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SPIXIANA	7	1	75-84	München, 1. März 1984	ISSN 0341-8391

Cranial and external characters of the larger fruit bats of the genus Artibeus from Amazonian Peru

(Chiroptera, Phyllostomidae)

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Abstract

Three sympatric species of larger fruit bats of the genus Artibeus can be distinguished in Amazonian Peru: Artibeus lituratus (Olfers, 1818), A. planirostris (Spix, 1823), and A. fuliginosus Gray, 1838. Besides cranial morphometrics, some pelage and skull characteristics are given for their identification.

1. Introduction

Current knowledge of the larger fruit bats of the genus Artibeus has been improved by recent investigations (e. g. DAVIS 1970, KOOPMAN 1978, PATTEN 1971), but several aspects of their systematics still remain uncertain, particularly regarding the *lituratus-jamaicensis* group from the Amazonian region.

TUTTLE (1970) was the first to suggest that bats from Amazonian Peru, formerly referred to Artibeus jamaicensis Leach, represent two or more distinct species. He distinguished an "unrecognized" species by its smaller size and dark pelage colour in comparison to typical *A. jamaicensis*. Also JONES & CARTER (1976) state that they are aware of an "undescribed" species of *jamaicensis*-like bats from Amazonian Ecuador, Peru and adjacent areas. Later on, KOOPMAN (1978) argued that the name *fuliginosus* Gray, 1838, be applied to this *jamaicensis*-like bat from Peru. He also remarked that the medium-sized bat of the *lituratus-jamaicensis* group from eastern Peru is not related to *A. jamaicensis trinitatis* Andersen, 1906, from Colombia, Venezuela, Trinidad, Tobago and Grenada, but instead can be associated with *A. planirostris* (Spix, 1823) from Brazil.

Including A. lituratus (Olfers, 1818), three larger species of the genus Artibeus can be recognized in Amazonian Peru. Anderson, KOOPMAN & CREIGHTON (1982) found the same systematic situation in Bolivia.

No detailed statistical analyses of skull characters have been carried out for the members of this species group distributed east of the Andes, and in the literature the differences in cranial and external features among them have been discussed only briefly (TUTTLE 1970, WEBSTER & JONES 1980). In our paper we attempt to provide some additional data for the recognition and differentiation of the three species mentioned above.

2. Specimens examined

Abbreviations: AMNH – American Museum of Natural History, New York City, USA; ZFMK – Zoologisches Forschungsinstitut und Museum Alexander König, Bonn, West Germany; ZMH – Zoologisches Institut und Zoologisches Museum Hamburg, West Germany; ZSM – Zoologische Staatssammlung München, West Germany. ©Zoologische Staatssammlung München;download: http://www.biodiversitylibrary.org/; www.biologiezentrum.at

Artibeus fuliginosus Gray: mouth of Río Curaray, Dept. Loreto: 2♂♂ (AMNH); Sta. Rosa, near Atalaya, Alto Ucayali, Dept. Ucayali: 1♂ (AMNH); Panguana, Río Llullapichis (= Yuyapichis), near Río Pachitea, Dept. Huánuco, 260 m.: 1♂, 3♀♀ (ZSM), 1♀ (AMNH); Cerros del Sira, Dept. Huánuco, 860–1120 m.: 1♂, 3♀♀ (AMNH); Río Ene, mouth of Río Saoreni (= Saoereni), near Puerto Prado, Dept. Junín, 340 m.: 1♀ (AMNH).

Artibeus planirostris (Spix): mouth of Río Curaray, Dept. Loreto: 13, 299 (AMNH); Panguana, Río Llullapichis, near Río Pachitea, Dept. Huánuco, 260 m.: 19 (AMNH), 333, 1199 (ZSM); Cerros del Sira, Dept. Huánuco, 1120 m.: 13, 19 (AMNH); 2 mi. northwest San Ramón, Dept. Junín, ca. 970 m.: 733, 699 (AMNH); Chanchamayo valley, 3 mi. southwest San Ramon, Dept. Junín: 13 (AMNH); Río Ene, mouth of Río Saoreni, near Puerto Prado, Dept. Junín, 340 m.: 13 (AMNH); Río Madre de Dios, near Puerto Maldonado, Dept. Madre de Dios, ca. 255 m.: 19 (ZFMK).

