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A SYSTEMATIC REVIEW OF THE LARGE SPECIES OF *ARTIBEUS* LEACH, 1821 (MAMMALIA: CHIROPTERA), WITH SOME PHYLOGENETIC INFERENCES

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ABSTRACT — Artibeus *is a widespread genus of fruit-eating bats, occurring from Mexico to Argentina. These bats play an important role as seed dispersers in the reforestation and maintenance of the tropical rain forest. Although* Artibeus *was described by Leach in 1821, the systematics of the genus is still not well understood. Due to these systematic problems, and because the environment of these animals is threatened, an urgent study is needed to determine this important group's distribution, systematics, and biology for conservation issues. In this study the large species of* Artibeus *(subgenus* Artibeus*) are defined and redescribed with additional information about synonyms, type material, distribution, and natural history. Eight species are recognized. Cladistic analysis was conducted to discover the hierarchical pattern, i.e., how the species are related to each other. Two minimum-length equally parsimonious cladograms were produced with the computer program "Hennig86", each with a length of 55 steps, and a consistency index (C.I.) of 0.70. The only difference between the cladograms refers to the position of* Artibeus fraterculus *and* A. obscurus *in relation to the clade formed by* A. hirsutus *and* A. inopinatus. Artibeus lituratus *is the most distinctive species of* Artibeus, *having at least five autapomorphies.* Artibeus amplus *and* A. fimbriatus *are the species with the least number of advanced character states and could represent primitive species.* Artibeus jamaicensis *and the clade formed by* A. obscurus, A. fraterculus, A. hirsutus, *and* A. inopinatus *could represent intermediate species in terms of evolution.* Artibeus hirsutus, *and* A. inopinatus *are considered sister species, and may form a clade with* A. fraterculus. *Conservation strategies are suggested for* Artibeus *species based on evolution and biogeography of the taxa. It seems that the tropical rain forest of South America and the dry places on the Pacific side of Central and South America should be the focus of our efforts. The selection of areas to be protected in those regions, however, depends on additional knowledge of geographic variation of the* Artibeus *species, and comparison with other taxonomic groups. The present study is open for future research in which systematics is the basis for conservation biology.*

KEY WORDS: Chiroptera; Phyllostomidae; *Artibeus*; Bats; Revision; Taxonomy; Cladistics; Conservation.

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RESUMO — *Uma revisão sistemática das espécies maiores de* Artibeus *Leach, 1821, (Mammalia: Chiroptera) com algumas inferências filogenéticas.* Artibeus *é um gênero de morcegos frugívoras de ampla distribuição, ocorrendo desde o México até a Argentina. Estes morcegos desempenham um papel importante como dispersores de sementes no reflorestamento e manutenção da floresta chuvosa tropical. Embora* Artibeus *tenha sido descrito por Leach em 1821, a sistemática do gênero ainda apresenta problemas. Neste estudo, as grandes espécies de* Artibeus *(subgênero* Artibeus*) foram definidas e redescritas com informação adicional sobre sinonímia, material tipo, distribuição e história natural. Oito espécies são reconhecidas. Análises cladísticas foram feitas para revelar o padrão hierárquico (como as espécies estão relacionadas entre si). Dois cladogramas, de comprimento mínimo e igualmente parsimoniosos, foram produzidos com o programa de computador Hennig86, cada um com um comprimento de 55 passos e um índice de consistência de 0.70. A única diferença entre os cladogramas se refere à posição de* Artibeus fraterculus *e* A. obscurus *em relação ao clade formado por* A. hirsutus *e* A. inopinatus. Artibeus lituratus *é a espécie mais distinta de* Artibeus, *com pelo menos cinco autapomorfias.* Artibeus amplus *e* A. fimbriatus *são as espécies com o menor número de caracteres avançados e poderiam representar espécies primitivas.* Artibeus jamaicensis *e o clade formado por* A. obscurus, A. fraterculus, A. hirsutus, *e* A. inopinatus *poderiam representar espécies intermediárias em termos de evolução.* Artibeus hirsutus *e* A. inopinatus *são consideradas espécies irmãs e podem formar um clade com* A. fraterculus. *Estratégias de conservação são sugeridas para as espécies de* Artibeus *baseadas na evolução e biogeografia do taxa. O estudo conclui que a floresta chuvosa tropical da América do Sul e as áreas secas no lado Pacífico da América Central e do Sul deveriam ser o foco de estudos futuros. A seleção das áreas a serem protegidas nestas regiões, porém, depende do conhecimento futuro sobre a variação geográfica das espécies de* Artibeus *e comparação com outros grupos taxonômicos.*

PALAVRAS-CHAVE: Chiroptera; Phyllostomidae; *Artibeus*; Morcegos; Revisão; Taxonomia; Cladística; Conservação.

INTRODUCTION

There are approximately 1,000 species of bats found almost world-wide; the majority, however, inhabit tropical forests. Size varies from the bumble bee bat (*Craseonycteris thonglongyai*) of Thailand (one of the world's smallest mammals, weighing less than 2 g) to some species of Old World flying foxes (*Pteropus vampyrus*), weighing more than 900 g (Grassé 1955; Hill 1974; Slaughter & Walton 1970).

In Latin America, there are more than 270 species of bats in 10 families. At least 140 of this total belong to the family Phyllostomidae, American leaf-nosed bats. These bats are best represented in museum collections, as they are relatively easy to capture (e.g., Davis 1980; Koopman 1978; Handley 1987, 1990, 1991; Hill 1980; Taddei et al. 1983; for a summary see Hall 1981; Honacki et al. 1982; Koopman 1982; Marques in press; Nowak 1991).

Bats of the neotropical genus *Artibeus* (Phyllostomidae: Stenodermatinae) are widespread fruit-eating species, occurring from Mexico to northern Argentina (Figures 1-3; Hall 1981; Honacki et al. 1982; Jones & Carter 1976; Koopman 1976, 1982; Marques in press; Nowak 1991). In his summary on fossil bats, Smith (1976) listed specimens of *Artibeus* from the late Pleistocene and sub-Recent.

Tuttle (1989) stated that pollination and dispersal of seeds by bats are vital to the survival of the rain forest. These plants provide more than 450 economically important products valued in the hundreds of millions of dollars annually, such as for food, beverages, medicine, timber, wood products, ornaments, fiber, and fuel, among others. Some examples of these plants are *Ceiba pentandra* (kapok), *Durio zibethinus* (durian), *Ficus* spp. (figs), and *Ochroma lagopus* (balsa). The value of tropical bats in forest maintenance alone is enormous.

Gardner (1977b), in his review of the food habits of the Phyllostomidae, listed 112 species of plants used by *Artibeus*, including pioneer species (first species to come after deforestation; e.g., *Cecropia* spp., *Piper* spp., *Solanum* spp.) and persistent species (species of the mature forest; e.g., *Bombax* sp., *Ceiba pentandra*, *Dipteryx odorata*, *Ochroma lagopus*). Although *Artibeus* is primarily frugivorous, it consumes pollen, nectar, flower parts, and insects as well. Some important papers and revisions about fruits and seed dispersal by *Artibeus* include Bonaccorso et al. (1980), Fleming et al. (1972), Handley et al. (1991), Handley & Leigh (1991), Heithaus (1982), Heithaus et al. (1975), Jimbo & Schwassmann (1967), Morrison (1978), Reis & Guillaumet (1983), Reis & Peracchi (1987), and Wilson (1989). These bats seem to play an important role in maintaining the diversity of tropical forests as well as in secondary succession.

The Amazonian region is one of the richest environments on earth in terms of the diversity of fauna and flora. However, without adequate protection, this diversity could disappear. As stressed by Fearnside (1989) in his article about deforestation in Brazilian Amazonia, "Although only a small proportion of Amazonia has been cleared, the rate of destruction is virtually exponential and if it continues the forests will be gone in a matter of decades..."

Since most of the range of *Artibeus obscurus* falls within the Amazonian Basin, these animals are threatened, and it is urgent that systematic and ecological studies be conducted. *Artibeus fimbriatus* is present in eastern and southern Brazil, and eastern Paraguay in the tropical humid forest (Handley 1990, 1991); its habitat is also doomed to disappear if proper precautions are not taken, as now seems the case in northeastern Brazil (Handley 1991). Concerning *Artibeus amplus*, this species was recently described from northern South America, and it is found mainly in evergreen forest (Handley 1987), a habitat also susceptible to change.

The importance of systematics in conservation biology was stressed by Wheeler (1990): the biodiversity crisis demands an urgency to inventory species diversity, and this task should be "accompanied by a similarly great need for the continued expansion and application of theoretical advances in systematic biology." Erwin (1991) further commented that the knowledge of the relationships between species, and their distribution range, i.e., phylogeny and biogeography, are essential for conservation strategies. Current conservation strategies give priority to protection of endemic forms occurring in small areas, without concern for their evolutionary status. Several authors, however, suggested that more recently evolved lineages should have priority in conservation because, according to the phylogenetic theory, such taxa carry the potential for species radiation that is occurring today (Erwin 1991). Still other authors suggested that distantly related taxa should have priority in conservation because genetic diversity, not just species number, is maximized (Mares 1992; Vane-Wright et al. 1991; see also Dizon et al. 1992; Pielou 1975).

Over 100 years ago, Peters (1865) stressed that the taxonomy of Stenodermatinae, which includes *Artibeus*, is confused. Currently, despite the large number of specimens in museum collections, this observation seems to be still valid for *Artibeus* as: (1) new species are being described (e.g., *Artibeus amplus*, Handley 1987), (2) other species are being revalidated (e.g., *Artibeus obscurus* and *A. fimbriatus*, Handley 1990), (3) still other species are being invalidated (e.g. *Artibeus planirostris*, Handley 1991), and (4) the synonymy is extensive.

Recent tradition has been to treat *Artibeus* Leach as monophyletic. *Enchisthenes* Andersen was considered part of *Artibeus* (e.g. Anderson et al. 1982; Handley 1976, 1987; Honacki et al. 1982; Koopman 1978; Simpson 1945), as well *Dermanura* Gervais (Trouessart 1897, and following authors until Owen 1987). Several authors, however, working at the molecular level, have suggested that *Artibeus* is paraphyletic (Koop & Baker 1983; Straney 1981; Straney et al. 1979; Tandler et al. 1986). Owen (1987), working at the morphological level, based on a phylogenetic analysis, expanded that theme and has suggested that *Artibeus* is polyphyletic. He placed the smaller species in the genus *Dermanura* Gervais 1856, while commenting that the relationships of *Enchisthenes hartii* and *Artibeus concolor* may not lie within *Dermanura*. Although retaining *hartii* and *concolor* under *Dermanura* in his discussion, elsewhere in the same publication (p. 61-63) Owen listed *Enchisthenes* and *A. concolor* apart from both *Artibeus* and *Dermanura*. In 1991, Owen proposed *Koopmania* as the name of a new genus to include *concolor*. Therefore, Owen (1987, 1991) proposed the split of *Artibeus* (*sensu lato*) into four genera: *Artibeus*, *Dermanura*, *Enchisthenes*, and *Koopmania*. Lim (1993), on the other hand, working at the morphological level, supplemented with karyotypic information, based on a phylogenetic analysis, did not refute the traditional systematic view of *Artibeus* being monophyletic. He suggested that previous analyses failed in finding such conclusion because they did not base the relationships of the taxa only on shared derived characteristics.

