.6 km by road S Tobatí (UMMZ 125878); Paraguarí, Parque Nacional Ybycuí (UMMZ 133732); Paraguarí, Saltos de Pirareta (UMMZ 133733); Paraguarí, Sapucai (AMNH 23770–23773; FMNH 48791*).

Platyrrhinus masu: **Bolivia:** Cochabamba, 50 km NW Villa Tunari (UMMZ 126759–126760); La Paz, Serranía Bellavista (AMNH 246610–246614); La Paz, Serranía Bellavista, 47 km by road N Caranavi (UMMZ 158068); **Peru:** Cuzco, 3 km E Amaybamba (MUSM 989–992); Cuzco, La Convención, Kimbiri, Camp. Llactahuaman (MUSM 14559–14560, 14562*, 14565, 14566*); Cuzco, La Convención, Kimbiri, Camp. Wayrapata (MUSM 14568, 14570, 14572); Cuzco, La Convención, Río Urubamba, Kiteni (MVZ 166595*); Cuzco, Paucartambo, 72 km by road NE Paucartambo (UMMZ 160627, 160633); Cuzco, Paucartambo, Challabamba, P. V. Acjanaco (FMNH 170112*; MUSM 8851); Cuzco, Paucartambo, Consuelo, km 165, 17 km by road W Pilcopata (FMNH 123917*; MUSM 9854); Cuzco, Paucartambo, La Esperanza (FMNH 174759*, 174760); Cuzco, Paucartambo, Pillahuata (MUSM 11793, 11794, 11795*); Cuzco, Paucartambo, Quitacalzon, Carretera Paucartambo-Pilcopata km 163 (MUSM 8852); Cuzco, Paucartambo, San Pedro (FMNH 172100* ; MUSM 8853–8854, 11792); Cuzco, Paucartambo, Suecia, km 138.5 road to Shintuya (FMNH 170113*); Cuzco, Quispicanchi, Camante (FMNH 68455*); Cuzco, Quispicanchi, Collpa de San Lorenzo (FMNH 93594*); Cuzco, Quispicanchi, Hacienda Cadena (FMNH 93588*); Madre de Dios, Manu, Cerro de Pantiacolla (FMNH 122136*); Madre de Dios, Manu, Cerro de Pantiacolla, upstream Río Palotoa (FMNH 139597–139599*, 139601–129603*, 139606–139607*; MUSM 9849–9853, 9868, 9966); Madre de Dios, Manu, Río Alto Madre de Dios, Hacienda Amazonia (FMNH 139590–139591*, 139593*; MUSM 9848); Huánuco, Huánuco, Chinchao, Cordillera de Carpish (MUSM 18265*, 18266*); Pasco, Oxapampa, San Alberto (MUSM 10272–10273); Pasco, Pasco, Paucartambo, Auquimarca, Anexo Santa Isabel (MUSM 15881–15884).

Platyrrhinus matapalensis: **Ecuador:** Bolívar, Barraganete, 3 km SW Echeandía (EPN 80.4.1, 80458); Esmeraldas, Borbón, Río Cayapas, Río Chimbocal, Comuna Corriente Grande (QCAZ 2155); Esmeraldas, Borbón, Río Cayapas, Community of Zapote (QCAZ 2066); Esmeraldas, Comunidad Valle del Sade, 8 km E mouth of the Río Sade in the Río Esmeraldas (EPN 85904); Esmeraldas, Eloy Alfaro, Borbón, Río Santiago, Estero María, Comuna Selva Alegre (QCAZ 1921); Esmeraldas, Eloy Alfaro, San Miguel, Río Cayapas, R. E. Cotacachi-Cayapas (QCAZ 508); Guayas, Naranjal, La Unión (QCAZ 2124); Guayas, El Triunfo, El Piedrero (QCAZ 2624); Los Ríos, Quevedo, Río Palenque (QCAZ 509); Pichincha, Nanegal, Chacapata, Recinto Playa Rica (QCAZ 1900); **Peru:** Tumbes, Zarumilla, Z.R. Tumbes, Quebrada Los Naranjos, Campo Verde (MUSM 10725–10726*); Tumbes, Zarumilla, Matapalo (FMNH 81079–81081*).