Artibeus lituratus (Olfers): Yarinacocha, near Pucallpa, Dept. Ucayali, 150 m.: 10^o (ZSM); Panguana, Río Llullapichis, near Río Pachitea, Dept. Huánuco, 260 m.: 19 (ZMH), 20^o0, 599

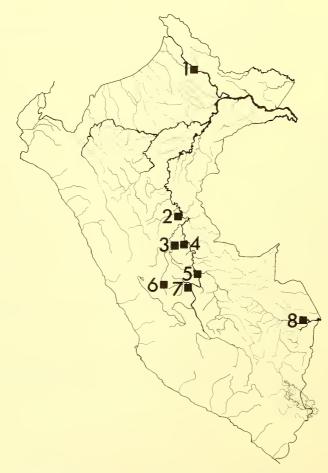


Fig. 1: Map of Peru showing locality records. 1 – mouth of Río Curaray; 2 – Yarinacocha; 3 – Panguana/Río Llullapichis; 4 – Cerros del Sira; 5 – Sta. Rosa/Alto Ucayali; 6 – San Ramón; 7 – Río Ene/mouth of Río Saoreni; 8 – Río Madre de Dios/Puerto Maldonado.

©Zoologische Staatssammlung München; download: http://www.biodiversitylibrary.org/; www.biologiezentrum.at (ZSM); Río Madre de Dios, near Puerto Maldonado, Dept. Madre de Dios, ca. 255 m.: $2 \circ \circ$, $2 \circ \circ$ (ZFMK).

For the localities of the collection sites see fig. 1.

Due to the taxonomic uncertainty regarding the large fruit bats of the genus Artibeus, some of the labels attached to specimens of the AMNH give different identifications, such as *jamaicensis planirostris* for *fuliginosus* and *hercules fallax* for *planirostris*.

Skull and external measurements were taken with a caliper according to FREEMAN (1981). The upper toothrow was always measured from the anteriormost alveolar border of the canine to the posteriormost alveolar border of the second molar, even in those specimens which possess the third upper molar.

Capitalized colour names are according to RIDGWAY (1912).

2. Results

2.1 Cranial characters

Artibeus fuliginosus is considerably smaller than the other two species (table 1). Our own measurements for *fuliginosus* are within the range indicated by WEBSTER & JONES (1980) for specimens from Bolivia, whereas PATTEN (1971) recorded skull lengths up to 29,5 mm for *fuliginosus* from Ecuador, and 29,3 mm for specimens from Huánuco, Peru.

Most skull dimensions are reliable characters that serve to separate *fuliginosus* from *planirostris* and *lituratus* (see table 1). In the latter two species, nearly all skull measurements overlap to a high degree. It is amazing that in some skull dimensions *planirostris* exceeds *lituratus*, the latter which is generally considered to be the largest species of the genus *Artibeus*.

Postorbital constriction is the best character to distinguish the two larger species. Only three of the examined specimens of *A. planirostris* have a postorbital width of 7,2 mm or less, values which are at the upper extreme of this character measured for *A. lituratus*.

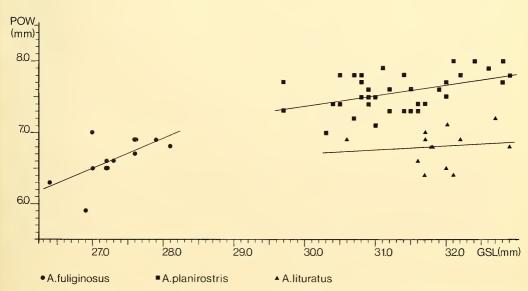


Fig. 2: Scatter diagramm correlating greatest skull length (GSL) with postorbital width (POW) in samples of Peruvian *Artibeus*. Regression lines are given for each species.

Tab. 1: Selected cranial and external measurements of species examined (mean, standard deviation, range, and sample size). All measurements in mm.