My research focuses on the large species of the traditionally recognized genus *Artibeus*. It is beyond the scope of this study to question taxonomic rank within *Artibeus*, (i.e., whether its component clades are genera or subgenera). I follow Owen (1987, 1991) to the extent that I recognize *Dermanura*, *Enchisthenes*, and *Koopmania* as subgenera of *Artibeus*; the large species of *Artibeus* comprise the subgenus *Artibeus*. The four subgenera are distinct from each other by the possession of advanced character states (see Diagnosis section under each subgenus and Phylogenetic Analysis section).

Artibeus (Artibeus) includes at least eight species: *A. amplus*, *A. fimbriatus*, *A. fraterculus*, *A. hirsutus*, *A. inopinatus*, *A. jamaicensis*, *A. lituratus*, and *A. obscurus* (Handley 1987, 1990, 1991). Koopman (1982), Owen (1987) and Nowak (1991) recognized two additional species, *A. intermedius* from Central America, and *A. planirostris* from South America. Davis (1984) revalidated *A. intermedius* to be a species distinct from *A. lituratus*. Earlier authors had considered it to be a subspecies of *A. lituratus* (Cabrera 1958; Goodwin 1969; Jones & Carter 1976). The problem, however, is not completely resolved, as individuals in the overlap zone were considered to be "probable hybrids" of *A. lituratus* and *A. intermedius* , and not variations within a single species. Moreover, Handley (1991) referred to *A. planirostris* as a subspecies of *A. jamaicensis*, ". . . intergrading with *A. j. fallax* Peters, but still recognizable as *A. j. planirostris* south to Mato Grosso [Brazil] and eastern Paraguay."

Concerning the phylogeny of the species of *Artibeus*, Owen (1987), working with all of the Stenodermatinae, could resolve only partially how the members of this genus are related. This is perhaps due to the selection of characters that would be valid for the entire subfamily.

The objectives of this research are:

1. To define and redescribe each species of *Artibeus (Artibeus)* Leach, with additional information about synonyms, type material, distribution, and natural history.
2. To do a phylogenetic (cladistic) analysis for *Artibeus (Artibeus)* to evaluate phylogeny, and to give new insights for conservation biology of the taxa.

MATERIALS AND METHODS

Material examined

Each species account is arranged in the following sequence: number of specimens of the species examined, collection locality of specimens, institutional abbreviation, catalog number, and sex. Geographic descriptors are in the sequence of country (capitalized) then state, province, department or district, followed by more specific locality data. Information on the material examined of the outgroups is placed in Appendix 1-3.

Abbreviations

The following abbreviations for institutions and collections are used for the examined material: MVZ – Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; USNM – National Museum of Natural History (formerly the United States National Museum), Washington, D.C., USA.

The following abbreviations for teeth are used: P4 - fourth upper premolar; M1 - first upper molar; M2 - second upper molar; m2 - second lower molar; M3 - third upper molar; m3 - third lower molar.

Morphometric Data

External and cranial measurements were made with digital or dial calipers, and data were recorded to tenths of a millimeter. Measurements were made on the left side of the specimens whenever possible.

Usually twenty specimens (10 males and 10 females) of each species were sampled for a set of four measurements: total length (head and body), forearm length, greatest length of skull, and maxillary toothrow length (Figures 1, 7, 9). Exceptions were: 1. *Artibeus fimbriatus*: Handley's data (1990) were used in this study because only six specimens were available for the whole set of measurements; 2. *Artibeus inopinatus*: Davis and Carter's data (1964) were used in this study because only three specimens were available for the whole set of measurements.

The cranial measurements were first defined by Handley in 1959, and the whole set, composed of nine measurements, was first used in 1960 by Handley. This set has proved to be useful for geographic comparisons (Handley 1960; Davis 1969, 1970a, 1970b, 1984; Owen 1988). Mean, maximum, and minimum are presented in the Description section of each species account.

Phylogenetic Analysis of ***Artibeus (Artibeus)***

1. Construction of Cladograms

The data were analyzed with the computer program "Hennig86" (Farris 1988). Cladograms were constructed with both the ie command, and the mhennig* and bb* commands in combination. To polarize the characters, outgroup comparison was used (Kluge & Farris 1969; Farris 1982). If a character state occurs in the ingroup (subgenus *Artibeus*) and the outgroup, it is most parsimonious (i.e. logical) to conclude that the state would be the primitive character state; the alternate character states would be derived (advanced) character states. *Dermanura*, *Enchisthenes* and *Koopmania*, considered as other subgenera of *Artibeus*, were used as outgroups to root the tree. *Enchisthenes* and *Koopmania* are monotypic, but *Dermanura* has at least eight species; *Artibeus (Dermanura) gnomus* was selected to represent the genus in this analysis because of the large number of specimens at the USNM, although all other species were studied for the polarization of the characters to make sure it does not vary. *Uroderma* and *Platyrrhinus* (*Vampyrops* is the name commonly used, but see Gardner & Ferrell 1990), genera considered closely related to *Artibeus* by Owen (1987) and Gardner (1977a), were used as extra outgroups for the characters that varied within the outgroups (Characters 7, 8, 10, 20, 23, 25, 26, 29).

To determine transformation series of the states of multistate characters, the method described by Lipscomb (1992) was used (see also Lipscomb & Mickevich 1991). The character state transformation series list is in Appendix 4. See also Figures 1 and 5-10. The "MST" program (Farris 1989) was used to convert branching transformation series of the multistate characters to additive binary coding so that they could be read by "Hennig86."

2. Characters Used in the Phylogenetic Analysis

A set of 31 characters (11 external morphology and 20 cranial) that did not vary between members of a species at the specific level, was used in this analysis. Of the 31 characters, 27 were binary and 4 were multistate in the subgenus *Artibeus*.

Four other characters were not included in this analysis because they varied among the members of some species (Andersen 1908; Davis 1970; Hall 1981; Handley 1987, 1990; Herskovitz 1949, Husson 1962, 1978): 1. interfemoral membrane hairiness; 2. development of facial stripes; 3. wingtip coloration; 4. presence and size of the third upper molar (M3).

In my descriptions of morphology I follow the terminology of Davis (1970a, 1984), Davis & Carter (1964), Handley (1965, 1987, 1990, 1991), Koepcke & Kraft (1984), and Owen (1987).

Similarity criterion was applied to the characters that are multistate in the subgenus *Artibeus* to produce initial hypothesis of transformation. These are described individually below:

External Character:

Character 10. Lower edge of horseshoe of noseleaf (Figure 1b). *Artibeus* has horseshoe of noseleaf free, bound down and rimmed on lower edge, or completely fused. *Dermanura* and *Koopmania* have horseshoe of noseleaf free, and *Enchisthenes* has it completely fused. The extra outgroups *Uroderma* and *Platyrrhinus* have it free. Therefore, horseshoe of noseleaf free is considered the primitive character state. Horseshoe of noseleaf free is more similar to bound down and rimmed on lower edge than to completely fused; horseshoe of noseleaf completely fused is also more similar to bound down and rimmed on lower edge than to free. Based on the degree of similarity among the character states, the proposed transformation series of the states is: horseshoe of noseleaf free, bound down and rimmed on lower edge, and completely fused.

Cranial Characters:

Character 14 (Figures 4 & 5). Preorbital process development. *Artibeus* has preorbital process poorly, moderately, or well developed. *Dermanura*, *Enchisthenes*, and *Koopmania* have preorbital process only poorly developed. Therefore, preorbital process poorly developed is considered to be the primitive character state. Preorbital process poorly developed is more similar to moderately developed than to well developed; preorbital process well developed is also more similar to moderately developed than to poorly developed. Based on the degree of similarity among the character states, the proposed transformation series of the states is: poorly developed, moderately developed, and well developed.

Character 15. Postorbital process development (Figures 4 & 5). *Artibeus* has postorbital process poorly, moderately, or well developed. The postorbital process in *Dermanura*, *Enchisthenes*, and *Koopmania* is poorly developed. Therefore, postorbital process poorly developed is considered to be the primitive character state. Postorbital process poorly developed is more similar to moderately developed than to well developed; postorbital process well developed is also more similar to moderately developed than to poorly developed. Based on the degree of similarity among the character states, the proposed transformation series of the states is: poorly developed, moderately developed, and well developed.

Character 26. Development of hypocone of first upper molar (M1). Species of *Artibeus* have hypocone of M1 moderately to well developed. The hypocone of *Enchisthenes* and *Koopmania* moderately developed. *Dermanura* have hypocone of M1 absent or only weakly developed. The hypocone of M1 is also absent or weakly developed in the outgroups *Uroderma* and *Platyrrhinus*. Therefore, hypocone of M1 absent or weakly developed is considered to be the primitive character state. Hypocone of M1 absent or only weakly developed is more similar to moderately than to well developed; hypocone of M1 well developed would also be more similar to moderately than to weakly developed or absent. Based on the degree of similarity among the character states, the proposed transformation series of the states is: absent or only weakly developed, moderately developed, and well developed.

3. Character Matrix for *Artibeus (Artibeus)*

The distribution of the characters and character states among the species of *Artibeus (Artibeus)* is found in Appendix 5.

4. Phylogeny of *Artibeus (Artibeus)*

The hypothesis of evolutionary relationships (phylogeny) within *Artibeus (Artibeus)* is proposed following the principles of phylogenetic systematics (cladistics) first formalized by Hennig (1950, 1965, 1966) and subsequently discussed and expanded by many authors (e.g., Farris 1970, 1979, 1983; Nelson & Platnick 1981; Sober 1983; Schoch 1986; Wiley 1981). A goal of cladistics is to discover the hierarchical pattern of synapomorphies (=homologies) that must exist in nature, given that all life has a common origin. Therefore, cladistics reconstructs the sister-group relationships of taxa and not ancestor-descendant relationships. In a phylogenetic analysis, recognized taxa must be monophyletic in including all descendants of an hypothesized common ancestor. Monophyletic groups are defined on the basis of the possession of shared derived characters (synapomorphies). It is generally accepted that the species of *Artibeus (Artibeus)* form a monophyletic group (Brosset & Charles-Dominique 1990; Emmons & Feer 1990; Handley 1987, 1988; Jones et al. 1988; Owen 1987).

The hypothesis of sister-group relationships of the members of a group that requires the fewest *ad hoc* assumptions about character transformation (i.e. the principle of parsimony) is preferred and used in this study. The use of this principle does not imply that evolutionary mechanisms are necessarily always parsimonious. Neither is there an underlying assumption that convergencies (homoplasies) are relatively rare (Farris 1983). Parsimony is considered to be the best inferential principal for such analysis, because it provides the most informative summary of our observations (Farris 1979).