Platyrrhinus nigellus: **Bolivia:** La Paz, 20 km

NNE Caranavi (UMMZ 127174); La Paz, Serranía Bellavista, 35 km N Canavari (AMNH 246616–246620); Santa Cruz, 4.5 km N and 1.5 km E Cerro Amboro, Río Pitasama (AMNH 261665); **Colombia:** Cesar, San Sebastián (FMNH 69484*); Nariño, El Carmen (FMNH 113891–113892, 113894–113897); **Ecuador:** Azuay, Valle Yunguilla (FMNH 53504*); Loja, Loja, Masanamaca, 12 km S Vilcabamba (QCAZ 1210); Morona Santiago, P. N. Sangay Sardinayacu (EPN 964718); Napo, Loreto, P. N. Napo-Galeras, W side, line 28 (QCAZ 1525); Napo, Loreto, P. N. Napo-Galeras, W side, line 30 (QCAZ 1388–1389); Napo, San Rafael Cascada (FMNH 124987*); Napo, Tena, Atacapi, Cordillera de Los Guacamayos (QCAZ 1264); Pichincha, Nanegal, Gavilán de Orongo (QCAZ 1974); Pichincha, Estación Forestal La Favorita, close to Chiriboga (EPN 799–10); Pichincha, Reserva Río Guajalito (QCAZ 3159); **Peru:** Amazonas, Cordillera del Cóndor (MUSM 10628); Ayacucho, Huanhuachayo (AMNH 233644–233684); Cajamarca, San Ignacio (MUSM 12890–12892); Cuzco, La Convención, Kimbiri, Camp. Wayrapata (MUSM 14579*); Cuzco, La Convención, Kimbiri, Camp. Llactahuamán (MUSM 14561, 14575*, 14576–14578); Cuzco, Paucartambo, Bosque de las Nubes, km 150 by road Paucartambo-Pilcopata (MUSM 8857); Cuzco, Paucartambo, Consuelo, km 165 by road Paucartambo-Shintuya (FMNH 123947*, 174777*, 174779*, 174781*, 174783*; MUSM 9970–9971, 9975); Cuzco, Paucartambo, Quitacalzón, road Paucartambo-Pilcopata km 163 (MUSM 8858, 8860); Cuzco, Paucartambo, San Pedro (MUSM 11796); Cuzco, Quispicanchi, Collpa de San Lorenzo (FMNH 93589–93593*, 93595–93597*, 93607*); Cuzco, Quispicanchi, Hacienda Cadena (FMNH 93598–93606*); Madre de Dios, Manu, Cerro de Pantiacolla, headwaters of Río Palotoa (FMNH 139577–139578*, 139580*; MUSM 9969); Madre de Dios, Manu, Hacienda Amazonia (FMNH 126031–126032*; MUSM 9955); Huánuco, Huánuco, Chinchao, Cordillera de Carpish (MUSM 18263*, 18264*, 18273*); Pasco, Oxapampa, Pozuzo, Palmira (MUSM 10943–10944, 10971); San Martín, Huallaga, La Morada (MUSM 16170–16172, 16176); San Martín, Las Palmas, 32 km NE Pataz (MUSM 7295–7296).

Platyrrhinus recifinus: **Brazil:** São Paulo (USNM 545002); São Paulo, Guaratuba (USNM 542612); São Paulo, Iguapẽ (USNM 542613); São Paulo, Municĩpio Ilhabela, Ilha de São Sebastião, Parque Estadual Ilhabela (MVZ 185604*, 185605, 185606*, 185607–185608, 185609–185611*); São Paulo, Município Salesópolis, Museu de Zoologia USP, Estação Biológica Boracéia (MVZ 185901*).

Platyrrhinus vittatus: **Colombia:** Magdalena, Valparaíso (AMNH 15100–15101*); Nariño, Ricaurte (AMNH 34232*); **Costa Rica:** Puntarenas, Monteverde (UMMZ 116681–116682*); **Panama:** Darién, ca. 6 km NW Cana, E slope Cerro Pirre (LSUMZ 25464–25466*); Darién, Cerro Mali (AMNH 238203–238209); Darien, Cerro Tacarcuna, Río Pucuro (AMNH 238210–238218); **Venezuela:** Carabobo, Puerto Cabello (ZMB 568).

Carollia subrufa: **Mexico:** Chiapas, 7.5 mi SW by road Ixtapa (AMNH 249087); Oaxaca, Juchitán, San Jerónimo (AMNH 36037–36038); Oaxaca, Juchitán, 10 mi S Tapanatepec (AMNH 177625–177626); Oaxaca, Tehuantepec, Limón (AMNH 208238–208240, 167028, 171642–171644, 171648); Oaxaca, Tehuantepec, Cerro San Pedro (AMNH 146150); Oaxaca, 60 mi Tehuantepec (AMNH 189729).