	A. fuliginosus	A. planirostris	A. lituratus
Greatest length of skull	27,31 [±] 0,45 (26,4 - 28,1) n = 13	31,32 ± 0,82 (29,7 - 32,9) n = 36	31,91 [±] 0,56 (30,6 - 32,9) n = 13
Upper ₂ toothrow c - m	9,62 [±] 0,25 (9,0 - 10,0) n = 13	l1,49 [±] 0,28 (l1,0 - l2,2) n = 36	11,15 ± 0,22 (10,8 - 11,6) n = 13
Postorbital width	6,62 ⁺ 0,30	7,57 ± 0,26	6,79 ± 0,25
	(5,9 - 7,0)	(7,0 - 8,0)	(6,4 - 7,2)
	n = 13	n = 36	n = 13
Width across	7,78 [±] 0,23	9,08 ± 0,25	8,94 ± 0,36
cingula of +1)	(7,4 - 8,1)	(8,6 = 9,8)	(8,4 - 9,6)
upper canines +1)	n = 13	n = 36	n = 13
Width across	ll,93 ± 0,31	13,68 [±] 0,46	13,39 ± 0,42
alveolar border	(ll,2 - 12,3)	(12,6 - 14,7)	(12,5 - 14,3)
of upper m2 +1)	n = 13	n = 36	n = 13
Zygomatic breadth	l6,79 [±] 0,44	19,51 [±] 0,71	19,21 ± 0,65
	(15,9 - 17,5)	(18,1 - 20,9)	(17,9 - 20,6)
	n = 13	n = 30	n = 13
Breadth of brain- case	12,0 [±] 0,33 (11,5 - 12,5) n = 13	13,41 [±] 0,29 (12,9 - 14,0) n = 36	13,55 ± 0,25 (13,1 = 13,8) n = 13
Height of brain- case	ll,69 [±] 0,32 (ll,0 - 12,1) n = 13	12,87 [±] 0,51 (11,8 - 13,8) n = 32	13,38 ± 0,31 (12,9 = 13,8) n = 12
Dentary length	18,84 [±] 0,30	22,11 [±] 0,58	22,22 ± 0,43
	(18,3 - 19,2)	(21,2 - 23,5)	(21,5 - 23,2)
	n = 13	n = 36	n = 13
Lower toothrow c - ^m 2	l0,05 ± 0,24 (9,6 - 10,5) n = 13	12,02 [±] 0,32 (11.4 - 12,8) n = 36	11,72 ± 0,33 (11,2 - 12,3) n = 13
Height of mandible at coronoid process	7,47 [±] 0,31 (7,0 - 8,1) n = 13	9,17 ± 0,29 (8,5 - 9,8) n = 36	10,15 ± 0,61 (9,1 - 11,3) n = 13
Forearm	60,02 ± 2,10	67,38 [±] 1,58	72,99 ± 2,01
	(56,7 - 63,4)	(64,2 - 70,4)	(68,9 - 77,4)
	n = 10	n = 30	n = 13
Third metacarpal	57,91 [±] 1,89	64,01 [±] 1,80	70,36 ± 2,86
	(54,4 - 61,3)	(59,2 - 67,6)	(64,6 - 74,7)
	n = 13	n = 35	n = 13

+1) measured from the labial side

©Zoologische Staatssammlung München:download: http://www.biodiversitylibrary.org/; www.biologiezentrum.at In fig. 2 greatest skull length is plotted against postorbital width. From this figure the marked con-

In fig. 2 greatest skull length is plotted against postorbital width. From this figure the marked contrast in size between fuliginosus and the other two species is clearly evident. Furthermore, it demonstrates the differences in skull proportions between the larger two species: specimens of *lituratus* and *planirostris* with the same skull length can usually be separated by the difference in postorbital width.

Discriminant function analysis¹): In order to decide whether a newly caught specimen supposed to belong to this group of three species studied has to be allocated to *A. lituratus*, *A. fuliginosus* or *A. planirostris* a discriminant function analysis after FISHER (1936) was applied. The calculated functions, or more exactly, inequalities, are as follows:

- (1) If GSL 2.2637 POW < 15.36 the specimen belongs to A. planirostris
- (2) If GSL 2.2637 POW > 15.36 the specimen belongs to A. lituratus
- (3) If GSL + 2.8777 POW < 49.52 the specimen belongs to A. fuliginosus
- (4) If GSL + 2.8777 POW > 49.52 the specimen belongs to either A. *planirostris* or A. *lituratus* and the inequalities (1) and (2) have to be applied.