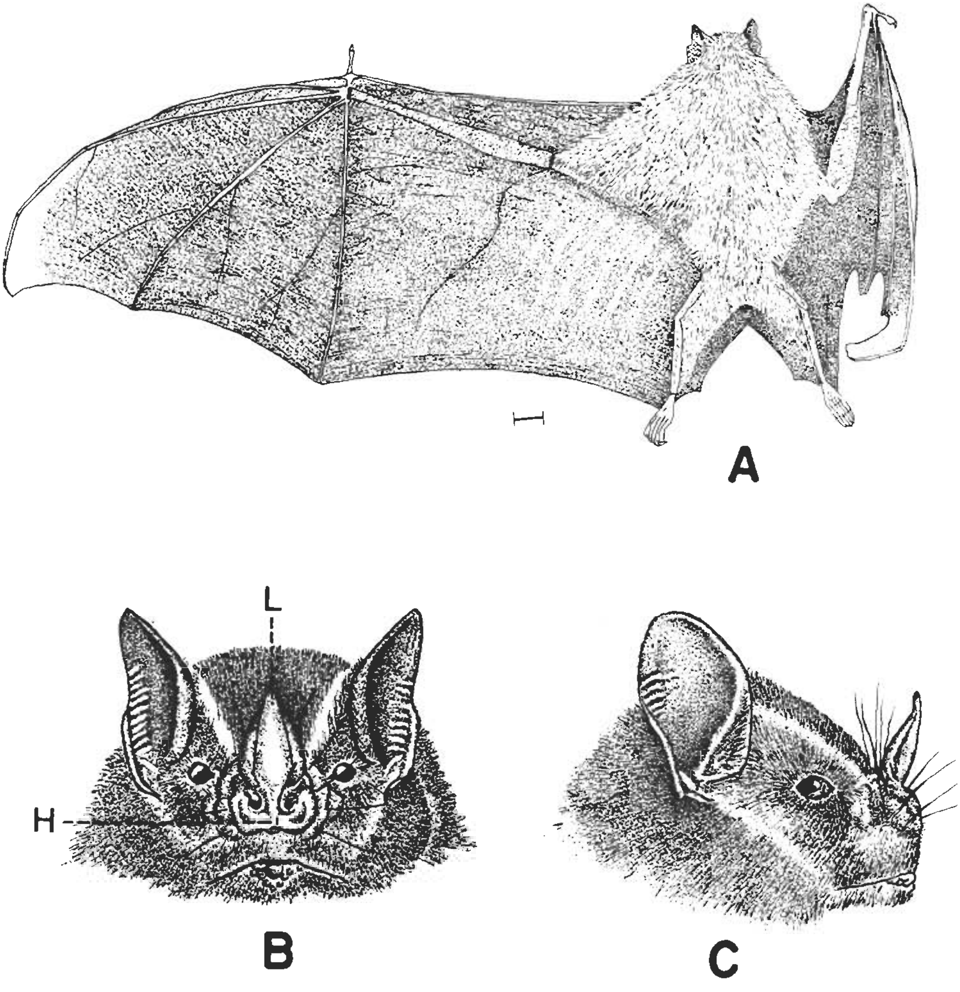

Figure 1 — External View of *Artibeus lituratus*. (A) Dorsal View of Body (F. forearm length, H. head and body (total length), P. plagiopatagium (wing membrane), U. uropatagium (interfemoral membrane)) (B) Front View of Head (H. horseshoe of noseleaf, L. noseleaf) (C) side view of head.

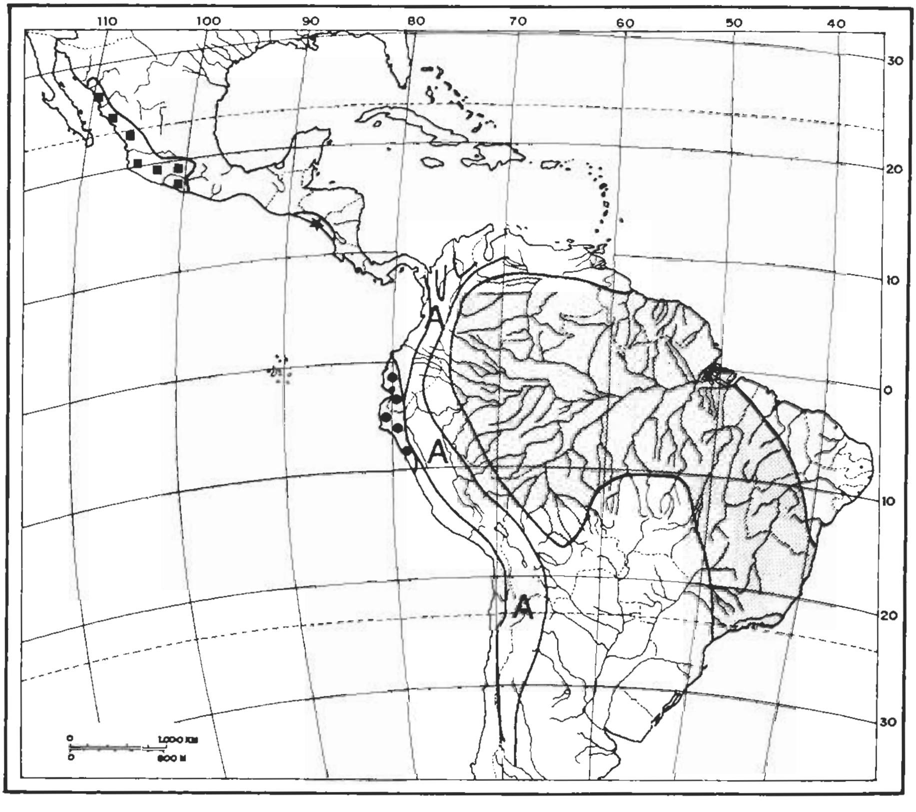

Figure 2 — Distribution of: ■ *A. hirsutus*; * *A. inopinatus*; ● *A. fraterculus*; ⁞⁞⁞ *A. obscurus*; (A – Andes).

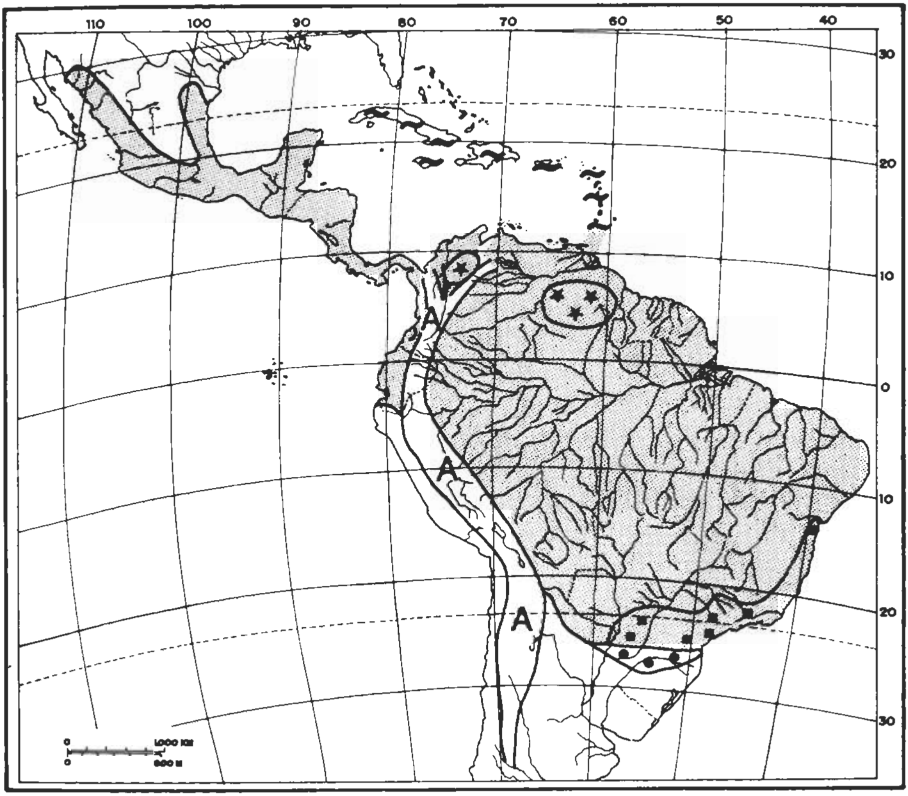

Figure 3 — Distribution of: ▒ ~ *A. jamaicensis*; ▒ ● *A. lituratus*; * A. amplus; ■ *A. fimbriatus*; (A – Andes).

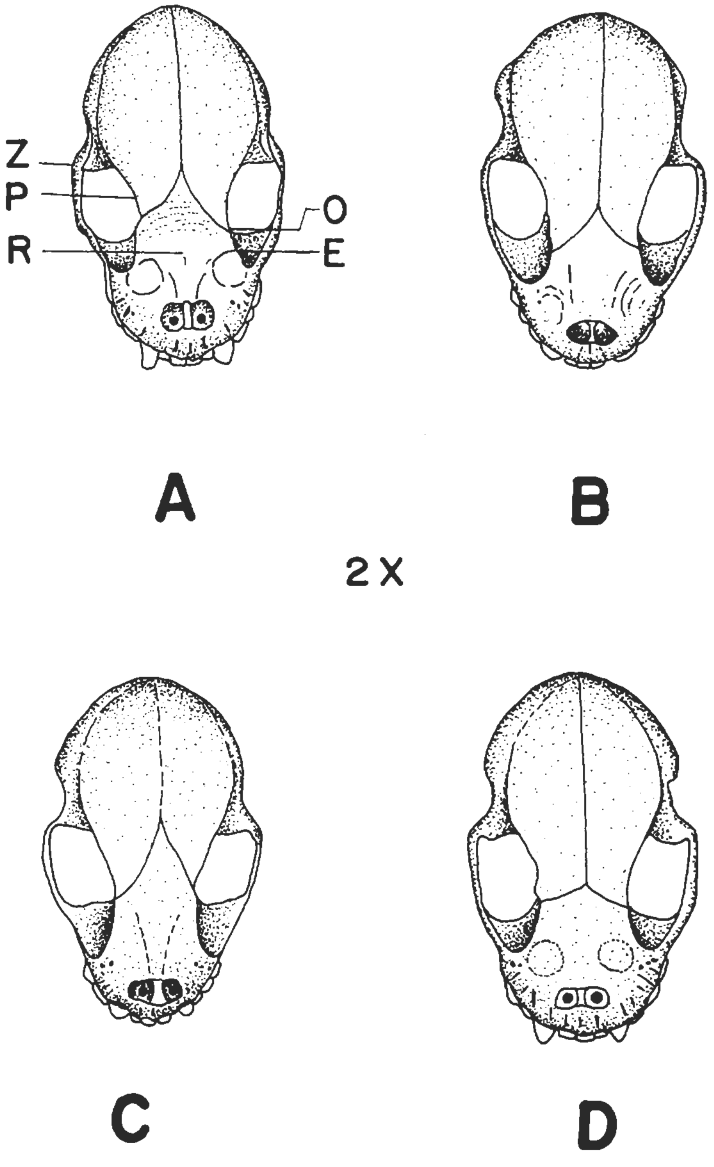

Figure 4 — Skull dorsal view of: (A) *A. fraterculus* (USNM 498941 ♀, Ecuador); (B) *A. hirsutus* (USNM 511396 ♀, Mexico); (C) *A inopinatus* (USNM 564900 ♀, Honduras); (D) *A. obscurus* (USNM 549451 ♂, Brazil); (E. preorbital process, O. postorbital process, P. postorbital constriction, R. rostrum, Z. zygomatic arch).