Sturnira erythromos: **Peru:** Amazonas, ca. 20 km by road W Leymebamba (MUSM 4908–4910); Ayacucho, Yuraccyacu (MUSM 5269); Cuzco, Paucartambo, Morro Leguia, km 135 road Paucartambo-Shintuya (MUSM 8866–8868); Cuzco, Paucartambo, Challabamba, P. V. Acjanaco (MUSM 8876–8877); Cuzco, Paucartambo, Pillahuata (MUSM 9980); Cuzco, Paucartambo, San Pedro (MUSM 11799); Huánuco, Huánuco, Cordillera Carpish (MUSM 172); Huánuco, Unchog pass between Chunchubamba and Hacienda Paty, NNW Acomayo (MUSM 5260); La Libertad, Mashua, E of Tayabamba, road to Ongón (MUSM 5285); La Libertad, Utcubamba, road to Ongón (MUSM 5310).

Uroderma magnirostrum: **Peru:** Cuzco, La Convención, Camisea, Armihuari (MUSM 14019); Cuzco, La Convención, Camisea, Konkariari (MUSM 14841–14842); Cuzco, La Convención, Camisea, Pagoreni (MUSM 14026); Cuzco, La Convención, Camisea, San Martín (14027–14037); Cuzco, La Convención, Camisea, Segakiato (14843–14844); Ucayali, Padre Abad, Bosque Nacional Alexander von Humboldt (MUSM 8630–8631).

Vampyrodes caraccioli: **Costa Rica:** Puntarenas, 2 km SW Rincon de Osa (MSB 26965–26969); **Ecuador:** Pichincha, Estación Forestal La Favorita, close to Chiriboga (EPN 799–12, 799–15); Sucumbíos, Shushufindi, Limoncocha (QCAZ 514); **Peru:** Cuzco, La Convención, Cam-

isea, Armihuari (MUSM 14070–14072); Cuzco, La Convención, Camisea, Pagoreni (MUSM 14073); Cuzco, La Convención, Camisea, San Martín (MUSM 14075–14078); Loreto, Río Samiria, Tacshacocha (MUSM 1017); Madre de Dios, Manu, Cerro de Pantiacolla (MUSM 10102); Madre de Dios, Manu, Pakitza (MUSM 739, 12625–12624); Madre de Dios, Manu, Hacienda Amazonia (MUSM 10100–10101, 10106); Pasco, Oxapampa, Pozuzo (MUSM 10997); Pasco, Oxapampa, Pozuzo, Río Negro (MUSM 10996); Ucayali, Atalaya, Sepahua (MUSM 12809).

Appendix 2: Data Matrix

This data matrix includes all the taxa examined (ingroup and outgroup) and all the characters used in the phylogenetic analysis. Polymorphisms are shown between brackets.

Carollia subrufa
0–02 10202 01120 10021 10000 00000 00000 0–110 00000 10200 01001 000{01}0
Sturnira erythromos
0–10 02000 00232 12001 0000{01} 00000 00000 0–010 00000 00110 00000 00020
Uroderma magnirostrum
10012 03022 21110 {01}0022 00011 11110 00101 11010 00101 11110 01102 10201
Vampyrodes caraccioli
10013 03121 31021 01{01}11 10100 11110 {01}0121 0–111 10010 11011 01102 11121
Platyrrhinus aurarius
10103 03122 20221 12112 12100 11111 00021 20111 10101 01010 01212 11221
Platyrrhinus brachycephalus
10012 14121 {23}112{01} 11{01}00 101{01}{01} 11111 {01}1{01}11 {12}0{01}01 10101 01022 11212 112{01}1
Platyrrhinus chocoensis
10102 0{23}1{12}2 2{12}111 11{01}0{01} 1{01}100 11111 00021 {12}0{01}21 1{01}102 01010 01212 102{12}1
Platyrrhinus dorsalis
10103 03121 20121 {01}1101 12100 11111 {01}0021 {12}0121 {01}{01}112 01020 01212 112{12}1
Platyrrhinus dorsalis "Norte"—*Platyrrhinus ismaeli* sp. nov.
10103 03121 20122 121{01}1 1110{01} 11111 {01}0{01}21 21121 {01}11{01}1 01020 01211 11221
Platyrrhinus dorsalis "Centro-Sur"—*Platyrrhinus masu* sp. nov.
10103 011{12}2 31122 12{01}01 1{01}101 11111 {01}0021 20111 {01}11{01}1 01020 01212 112{12}1
Platyrrhinus helleri "Eastern"—*Platyrrhinus helleri*
1001{12} {01}312{12} {23}1111 {01}2{01}11 101{01}0 11111 01{01}11 10{01}21 10101 01021 11212 {01}1201
Platyrrhinus helleri "Western"—*Platyrrhinus matapalensis* sp. nov.
10012 03221 211{01}0 {01}2{01}00 101{01}{01} 11111 {01}1{01}11 10{01}11 1010{12} 01020 11212 11{12}01
Platyrrhinus infuscus
10103 {01}32{12}{12} 12120 {01}1{01}12 111{01}{01} 11111 11{01}21 20111 1111{12} 01020 01210 102{12}1
Platyrrhinus lineatus
10012 03121 31122 12022 1010{01} 11111 0{01}0{12}1 20111 101{01}{12} 01020 01210 11221
Platyrrhinus nigellus
10103 {01}3122 {23}0122 {01}2{01}01 1{12}100 11111 {01}0{01}{12}1 {12}0111 10{01}0{12} 01020 0{01}21{12} 11221
Platyrrhinus recifinus
10012 03021 31222 12011 111{01}0 11111 11011 10111 10102 01020 01212 10201
Platyrrhinus vittatus "Northern"—*Platyrrhinus vittatus*
11103 03222 30112 {01}1{01}11 10100 11111 10021 201{01}1 11111 01021 01211 11221
Platyrrhinus vittatus "Southern"—*Platyrrhinus albericoi* sp. nov.
11003 03{12}21 20112 12{01}12 1010{01} 11111 10121 20111 11011 01020 01211 11211