The probability that a skull of *A. planirostris* will be erroneously allocated to *A. lituratus* or vice versa by these rules without using any other characters equals to 11%. For the distinction between *A. fuliginosus* and the *A. planirostris-A. lituratus*-group the error will only be 2%.

Apart from cranial measurements, *Artibeus lituratus* can be easily distinguished from the other two species by the shape of the skull (fig. 3): the postorbital constriction in *lituratus* is very narrow and situated immediately behind the orbitonasal shield; in dorsal view there is a strong contrast between the broad posterior border of the orbitonasal shield and the postorbital constriction. In *planirostris* the postorbital constriction is less accentuated, and there is no step in the outline of the orbital region. The skull of *lituratus* possesses well-developed postorbital and, with few exceptions, preorbital processes. A prominent ridge connects both processes, forming the conspicious orbitonasal shield. In *fuliginosus* and *planirostris* such ridges are less prominent or hardly visible. In *A. planirostris* preorbital processes are usually absent, and postorbital processes are also lacking or are only faintly developed. Only two of the specimens examined show striking pre- and postorbital processes comparable with those of *Artibeus lituratus*.

No obvious difference exists between *lituratus* and *planirostris* in the development of the ridges connecting the postorbital processes and the sagittal crest ("interorbital ridges" in the sense of PATTEN [1971]). Even in *A. lituratus* they are never as prominent as suggested by DAVIS (1970) for Central American populations of *lituratus*.

Generally, the skull of *lituratus* appeares more slender in contrast to the more compact skull of *planirostris*. In *fuliginosus* the shape of the skull resembles that of *planirostris*, but with even more obscured pre- and postorbital processes.

A. fuliginosus and planirostris usually possess the third upper molars, only 1 of 13 specimens of fuliginosus and 1 of 36 specimens of planirostris lack them. All A. lituratus examined have two upper molars on each side.

2.2 External characters

Though A. fuliginosus resembles A. planirostris in general appearance, these closely related species can be distinguished by several pelage characteristics from each other and from *lituratus*. From our examination we may summarize the most useful external features for their recognition as follows:

Artibeus fuliginosus Gray – General appearance of dorsal fur Blackish Brown to Mummy Brown, conspicuously darker than in *A. planirostris*. Single hair pale from base, about Light Drab to Drab, evenly becoming darker towards the tip. The fur on neck and shoulder is relatively long and soft when compared with *planirostris*. Hairs of shoulder and venter white tipped, giving a frosted appearance.

¹) Calculation carried out by Dr. Hubert FECHTER, Zoologische Staatssammlung München

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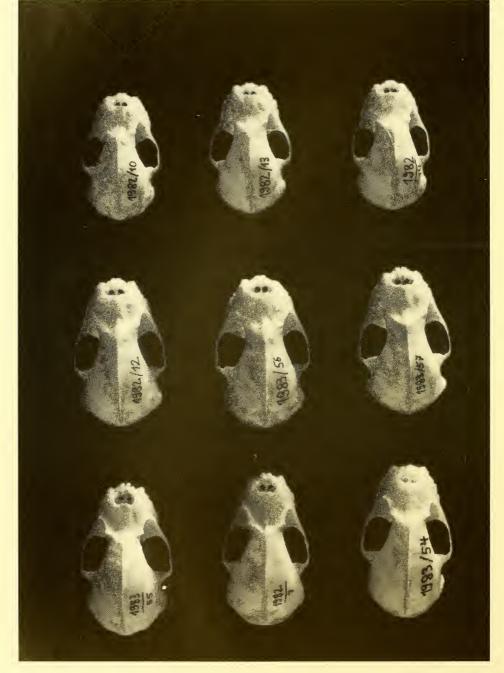
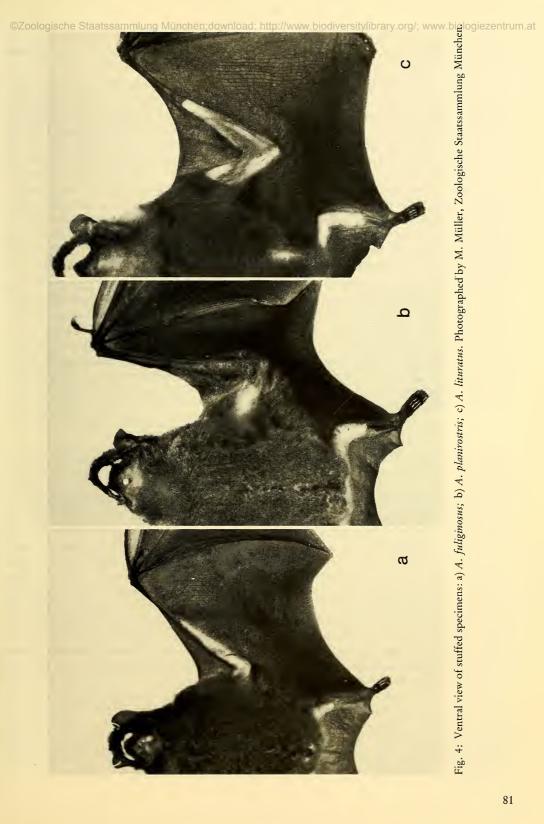