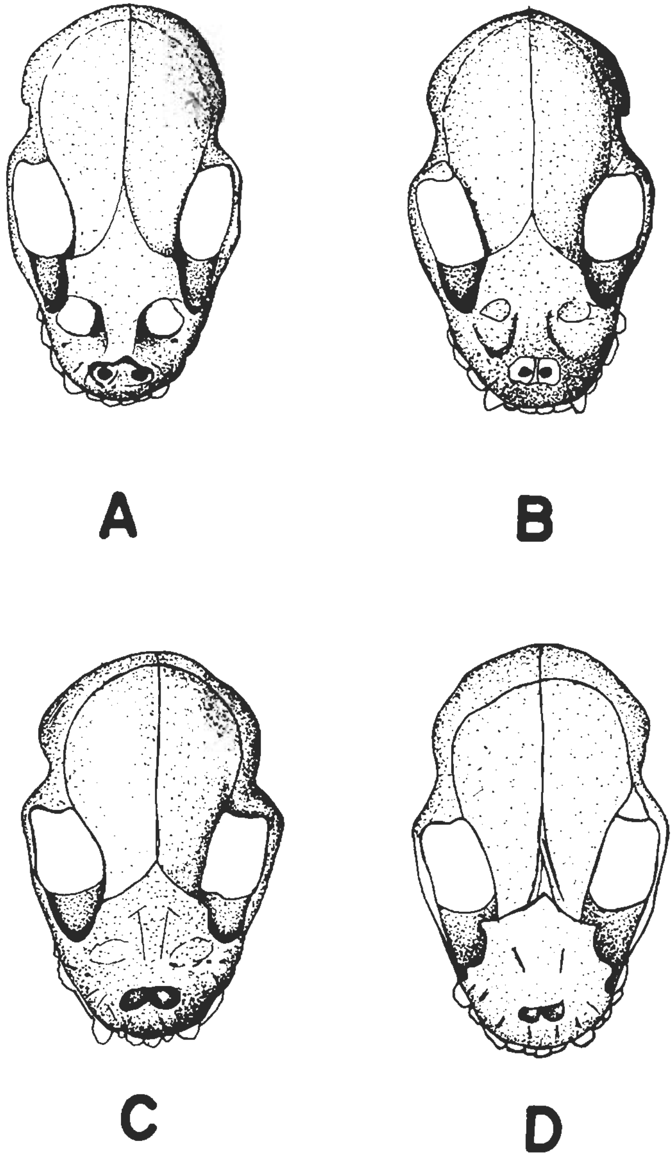

Figure 5 — Skull dorsal view of: (A) *A. amplus* (USNM 405309 ♀, Venezuela); (B) *A. fimbriatus* (MVZ 144431 ♀, Paraguay); (C) *A. jamaicensis* (USNM 499114 ♂, Peru); (D) *A. lituratus* (USNM 549476 ♀, Brazil).

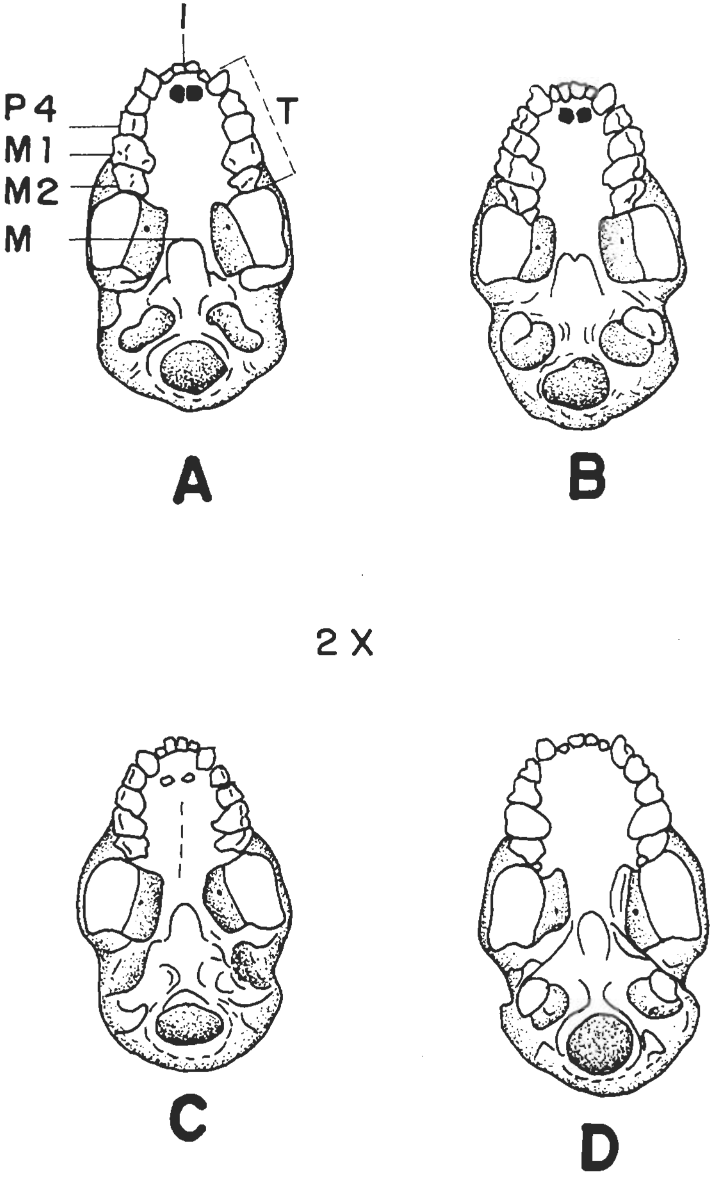

Figure 6 — Skull ventral view of: (A) *A. fraterculus*; (B) *A. hirsutus*; (C) *A. inopinatus*; (D) *A. obscurus* (I. inner incisors, M. anterior side of mesopterygoid fossa, M1. first upper molar, M2. second upper molar, P4. fourth upper premolar, T. maxillary toothrow length).

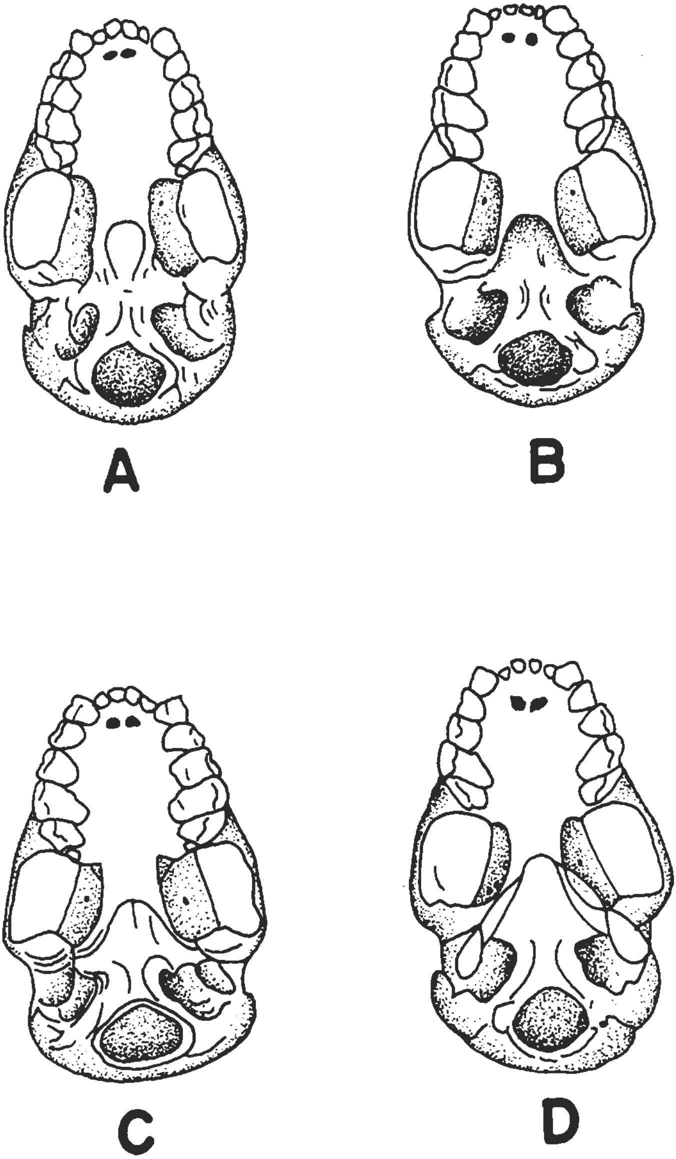

Figure 7 — Skull ventral view of: (A) *A. amplus*; (B) *A. fimbriatus*; (C) *A. jamaicensis*; (D) *A. lituratus*.