Appendix 3: Optimization of Characters

The following apomorphies support the monophyletic clades shown in Figure 29. Both ACCTRAN and DELTRAN optimizations are given for each clade. Diagnosis for each character is given as follow: (character number; consistency index) character state description, state number → state number. Unambiguous transformations are indicated by a double arrow "⇒," transformations

FIG. 29. Strict consensus tree with nodes numbered as a reference for Appendix 3, which presents apomorphies of the clades.

that occur in only one optimization are indicated by a single arrow "→."

Platyrrhinus **(Node 1)**—ACCTRAN: (30; 1.000) Sulcus present on the anterior face of P4, 0 ⇒ 1; (33; 0.333) M1 mesostyle absent, 1 → 0; (36; 0.667) Stylar cusp present on the lingual cingulum of the M1 metacone, 0 ⇒ 2; (45; 0.500) lingual cingulum of the M2 metacone continuous to the paracone, 0 ⇒ 2; (46; 0.500) M2 hypoconal basin developed, 1 ⇒ 0; (49; 0.500) both labial and lingual cingula present on p4, 1 ⇒ 2; (53; 1.000) both labial and lingual cingula present on m1, 1 ⇒ 2; (54; 1.000) stylid cusps present on the anterior face of the m1 protoconid, 0 ⇒ 1. DELTRAN: (30; 1.000) Sulcus on the anterior face of P4, 0 ⇒ 1; (36; 0.667) Stylar cusp present on the lingual cingulum of the M1 metacone, 0 ⇒ 2; (43: 0.333) M2 metastyle present, 0 → 1; (45; 0.500) lingual cingulum of the M2 metacone continuous to the paracone, 0 ⇒ 2; (46; 0.500) M2 hypoconal basin developed, 1 ⇒ 0; (53; 1.000) both labial and lingual cingula present on m1, 1 ⇒ 2; (54; 1.000) stylid cusps on the anterior face of the m1 protoconid, 0 ⇒ 1.

Node 2—ACCTRAN: (3; 0.500) dark facial stripes, 0 ⇒ 1; (4; 0.500) Absence of a basal protuberance, where the genal vibrissae are implanted, 1 ⇒ 0; (10; 0.333) folds in the pinna well marked, 1 → 2; (11; 0.429) dorsal stripe definite, but narrow, 3 → 2; (18; 1.000) posterior border of the hard palate "V"-shaped, 0 → 1; (19; 0.286) postorbital process absent or poorly developed, 1 ⇒ 0; (39; 0.400) M1 protocone small and blunt, 1 → 2. DELTRAN: (3; 0.500) dark facial stripes, 0 ⇒ 1; (4; 0.500) Absence of a basal protuberance, where the genal vibrissae are implanted, 1 ⇒ 0; (11; 0.429) dorsal stripe definite, but narrow,

3 → 2; (19; 0.286) postorbital process absent or poorly developed, 2 → 0.

Node 3—ACCTRAN: (5; 0.667) six vibrissae surrounding the margins of the noseleaf in a single array, 2 ⇒ 3; (12; 0.500) dorsal fur > 8 mm, 1 ⇒ 0; (22; 0.500) A deep fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, 0 ⇒ 2. DELTRAN: (5; 0.667) six vibrissae surrounding the margins of the noseleaf in a single array, 2 ⇒ 3; (12; 0.500) dorsal fur > 8 mm, 1 ⇒ 0; (18; 1.000) posterior border of the hard palate "V"-shaped, 0 → 1; (22; 0.500) A deep fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, 0 ⇒ 2.