Fig. 3: Dorsal view of skulls of Peruvian Artibeus (from ZSM). Upper row: A. fuliginosus; middle row: A. planirostris; lower row: A. lituratus. Photographed by M. Müller, Zoologische Staatssammlung München.



Zoologische Staatssammlung München;download: http://www.biodiversitylibrary.org/; www.biologiezentrum.al Tragus, ears, lips, and nose leaf blackish, contrasting with the somewhat paler fur of head. No facial stripes. Ventral surface of propatagium and mesopatagium between flanks and middle of forearm thinly haired (fig. 4a). Uropatagium very sparsely haired or naked.

Artibeus planirostris (Spix) – General appearance of dorsal fur Fuscous to Fuscous Black, due to the dark tips of hairs. Individual hairs bicoloured with a sharp demarcation line between the pale basal four fifths and the dark terminal part. Specimens from Huánuco show little variation in colour, having the basal part of hairs about Drab Gray, whereas in those from Junín and Loreto basal parts of dorsum hairs vary from yellowish (Avellaneous to Vinaceous Buff) to Drab Gray. The specimens from the mouth of the Río Curaray have a somewhat darker band in the light basal zone. General coloration of dorsum somewhat lighter than in *A. fuliginosus*. Shoulder and belly with conspicuous frosting; in some specimens the hairs on the back are also slightly tipped with white or Drab Gray. Tragus brown; lips, ears, and nose leaf not conspicuously darker than surrounding fur. Supraorbital streaks usually faintly developed, although in some specimens well-defined. Infraorbital streaks always hardly visible. Underparts of propatagium and mesopatagium in an area extending from flanks around elbow to the middle of forearm densely covered with whitish hairs (fig. 4b). Ventral side of uropatagium thinly haired in a triangle between middle of its posterior border and knees, upper side very sparsely haired or nearly naked.

Artibeus lituratus (Olfers) – Pelage rather uniformly reddish brown or greyish brown with reddish tinge. Colour of basal parts of dorsum hairs very variable in different specimens, being more or less paler than terminal tips. Belly only slightly paler than upper side, without any trace of frosting. Tragus yellowish, supra- and infraorbital streaks prominent. Ventral surface of propatagium and mesopatagium between flanks and middle of forearm densely covered with reddish brown hairs (fig. 4 c). Upper surface of interfemoral membrane densely covered with thin hairs, under surface more or less haired only on its middle region.

3. Discussion

The larger fruit bats of the genus Artibeus on the Amazonian side of Peru represent three well-defined species. A fourth species, A. fraterculus Anthony, 1924, normally distributed on the Pacific side of the Andes, is said to extend into isolated arid localities east of the Andes in northern Peru (KOOPMAN 1978, PATTEN 1971). In accordance with KOOPMAN (1978), ANDERSON, KOOPMAN & CREIGHTON (1982), DAVIS & DIXON (1976), HANDLEY (1976), HONACKI, KINMAN & KOEPPL (1982), WEBSTER & JONES (1980) and JONES & CARTER (1979) we apply the name fuliginosus Gray to the smallest species of the lituratusjamaicensis group. PATTEN (1971) however asserts that the original description of Arctibeus fuliginosus Gray, 1838, is not sufficiently indicative to be applied to this species. In his Ph. D. dissertation, which is unpublished but available by microfilm-xerography, he indicated that he has redescribed this species as Artibeus davisi Patten, 1971, and announced this redescription as "in press". But it was not in fact published in the journal advertised by him and, to our knowledge, nowhere else. However, in his Ph. D. dissertation, he failed to provide the name *davisi* with the attribute "new species". Furthermore it is doubtful if microfilm-xerographies represent publications in the sense of the International Code for Zoological Nomenclature. Therefore we hesitate to consider this description as an original and valid one. To prevent further taxonomic confusion, we use the name fuliginosus Gray, 1838, for the small, blackish brown Artibeus from eastern Peru.