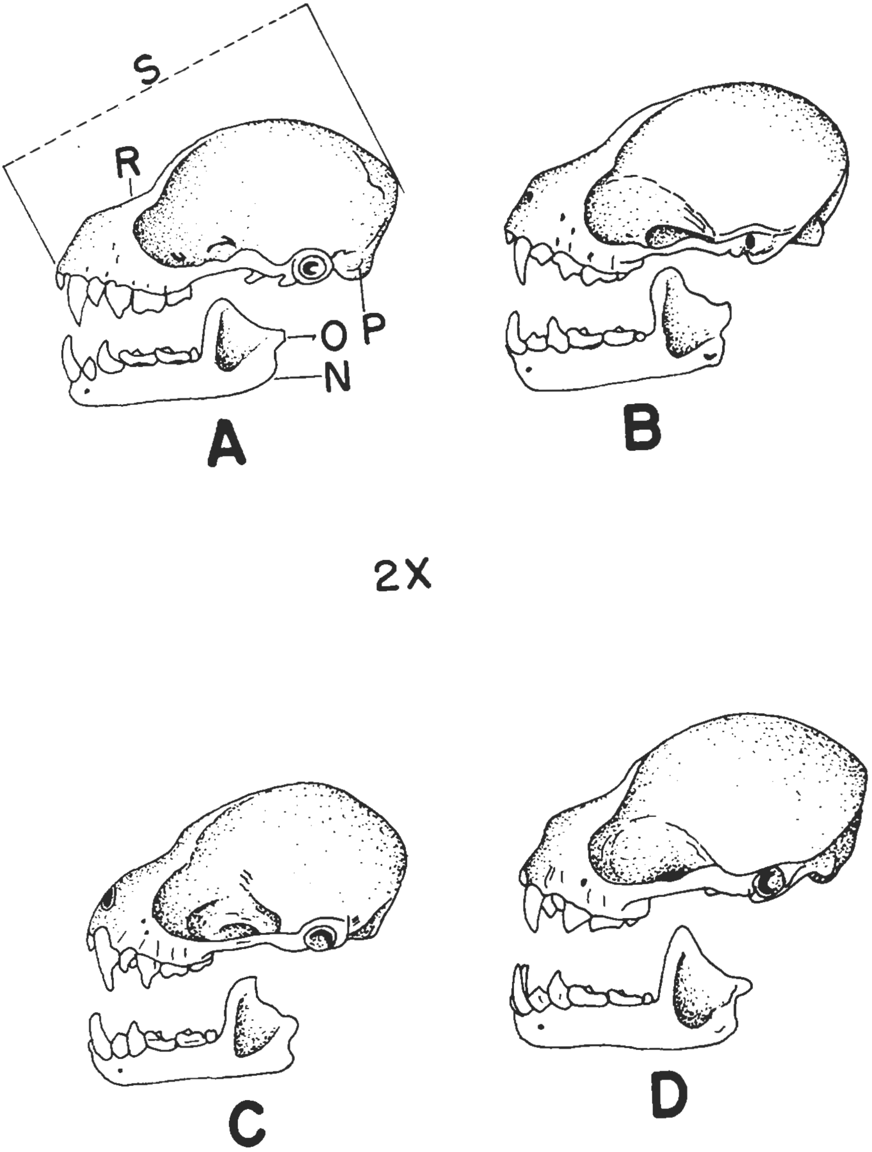

Figure 8 — Skull lateral view of: (A) *A. fraterculus*; (B) *A. hirsutus*; (C) *A. inopinatus* ; (D) *A. obscurus* (N. angular process, O. condylar process, P. paraoccipital process, R. rostrum, S. greatest length of skull).

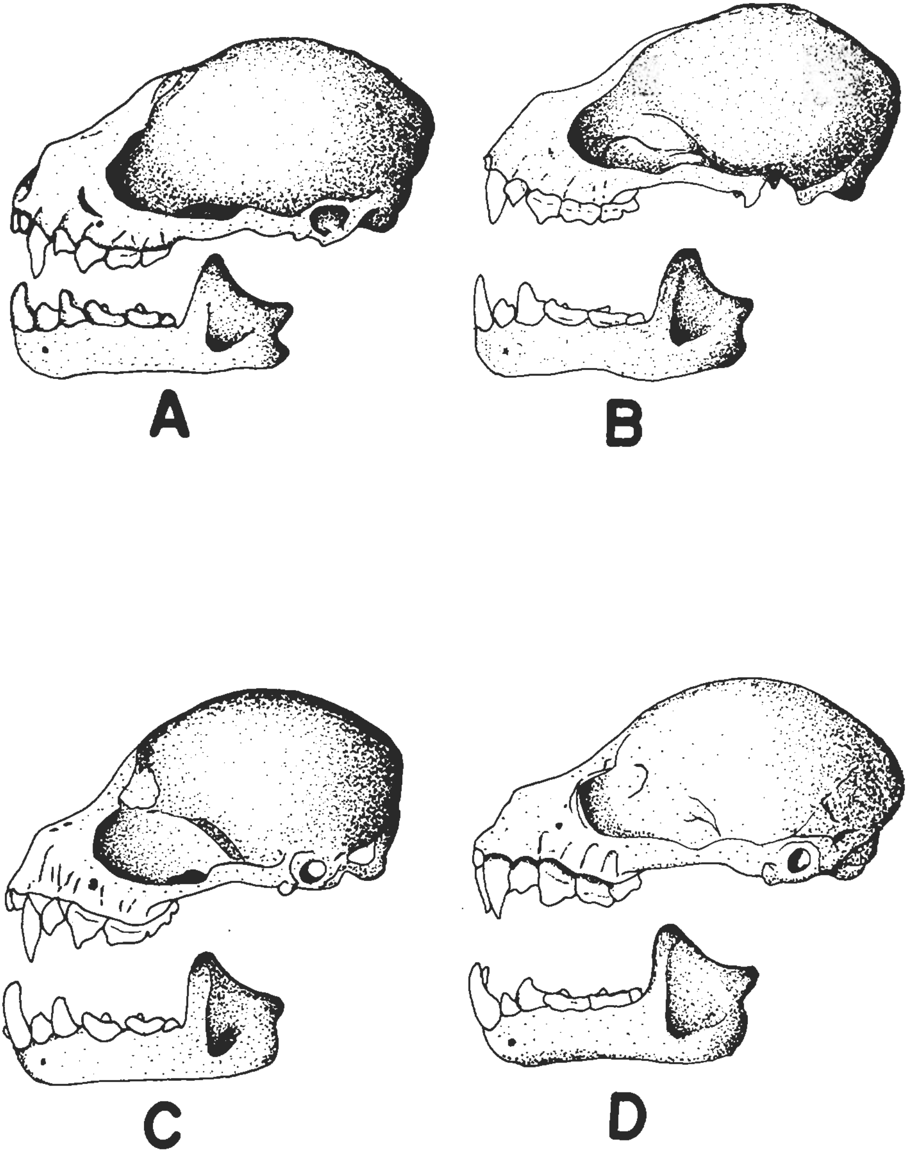

Figure 9 — Skull lateral view of: (A) *A. amplus*; (B) *A. fimbriatus*; (C) *A. jamaicensis*; (D) *A. lituratus*.

SYSTEMATIC TREATMENT

Artibeus (Dermanura) Gervais, 1856
Lesser Artibeus

Synonyms

Dermanura Gervais, 1856: 36; type species *Dermanura cinereum* Gervais, 1856, by monotypy.

Desmanura Kappler, 1881: 163 (incorrect subsequent spelling of *Dermanura* Gervais).

[Artibeus (Dermanura)] cinereum: Trouessart, 1897: 160 (name combination).

Dermanura: Owen, 1987: 47 (first modern use of *Dermanura* Gervais, 1856).

Diagnosis

Noseleaf longer than wide, index about 2.00 (1.92-2.13); paraoccipital process poorly developed; hypocone of first upper molar (M1) absent or weakly developed. Condylar (articular) process prominent and projected conspicuously from ramus is shared only by *Enchisthenes*. Rostrum short (rostral index equal to or less than 0.28), and fourth upper premolar (P4) lingual cusp absent or poorly developed are additional characters shared by *Enchisthenes* and *Koopmania*.

Species

Artibeus (Dermanura) consists of eight recent species: *A. (D.) anderseni, A. (D.) aztecus, A. (D.) cinereus, A. (D.) glaucus, A. (D.) gnomus, A. (D.) phaeotis, A. (D.) toltecus*, and *A. (D.) watsoni*.

Distribution

Dermanura is found in the Neotropical Region from Mexico (Sinaloa, Durango, Nuevo León), south throughout Central America, Lesser Antilles (Grenada), Trinidad and Tobago, and South America to southern Bolivia (Santa Cruz), and southeastern Brazil (São Paulo) (for a summary see Hall 1981; Handley 1987; Honacki et al. 1982; Koopman 1982; Marques in press; Nowak 1991).

Artibeus (Enchisthenes) Andersen, 1906
Hart's Artibeus

Synonyms

Artibeus hartii Thomas, 1892b: 409; type locality "Trinidad," Trinidad and Tobago; restricted to Botanic Gardens, Port-of-Spain by Thomas (1893a: 163).

[Artibeus (Artibeus)] Harti: Trouessart, 1897: 160 (name combination).

Enchisthenes harti: Andersen, 1906b: 419 (generic description and name combination; type species *Artibeus hartii* Thomas, 1892b, by monotypy).

Artibeus (Enchisthenes) harti: Koopman, 1978: 13 (name combination).

Dermanura hartii: Owen, 1987: 47 (name combination).

Diagnosis

Plagiopatagium attached at ankle; noseleaf as long as wide, index about 1.00 (1.00 - 1.10); tragus with a pointed projection on the inner margin near the tip; crowns of inner upper incisors simple (not bifid), and pointed; metacone and metaconule of second upper molar (M2) set apart as distinct lobes from the rest of tooth by a deep fissure; third upper (M3) and lower molars (m3) relatively large (about 35% the size of M2 and m2 respectively). Anterior margin of mesopterygoid fossa V-shaped (with sharp medial notch), resulting in straight lateral borders, is shared with some species of *Dermanura*. Condylar process prominent, projecting conspicuously from ramus is shared with all species of *Dermanura* only. Rostrum short (rostral index equal to or less than 0.28), and fourth upper premolar (P4) lingual cusp absent or poorly developed are shared with *Dermanura* and *Koopmania*.

Species

Artibeus (Enchisthenes) is monotypic (*A. (E.) hartii*).

Distribution

Enchisthenes hartii is known from southern USA (Tucson, Arizona), Mexico, Central America, Trinidad and Tobago, northern and western Venezuela (Distrito Federal, Falcón, Territorio Federal del Amazonas), eastern Colombia (Antioquia), eastern Ecuador (Bolívar, Morona-Santiago, Napo, Pichincha), eastern Peru (Ayacucho, Cuzco, Junín, Piura), western Bolivia (Cochabamba, La Paz) (for a summary see Hall 1981; Jones & Carter 1976; Marques in press; Nowak 1991).

Artibeus (Koopmania) Owen, 1991
Plain Artibeus

Synonyms

Artibeus concolor Peters, 1865c: 357; type locality "Paramaribo (Surinam)."
[Artibeus (Uroderma) planirostre] concolor: Trouessart, 1897: 159 (name combination).
Dermanura concolor: Owen, 1987: 47 (name combination).
Koopmania concolor: Owen, 1991: 21 (generic description and name combination; type species *Artibeus concolor* Peters, 1865c, by original designation).

Diagnosis

Fur on dorsum conspicuously tricolored; plagiopatagium attached at base of toes; paraoccipital process absent or very poorly developed; third upper (M3) and lower molars (m3) medium-sized (about 20% the size of M2 and m2 respectively). The presence of a short rostrum (rostral index equal to or less than 0.28) and absent or poorly developed fourth upper premolar (P4) lingual cusp are shared with *Enchisthenes* and *Dermanura*.

Species

Artibeus (Koopmania) is monotypic (*A. (K.) concolor*).