Node 4—ACCTRAN: (17; 0.286) A densely haired uropatagium fringe, 1 ⇒ 2; (39; 0.400) M1 protocone moderately developed, 2 → 1; (45; 0.500) lingual cingulum of the M2 metacone restricted to the metacone, 2 ⇒ 1. DELTRAN: (17; 0.286) A densely haired uropatagium fringe, 1 ⇒ 2; (45; 0.500) lingual cingulum of the M2 metacone restricted to the metacone, 2 ⇒ 1.

Node 5—ACCTRAN: (15; 0.286) dense and long hair on the dorsum of the feet, 1 ⇒ 2; (22; 0.500) A shallow fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, 2 → 1; (31; 0.500) A deep fossa on the hypoconal basin of P4, 0 → 1. DELTRAN: (15; 0.286) dense and long hair on the dorsum of the feet, 1 ⇒ 2; (49; 0.500) both labial and lingual cingula of p4 present, 1 → 2.

Node 6—ACCTRAN: (42; 1.000) stylar cusp present on the lingual face of the M2 paracone, 0 ⇒ 1; (44; 0.333) stylar cusp present on the lingual face of the M2 metacone, 0 → 1. DELTRAN: (22; 0.500) A shallow fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, 2 → 1; (42; 1.000) stylar cusp present on the lingual face of the M2 paracone, 0 ⇒ 1.

Node 7—ACCTRAN: (10; 0.333) folds in the pinna poorly marked but distinguishable, 2 → 1; (19; 0.286) postorbital process moderately developed, 0 → 1; (55; 0.400) poorly developed m1 metaconid, 2 ⇒ 1. DELTRAN: (55; 0.400) poorly developed m1 metaconid, 2 ⇒ 1.

Node 8—ACCTRAN: (8; 0.400) two interramal vibrissae present, 1 ⇒ 2; (17; 0.286) edge of the uropatagium, usually hairy, 2 → 1; (20; 0.333) A well-developed paraoccipital process, 1 → 2. DELTRAN: (8; 0.400) two interramal vibrissae present, 1 ⇒ 2; (19; 0.286) postorbital process moderately developed, 0 → 1; (31; 0.500) A deep fossa on the hypoconal basin of P4, 0 → 1; (44; 0.333) stylar cusp present on the lingual face of the M2 metacone, 0 → 1.

Node 9—ACCTRAN: (2; 1.000) dorsomedial facial stripe more marked than the ventrolateral stripe, 0 ⇒ 1; (14; 0.333) ventral fur bicolored, 2 ⇒ 1; (22; 0.500) An almost imperceptible fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, 1 ⇒ 0. DELTRAN: (2; 1.000) dorsomedial facial stripe more marked than the ventrolateral stripe, 0 ⇒ 1; (14; 0.333) ventral fur bicolored, 2 ⇒ 1; (22; 0.500) An almost imperceptible fossa on the squamosal end of the zygomatic arch, lateral to the glenoid fossa, 1 ⇒ 0.

Node 10—ACCTRAN: (15; 0.286) dense and long hair on the dorsum of the feet, 1 → 2; (17; 0.286) A densely haired uropatagium edge, 1 ⇒ 2; (32; 0.500) M1 parastyle present, 0 → 1; (34; 1.000) presence of a labial cingulum at the base of the M1 metacone, 2 → 1. DELTRAN: (10; 0.333) folds in the pinna poorly marked but distinguishable, 2 → 1; (17; 0.286) A densely haired uropatagium edge, 1 ⇒ 2; (49; 0.500) both labial and lingual cingula on p4 present, 1 → 2.

Node 11—ACCTRAN: (45; 0.500) lingual cingulum of the M2 metacone restricted to the metacone, 2 ⇒ 1; (51; 1.000) stylid cusp present on the posterior face of the main cone of p4, 0 ⇒ 1. DELTRAN: (45; 0.500) lingual cingulum of the M2 metacone restricted to the metacone, 2 ⇒ 1; (51; 1.000) stylid cusp present on the posterior face of the main cone of p4, 0 ⇒ 1.

Node 12—ACCTRAN: (19; 0.286) postorbital process, absent or poorly developed, 1 ⇒ 0; (20; 0.333) paraoccipital process, poorly developed, 1 ⇒ 0. DELTRAN: (19; 0.286) postorbital process, absent or poorly developed, 1 ⇒ 0; (20; 0.333) paraoccipital process, poorly developed, 1 ⇒ 0.

Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496
Telephone: (312) 665-7055