Nevertheless we are unable to decide whether or not *A. fuliginosus* represents a subspecies of *Artibeus jamaicensis* Leach, as has been suggested by ANDERSON, KOOPMAN & CREIGHTON (1982), or if it is to be regarded as an independent species. Likewise we cannot clarify the subspecific status of Peruvian *planirostris*. JONES & CARTER (1976, 1979) listed *planirostris* as a subspecies of *A. jamaicensis* Leach. But in contrast to them, ANDERSON, KOOPMAN & CREIGHTON (1982) give *planirostris* specific rank and use the name *A. planirostris fallax* Peters, 1865, for animals from Bolivia.

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Three species of bats of the *lituratus-jamaicensis* group are also reported to occur in Paraguay (MYERS & WETZEL 1979, BAUD 1981). They are listed as *A. lituratus*, *A. jamaicensis planirostris* and "*Artibeus* sp.". Measurements given by these authors for the latter unnamed species do not correspond with those of Peruvian *fuliginosus*; their taxonomic status therefore remains uncertain.

The three species studied in this paper occur sympatrically in Amazonian Peru. At Panguana, Dept. Huánuco, we netted *fuliginosus* and *planirostris* together at the same places, in a primary rain forest as well as on an adjacent cattle farm. A. *lituratus* was caught by us together with *planirostris* at clearings near the edge of the forest in the same area. Evidently, some specimens of *fuliginosus* and *planirostris* in the American Museum of Natural History were also caught at the same localities, e. g. those from Río Curaray, Río Ene, and some of those from Cerros del Sira.

Due to the fact that *fuliginosus* has been recognized only recently as independent from *planirostris*, nothing is known about ecological and behavioural separation between these closely related species.

Otherwise, *A. lituratus* was never captured in our mist nets set up in dense woods. We suggest that this species, in contrast to the smaller two, mostly forages at higher vegetation levels of the forest. Differential selection of roost sites may lead to specific niche separation; *lituratus* is said to roost usually in dense vegetation, hanging from tree branches under leaves, whereas the smaller *jamaicensis*-like species prefer darker diurnal retreats, such as caves, tree holes or hollow branches (BROSSET 1965, DALQUEST 1953, FELTEN 1956, MORRISON 1979).

Acknowledgements

We are greatly indebted to the following persons for the loan of material in their care: Dr. Rainer Hutterer, Zoologisches Forschungsinstitut und Museum Alexander König, Bonn; Dr. Karl F. Koopman, American Museum of Natural History, New York City; Prof. Dr. Harald Schliemann, Zoologisches Institut und Zoologisches Museum, Hamburg. We are especially grateful to Dr. Hubert Fechter, Zoologische Staatssammlung München, for providing the discriminant function analysis in chapter 2.1.

Zusammenfassung

Im Amazonas-Tiefland von Peru sind drei "große" Arten der Fledermausgattung Artibeus sympatrisch verbreitet: Artibeus lituratus (Olfers, 1818), A. planirostris (Spix, 1823) und A. fuliginosus Gray, 1838. In der vorliegenden Arbeit werden Schädel- und Fellmerkmale untersucht, die eine Unterscheidung dieser Arten ermöglichen.

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Zeitschrift/Journal: Spixiana, Zeitschrift für Zoologie

Jahr/Year: 1984

Band/Volume: 007

Autor(en)/Author(s): Koepcke Juliane, Kraft Richard

Artikel/Article: <u>Cranial external characters of the larger fruit bats of the genus</u> <u>Artibeus from Amazonian Peru (Chiroptera, Phyllostomidae) 75-84</u>