Distribution

Koopmania concolor is in eastern Peru (Ucayali), eastern Colombia (Vaupés), central and southern Venezuela (Bolívar, Territorio Federal del Amazonas), Guianas, and northern Brazil (Amazonas, Ceará, Pará, Piauí, Rondônia) (for a summary see Acosta & Owen 1993; Honacki et al. 1982; Koopman 1982; Marques in press; Nowak 1991).

Artibeus (Artibeus) Leach, 1821
Greater Artibeus
(Figures 1, 2, 3)

Synonyms

Phyllostomus: Olfers, 1818: 224 (part, not *Phyllostomus* Lacèpéde, 1799).
Artibeus Leach, 1821: 75; type species *Artibeus jamaicensis* Leach, 1821, by monotypy.

Madataeus Leach, 1821: 81; type species *Madataeus lewisii* Leach, 1821, by monotypy.
Medateus Gray, 1827: 74 (incorrect subsequent spelling of *Madataeus* Leach).
Arctibeus Gray, 1838: 487 (incorrect subsequent spelling of *Artibeus* Leach).
Pteroderma Gervais, 1856: 34; type species *Pteroderma perspicillatum* Gervais, 1856 (= *Phyllostoma perspicillatum* Geoffroy St. Hilaire, 1810; not *Vespertilio perspicillatus* Linnaeus, 1758), by monotypy.
Artibaeus Gervais, 1856: 34 (incorrect subsequent spelling of *Artibeus* Leach).
Artobius Winge, 1892: 10 (incorrect subsequent spelling of *Artibeus* Leach).

Diagnosis

Rostrum relatively long (rostral index equal to or more than 0.29), and fourth upper premolar (P4) lingual cusp moderately to well developed. *Artibeus* may be further distinguished from *Dermanura*, *Enchisthenes*, and *Koopmania* by the following combination of character states: fur on the back bicolored or inconspicuously tricolored; wing membrane attached at side of foot; noseleaf longer than wide by 1.57 (1.41-1.75); tragus without a pointed projection on the inner margin near the tip; paraoccipital process moderately to well developed; anterior shape of mesopterygoid fossa U-shaped resulting in curved lateral borders; crowns of inner upper incisors bilobed (bifid) and not pointed; hypocone of first upper molar (M1) moderately to well developed; metacone and metaconule of second upper molar (M2) not separated as distinct lobes from the rest of tooth; third lower molar (m3) small (peg-like); condylar (articular) process not prominent, projecting sligthly from ramus.

Artibeus may be distinguished from *Dermanura* by having: noseleaf longer than wide by an index of 1.57, opposed to 2.00; paraoccipital process moderately to well developed; hypocone of M1 moderately to well developed; condylar (articular) process not prominent, projecting slightly from ramus.

Artibeus may be distinguished from *Enchisthenes* by having: plagiopatagium attached at side of foot; noseleaf longer than wide by 1.57 opposed to 1.00; tragus without a pointed projection on the inner margin near the tip; anterior shape of mesopterygoid fossa U-shaped, resulting in curved lateral borders; condylar (articular) process not prominent, projecting slightly from ramus; crowns of inner upper incisors bilobed (bifid) and not pointed; metacone and metaconule of M2 not set apart as distinct lobes from the rest of tooth; M3 small (peg-like), or absent; m3 small (peg-like).

Artibeus may be distinguished from *Koopmania* by having: bicolored or inconspicuously tricolored fur on the back; plagiopatagium attached at the side of the foot; paraoccipital process moderately to well developed; M3 small (peg-like) or absent; m3 small (peg-like).

Description

Total length (head and body): 70.0-104.0 mm; forearm length: 48.0-75.3 mm; weight: 25.0-87.0 g. Coloration ranges from pale brownish to blackish, with ventral parts usually paler than dorsum and variably frosted with white; fur pale at base; facial stripes vary from prominent to indistinct or absent; dorsal stripe absent. Plagiopatagium attached to the side of foot. Wingtips whitish, undifferentiated, or grayish. There is no tail, and the interfemoral membrane is variably broad and hairy; proximal ventral side of forearm hairy; proximal dorsal side of forearm hairy, or with only scattered hair, practically naked. Fur is soft, 4.0-12.0 mm long on rump; ears medium sized (length: 18.0-26.0 mm) and triangular in outline; noseleaf longer than wide by an index of 1.57, and lower edge fused or not; tragus without a pointed projection on the inner margin near the tip. Skull characteristically short and broad (length of rostrum slightly more than half that of braincase), although longer than in *Dermanura*, *Enchisthenes*, and *Koopmania* (rostral index equal to or more than 0.29, contrasting to equal to or less than 0.28). Rostral shield (orbitonasal shield) developed or not; preorbital and postorbital processes developed or not; paraoccipital process moderately to well developed; supraorbital ridges nearly parallel to each other or converge posteriorly; position of postorbital constriction variable; zygomatic arches subparallel or diverge markedly posteriorly. Anterior shape of mesopterygoid fossa U-shaped, with lateral borders curved, and lacking distinct medial notch; mesopterygoid fossa constricted or not posteriorly on basicranium. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow or broad. Maxillary toothrows converge anteriorly (V-shaped) or are nearly parallel to each other (U-shaped). Upper incisors larger than the lower and crowded between canines; inner upper incisors larger than the outer, bilobed (bifid), and not pointed. Canines well developed and lacking secondary cusps. Upper premolars have a large triangular outer cusp and a low, broad, and somewhat concave inner basin; fourth upper premolar (P4) lingual cusp moderately to well developed. Lower premolars similar to upper premolars, but broader relative to length and lacking a posteromedial basin. First and second molars broad, usually with low cusps; third molars are reduced in size (peg-like) or absent; hypocone of first upper molar (M1) moderately to well developed; metacone and metaconule of second upper molar (M2) not set apart as distinct lobes from the rest of tooth; metaconid of second lower molar (m2) set apart, or not, by a deep fissure from the rest of tooth. Dental formula 2/2 1/1 2/2 2-3/3 x 2 = 30-32.

The subgenus *Artibeus* presents 10 pairs of metacentric or submetacentric autosomes, and 4 pairs of subtelocentric elements. The karyotype is 2n = 30 or 30-31, FN = 56, however data are lacking for three species (*A. amplus*, *A. fimbriatus*, and *A. fraterculus*) (Baker et al. 1979).

The stomachs of three species of *Artibeus* (*inopinatus*, *jamaicensis*, *lituratus*), studied by Forman et al. (1979), are substantially more complex and more specialized than stomachs of non-frugivorous bats (e.g., the Phyllostominae and Glossophaginae); in addition, *Artibeus* have greatly enlarged cardiac vestibules that permit storage of relatively large amounts of plant material (=fruit juice).

Nominal Species

Artibeus amplus Handley, 1987 (Giant Artibeus)
Artibeus fimbriatus Gray, 1838 (Fringed-lip Artibeus)
Artibeus fraterculus Anthony, 1924 (Western Artibeus)
Artibeus hirsutus Andersen, 1906 (Hairy Artibeus)
Artibeus inopinatus Davis & Carter, 1964 (Lesser hairy Artibeus)
Artibeus jamaicensis Leach, 1821 (Common fruit bat)
Artibeus lituratus (Olfers, 1818) (Striped large Artibeus)
Artibeus obscurus (Schinz, 1821) (Black Artibeus)

Distribution

Artibeus (Artibeus) is found in the Neotropical Region (Figures 2, 3), from Mexico (Sinaloa and Coahuila) south throughout Central America, Caribbean Islands, and South America to Paraguay (Central, and President Ayes), southern Brazil (Rio Grande do Sul), and northern Argentina (Misiones, Salta, and Tucumán). It has been reported (probably erroneously; see remarks under *A. jamaicensis*) from the lower Florida Keys, USA (for a summary see Hall 1981; Honacki et al. 1982; Koopman 1982; Marques in press; Nowak 1991).

Remarks

Some important papers concerning the systematics of this genus are Andersen (1906, 1908), Davis (1969, 1970a, 1970b, 1984), Dobson (1878), Handley (1987, 1990, 1991), Hershkovitz (1949), Husson (1962), Koepcke & Kraft (1984), Koopman (1978, 1982), Kraft (1982), Lim (1993), Marques (in press), Miller (1907), Owen (1987, 1988, 1991), and Taddei (1969, 1979).

Key to the Species of *Artibeus (Artibeus)* Leach

1. Interfemoral membrane narrow (≤ 7.0 mm) 2
   Interfemoral membrane broad (≥ 10.0 mm) 3
2. Interfemoral membrane conspicuously hairy; posterior border of palate usually with a broad spine . . . . *Artibeus hirsutus*
   Interfemoral membrane moderately hairy; posterior border of palate without a broad spine . . . . *Artibeus inopinatus*
3. Molars 3/3 4
   Molars 2/3 6
4. Fur long (more than 8.0 mm) and blackish . . . . *Artibeus obscurus* (part)
   Fur short (equal or less than 8.0 mm) and brownish or grayish 5
5. Interfemoral membrane slightly hairy and fringed medially; horseshoe of noseleaf bound down; maxillary toothrows nearly parallel to each other . . . . *Artibeus amplus*
   Interfemoral membrane almost naked and not fringed medially; horseshoe of noseleaf usually free; maxillary toothrows converge anteriorly . . . . *Artibeus jamaicensis* (part)
6. Upper parts grayish-brown or yellowish-brown (palest of the South American *Artibeus*); M1 triangular shaped in occlusal view; hypocone of M1 well developed *Artibeus fraterculus*
   Upper parts usually brown to black; M1 not triangular shaped in occlusal view; hypocone of M1 not well developed 7
7. Facial stripes prominent and well defined (some Central American specimens less prominent), underparts not conspicuously frosted with white . . . . *Artibeus lituratus*
   Facial stripes narrow, weakly defined, or absent, underparts frosted with white 8
8. Interfemoral membrane and legs distinctly hairy, horseshoe of noseleaf bound down and rimmed on lower edge . . . . *Artibeus fimbriatus*
   Interfemoral membrane and legs slightly haired or appearing naked, horseshoe of noseleaf free, or bound down but not rimmed on lower edge 9
9. Fur short (equal or less than 8.0 mm) and gray brown . . . . *Artibeus jamaicensis* (part)
   Fur long (more than 8.0 mm) and blackish . . . . *Artibeus obscurus* (part)

Artibeus amplus Handley, 1987
Giant Artibeus
(Figures 3, 5, 7, 9)

Synonyms

Artibeus amplus Handley, 1987: 164; type locality "Kasmera, 21 km SW Machiques, Estado Zulia, Venezuela, 270 m."

Type material

Holotype - USNM 440932, adult female with suckling young, skin and skull, collected 15 April 1968 by N. E. Peterson, F. P. Brown, Jr., and J. O. Matson, Smithsonian Venezuelan Project.

The holotype was collected in a damp cave in a cliff along the Río Yasa across from the Kasmera Biological Station, in the eastern foothills of the Sierra de Perijá (Handley 1987: 164).

Diagnosis

Horseshoe of noseleaf bound down but not rimmed on the lower edge is unique among *Artibeus* species, but is present in *Enchisthenes*. Maxillary toothrow nearly parallel to each other (U-shaped) is unique also among *Artibeus* species, but is present in *Dermanura* and *Koopmania*. *A. amplus* may be further distinguished from other species of *Artibeus* by the following combination of character states: preorbital and postorbital processes moderately developed; supraorbital ridges nearly parallel to each other. *Artibeus amplus* is the only known host of *Strebla paramirabilis* Wenzel and *Trichobius assimilis* Wenzel (Diptera: Streblidae) (Handley 1987).

Description

Total length (head and body) 93.5 mm (80.0-104.0); forearm length 69.2 mm (65.0-73.2; 75.3 from Handley, 1987); skull greatest length 31.0 mm (30.3-32.0; 32.8 from Handley, 1987); maxillary toothrow length 11.2 mm (10.7-11.7). Coloration of fur of upper parts varies from blackish brown to brown; underparts conspicuously frosted with white; fur on the back (mid-dorsum) short; base of forearm hairy on dorsal and ventral sides; facial stripes present but obscure; interfemoral membrane broad (equal to or more than 10.0 mm), slightly hairy (dorsal side) and fringed medially. Plagiopatagium attached at side of foot; wingtips undifferentiated or grayish. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf bound down, not rimmed on lower edge, or sometimes free. Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29); rostral shield (orbitonasal shield) not developed, rostrum arched; preorbital and postorbital processes moderately developed; supraorbital ridges nearly parallel to each other; postorbital constriction well behind postorbital process; postorbital constriction broad (postorbital constriction/ skull greatest length equal to or more than 0.23); zygomatic arches subparallel; paraoccipital process moderately developed. Mesopterygoid fossa not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch) resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 3/3 x 2 = 32; maxillary toothrows nearly parallel to each other (U-shaped); inner upper incisors bilobed, but only slightly bilobed in some specimens; P4 lingual cusp moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 set apart as a distinct lobe from rest of tooth by a deep fissure; M3 small (peg-like) and practically uncusped; m3 small (peg-like), but cusped.

No information is available on the karyotype of this species.

Subspecies

Artibeus amplus is monotypic.

Distribution

Artibeus amplus is found in northern Colombia (Antioquia), northwestern and southern Venezuela (Apure, Bolívar, Territorio Federal del Amazonas, and Zulia), and Guyana (Mazaruni-Potaro). It probably occurs in adjacent parts of Brazil (Handley 1987; Lim & Wilson 1993; Marques in press; Ochoa G. et al. 1988).

Natural History

Artibeus amplus has been found in Venezuela mainly in evergreen forest, near streams and other moist areas as well as forest openings such as yards and orchards. Handley (1987) reported the species roosting in the "twilight" zone of caves. The known elevational range is from 24 to 1,200 m. The diet of *A. amplus* probably is primarily tree fruits. Little is known about its reproduction or other aspects of its biology. The holotype is an adult female that was with a suckling young when collected in April in a damp cave in a cliff along the Río Yasa across from the Kasmera Biological Station in the eastern foothills of the Sierra de Perijá (Handley 1987: 164). Based on material at the National Museum of Natural History (USNM), two lactating females were collected in Colombia in May. In Venezuela, seven were pregnant in February; one was lactating in February and another in April. Handley (1987) mentioned *Strebla paramirabilis* Wenzel and *Trichobius assimilis* Wenzel (Diptera: Streblidae) as ectoparasites recorded only from *A. amplus*. The only other known ectoparasite is a species of argasid tick (Jones et al. 1972). No information is available on endoparasites of this species.

Remarks

Artibeus amplus is the *Artibeus* sp. "D" of Handley (1976).

Material examined: 22 specimens

COLOMBIA. Antioquia: 25 km S and 22 km W Zaragoza, La Tirana, 520 m (USNM 499507 ♀, USNM 499508 ♀).

GUYANA. Potaro-Siparuni: Kaieteur Falls (USNM 565531 ♂).

VENEZUELA. Bolívar: 85 km SSE El Dorado, Km 125 (USNM 387390 ♀; USNM 387395 ♂); 20.8 km N Icabarú, El Pauji, 851 m (USNM 441176 ♂). Territorio Federal del Amazonas: Cerro Duida, Cabecera del Caño Culebra, 1,200 m (USNM 405304 ♀, USNM 405305 ♀, USNM 405306 ♂, USNM 405307 ♂, USNM 405308 ♀, USNM 405363 ♀); Cerro Duida, Caño Culebra, 800 m (USNM 405301 ♂); Río Cunucunuma, Belén, 150 m (USNM 405297 ♂, USNM 405313 ♀, USNM 405316 ♀, USNM 405322 ♀, USNM 405336 ♂, USNM 405339 ♀, USNM 405341 ♀). Zulia: 10 Km S and 18 Km W Machiques, Kasmera, 270 m (USNM 440932 ♀, holotype of *Artibeus amplus* Handley); 3 km S and 19 km W Machiques, Novito, 1,135 m (USNM 441228 ♀).

Artibeus fimbriatus Gray, 1838
Fringed-lipped Artibeus
(Figures 3, 5, 7, 9)

Synonyms

Arctibeus fimbriatus Gray, 1838: 487; type locality "Brazil;" restricted to "Morretes, at the coastal foot of the Serra do Mar, state of Paraná," by Handley (1990: 455).

Artibeus fimbriatus, Wagner, 1855: 627 (first use of name combination).

Artibeus perspicillatus: Dobson, 1878: 519 (part, not *Vespertilio perspicillatus* Linnaeus, 1758).

Artibeus grandis Dobson, 1878: 520 (*nomen nudum*).

Artibeus lituratus: Thomas, 1902: 59 (part, specimens from Morretes, Paraná, Brazil [Handley, 1990: 458]; not *Artibeus lituratus* Olfers, 1818).

Artibeus jamaicensis lituratus: Andersen, 1908: 272 (part, *Artibeus grandis* in synonymy and all British Museum (Natural History) specimens of *Artibeus fimbriatus* [see Handley, 1990: 458]).

Artibeus fimbriatus: Myers, 1982: 86 (first modern use of current name combination).

Type material

Holotype - British Museum (Natural History), unregistered, adult (male ?), damaged skin without head or skull, collector, and date of collection unknown (Handley 1990).

Diagnosis

Horseshoe of noseleaf bound down and rimmed on lower edge is unique to *Artibeus fimbriatus*. This species may be further distinguished from other species of

Artibeus by the following combination of character states: fur on the back (middorsum) long; preorbital and postorbital processes poorly developed; supraorbital ridges nearly parallel to each other.

Description

Forearm length average 67.3 mm (n = 33); skull greatest length average 31.1 mm (n = 20) (Handley 1990). Coloration of fur on dorsum dark sooty-brown; underparts a little paler and conspicuously frosted with white; fur on the back (middorsum) long, more than 8.0 mm; forearm hairy at base on dorsal and ventral sides; facial stripes moderately developed; interfemoral membrane broad (equal to or more than 10.0 mm) and moderately hairy (dorsal side); wing membrane attached at side of foot; wingtips whitish. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf bound down and rimmed on lower edge. Tragus without pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29); rostral shield not developed; rostrum arched; preorbital and postorbital processes poorly developed; supraorbital ridges nearly parallel to each other; postorbital constriction broad and well behind postorbital process; zygomatic arch subparallel; paraoccipital process moderately developed. Mesopterygoid fossa not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch), resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 2/3 x 2 = 30; maxillary toothrow converge anteriorly (V-shape); crowns of inner upper incisors bilobed (bifid), and not pointed; P4 lingual cusp moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 set apart as a distinct lobe from rest of tooth by a deep fissure; M3 absent; m3 small (peg-like), and cusped.

No information is available on the karyotype of this species.

Subspecies

Artibeus fimbriatus is monotypic.

Distribution

Artibeus fimbriatus has been found only in eastern and southern Brazil (Bahia, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina), and in eastern Paraguay (Canendiyu, Central, and Ñeembucú (Handley 1990; Marques in press).

Natural History

Artibeus fimbriatus is a common bat in the tropical humid forest near latitude 25°S and has been found from near sea level in several localities to 530 m at Cruzeiro, São Paulo, Brazil (Handley 1990). The diet of *A. fimbriatus* probably is primarily tree fruits. Although few data are available, bimodal polyestry is the probable reproductive pattern. In Paraguay a juvenile male was recorded in January, and a pregnant female in July; in Brazil (Paraná), a juvenile female was collected in March, and a juvenile male in April (MVZ and USNM collections). No information is available on parasites and diseases.

Remarks

This species was overlooked by systematists for more than 150 years, and Patten (1971: 23) regarded *A. fimbriatus* Gray, as a *nomen nudum*. Handley (1990: 455), on the other hand, after studying the holotype in the Natural History Museum of London (BMNH), resurrected and redescribed *A. fimbriatus* Gray. *Artibeus grandis*, as listed by Dobson (1878), is one of Gray's unpublished manuscript names.

The apparent hiatus in distribution between Paraguayan and Brazilian localities may be a result of inadequate collecting. Handley (1990: 455) wrote "the range of the species may skirt the *Araucaria* forest of the interior of southern Brazil." In 1991, Handley suggested that the low number of specimens recorded from eastern Brazil is due to the dramatic decrease in the coastal forest. We know that northeastern, eastern, and southern Brazil were mostly forest covered. There is a record of *A. fimbriatus* in eastern Brazil (Bahia), and then only in Rio de Janeiro (southeastern Brazil) with a gap between. This gap could be due to a lack of collection in the area or, as suggested by Handley (1990), a real gap because the forest in that area is practically gone.

Material examined: 20 specimens

BRAZIL. Paraná: Salto Grande (USNM 141390 ♀, USNM 141391 ♂). São Paulo: Iguape (USNM 542630 ♀, USNM 542631 ♀, USNM 542634 ♂, USNM 542635 ♀, USNM 542636 ♂, USNM 542638 ♀, USNM 542639 ♂); Peruíbe (USNM 542645 ♂, USNM 542646 ♀, USNM 542647 ♂); Bertioga, Varjão do Guaratuba (USNM 542650 ♀, USNM 542651 ♂, USNM 542652 ♂). Santa Catarina: specific locality unknown (USNM 122139 ♂)

PARAGUAY. Central: Asunción (MVZ 144424 ♀, MVZ 144425 ♀, MVZ 144431 ♀). Paraguarí: Sapucay [= Sapucaí], 300 m (USNM 105588 ♂).

Artibeus fraterculus Anthony, 1924
Western Artibeus
(Figures 2, 4, 6, 8)

Synonyms

Artibeus fraterculus Anthony, 1924: 5; type locality "Portovelo, Provincia del Oro, Ecuador; altitude, 2000 ft."

A[rtibeus]. j[amaicensis]. fraterculus: Hershkovitz, 1949: 447 (name combination).

Type material

Holotype - American Museum of Natural History (AMNH 47248), adult female, skin and skull, collected 12 July 1920 by H. E. Anthony.

Diagnosis

Hypocone of M1 well developed is unique to *Artibeus fraterculus*. This species may be further distinguished from other species of *Artibeus* by the following combination of character states: fur on the back with a conspicuous silvery tinge; preorbital process poorly developed; postorbital process moderately developed; supraorbital ridges converge posteriorly; postorbital constriction immediately behind postorbital process.

Description

Total length (head and body) 86.1 mm (72-102); forearm length 56.2 mm (53.4-58.6); skull greatest length 26.9 mm (25.3-27.6); maxillary toothrow length 9.8 mm (9.1-10.1). Coloration of dorsal fur grayish-brown or yellowish-brown; underparts conspicuously frosted with white; fur on the back (mid-dorsum) short (equal or less than 8.0 mm); base of forearm, both dorsal and ventral sides hairy; facial stripes moderately developed; interfemoral membrane broad (equal to or more than 10.0 mm), slightly hairy, and fringed medially; wing membrane attached at side of foot; wingtips undifferentiated or grayish. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf free. Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29); rostral shield not developed and rostrum arched; preorbital process poorly developed; supraorbital ridges converge posteriorly; postorbital process moderately developed; postorbital constriction broad and immediately behind postorbital process; zygomatic arches subparallel; paraoccipital process moderately developed. Mesopterygoid fossa not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch) resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 2/3 x 2 = 30; maxillary toothrows converge anteriorly (V-shaped); crowns of inner upper incisors bilobed (bifid) and not pointed; P4 lingual cusp moderately to well developed; hypocone of M1 well developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 set apart as a distinct lobe from rest of tooth by a deep fissure; M3 absent; m3 small peg-like), and cusped.

No information is available on the karyotype of this species.

Subspecies

Artibeus fraterculus is monotypic.

Distribution

Artibeus fraterculus is in western Ecuador (Guayas, Loja, and Manabí), and western Peru (Cajamarca, Lima, Piura, and Tumbes) (Albuja 1983; Marques in press).

Natural History

Artibeus fraterculus inhabits the arid, or semi-arid coastal zone of southern Ecuador and Peru from sea level to 1,600 m. This bat may roost in caves or tree holes. Its diet is insects and fruits (Albuja 1983). Based on Ecuadorian material in the USNM, a female was pregnant/lactating in November, others were either lactating in July and November or pregnant in October and November. These data suggest bimodal polyestry. No information is available on parasites and diseases.

Remarks

Artibeus fraterculus appears to be the only *Artibeus* widely distributed on the arid Pacific side of Peru (Koopman 1978), and Ecuador.

Material examined: 20 specimens

ECUADOR. Guayas: 5 km E Manglaralto, El Refugio (USNM 522461 ♂, USNM 522462 ♀, USNM 522463 ♀, USNM 522464 ♀, USNM 522465 ♀). Loja: ca. 10 km W Catacocha, Hacienda Almenital (USNM 535096 ♀); ca. 10 km W Catacocha, Hacienda Casanga (USNM 535107 ♂). Los Rios: ca. 12 km NE Vinces, Cerezo, Abras de Mantequilla (USNM 522467 ♀); 7 km SW Puebloviejo, El Papayo, near San Juan (USNM 498940 ♀, USNM 522466 ♀); ca. 12 km NE

Vinces, Hacienda Santa Teresita, Abras de Mantequilla (USNM 522471 ♂, USNM 522473 ♂; USNM 522474 ♂, USNM 522478 ♂, USNM 522479 ♂, USNM 522480 ♂, USNM 522481 ♂, USNM 522493 ♀, USNM 522494 ♂); 4 km SW Puebloviejo, Lima Paresa (USNM 498941 ♀).

Artibeus hirsutus Andersen, 1906
Hairy Artibeus
(Figures 2, 4, 6, 8)

Synonyms

Artibeus hirsutus Andersen, 1906: 420; type locality "La Salada, Michoacan, Mexico."

Type material

Holotype - USNM 126449, adult male, skin, collected 16 March 1903 by Nelson and Goldman, collector's number 16168.

Diagnosis

Interfemoral membrane (dorsal side) conspicuously hairy is a character unique among species of *Artibeus*. Facial stripes moderately developed distinguish *A. hirsutus* from *A. inopinatus*, its sister species. *A. hirsutus* may be further distinguished from other *Artibeus* by the following combination of character states: fur on back with conspicuous silvery tinge; interfemoral membrane narrow; preorbital and postorbital processes poorly developed; supraorbital ridges converge posteriorly; zygomatic arches diverge markedly posteriorly; mesopterygoid fossa constricted posteriorly on basicranium (internal margin of pterygoid with a ridge); metaconid of m2 not set apart from rest of tooth.

Description

Total length (head and body) 80 mm (70-89); forearm length 55.4 mm (53.7 - 57.3); skull greatest length 26.7 mm (25.3-27.6); maxillary toothrow length 9.8 mm (9.3-10.2). Coloration of dorsal fur drab with a conspicuous silvery tinge; underparts a little paler and conspicuously frosted with white; fur on the back (middorsum) short (equal to or less than 8.0 mm); base of forearm, both dorsal and ventral sides, hairy; facial stripes moderately developed; interfemoral membrane narrow (equal to or less than 7.0 mm) and conspicuously hairy; wing membrane attached at side of foot; wingtips undifferentiated or grayish. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf free. Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29); rostral shield not developed and rostrum arched; preorbital and postorbital processes poorly developed; supraorbital ridges converge posteriorly; postorbital constriction broad and well behind postorbital process; zygomatic arches diverge markedly posteriorly; paraoccipital process moderately developed. Mesopterygoid fossa constricted posteriorly on basicranium (internal margin of pterygoid ridged); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch) resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 2-3/3 x 2 = 30-32; maxillary toothrows converge anteriorly (V-shaped); crowns of inner upper incisors bilobed (bifid) and not pointed; P4 lingual cusp moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 not separated as a distinct lobe from rest of tooth; M3 small (peg-like and practically uncusped), or absent; m3 small (peg-like), but cusped.

The karyotype is 2n = 30-31, FN = 56, with a Y_1, Y_2 chromosome system (X-autosome fusion); X and Y_1 chromosomes subtelocentric, and Y_2 chromosome acrocentric (Baker 1973; Baker et al. 1979).

Subspecies

Artibeus hirsutus is monotypic.

Distribution

Artibeus hirsutus is limited to tropical western Mexico (central Sonora southeastward to Morelos and Guerrero) (Jones & Carter 1976; Hall 1981).

Natural History

The hairy Artibeus is present in semi-desert lowlands, and arid uplands (Davis & Russel 1952); it occurs from near sea level to 2,575 m (Webster & Jones 1983). This bat roosts in abandoned mines, small caves, buildings, and beneath boulders (Webster & Jones 1983). Villa-R. (1967) reported *A. hirsutus* roosting in association with *Desmodus rotundus*, *Balantiopteryx plicata*, *Leptonycteris nivalis*, *Anoura geoffroyi*, and *Pteronotus parnellii*. The diet probably is fruits (Gardner 1977b); Villa-R. (1967) suggested that the general habits are similar to those of *A. jamaicensis* and *A. lituratus*.

Anderson (1960) suggested that *A. hirsutus* does not have a restricted breeding season. In support of this claim, Findley and Jones (1965) found that spermatogenesis, copulation, parturition, and lactation apparently occur at the same time in a population of Sonora, Mexico. Wilson's (1979) summary on reproduction cited pregnant females from February to September, except March, and lactating females from June, August, and September. Based on the USNM collection, juveniles were collected in May.

Webb and Loomi's (1977) summary of ectoparatsites listed *Perissopalla beltrani* (Trombiculidae) and *Tricobius intermedius* (Streblidae). No information is available on endoparasites and diseases.

Material examined: 19 specimens

MEXICO. Guerrero: Papayo (USNM 126553 ♀); 8.5 mi. S Río Mezcala (USNM 559630 ♂). Jalisco: Itzatlan (USNM 52101 ♀). Michoacan: La Salada (USNM 126447 ♂; USNM 126449 ♂, holotype of *Artibeus hirsutus* Andersen; USNM 126450 ♀). Morelos: 3 km S Tetecalita, Cueva del Salitre (USNM 559624 ♂, USNM 559627 ♀, USNM 559628 ♀). Nayarit: 2 mi. WNW Mesa del Nayar, Arroyo Taberna, 4,900 ft. (USNM 511392 ♀, USNM 511393, USNM 511394 ♀, USNM 511395 ♀, USNM 511396 ♀); Mesa del Nayar, 4,500 ft. (USNM 511397 ♀, USNM 511398 ♀, USNM 511399 ♀, USNM 511400 ♀); Rancho Sapotito, 3,500 ft. (USNM 511401 ♀).

Artibeus inopinatus Davis and Carter, 1964
Lesser hairy Artibeus
(Figures 2, 4, 6, 8)

Synonyms

Artibeus inopinatus Davis and Carter, 1964: 119; type locality "Choluteca, 10 ft, Depto. de Choluteca, Honduras."

Type material

Holotype - Texas Cooperative Wildlife Collections (TCWC 9517), adult female, skin and skull, collected 1 August 1963 by J. V. Mankins, original No. 4576.

Diagnosis

Interfemoral membrane (dorsal side) moderately hairy and facial stripes obscure or even indistinct, separate *A. inopinatus* from *A. hirsutus*, its sister species. *A. inopinatus* may be further distinguished from other *Artibeus* by the following combination of character states: fur on the back with a conspicuous silvery tinge; interfemoral membrane narrow; preorbital and postorbital processes poorly developed; supraorbital ridges converge posteriorly; zygomatic arches diverge markedly posteriorly; mesopterygoid fossa constricted posteriorly on basicranium (internal margin of pterygoid ridged); metaconid of m2 not set apart from rest of tooth.

Description

Forearm length 48 - 51 mm; skull greatest length average 25.5 mm (25.0 - 26.0; 8 ♀♀) (Davis & Carter 1964); USNM 564900 forearm length: 54 mm). Coloration of dorsal fur medium drab with a conspicuous silvery tinge; underparts conspicuously frosted with white; fur on back (mid-dorsum) short (equal to or less than 8.0 mm); base of forearm hairy on both dorsal and ventral sides; facial stripes obscure or indistinct; interfemoral membrane narrow (equal to or less than 7.0 mm) and moderately hairy; wing membrane attached at side of foot; wingtips undifferentiated or grayish. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf free. Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29); rostral shield not developed and rostrum arched; preorbital and postorbital processes poorly developed; supraorbital ridges converge posteriorly; postorbital constriction broad and well behind postorbital process; zygomatic arches diverge markedly posteriorly; paraoccipital process moderately developed. Mesopterygoid fossa constricted posteriorly on basicranium (internal margin of pterygoid with a ridge); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch) resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 2-3/3 x 2 = 30-32; maxillary toothrows converge anteriorly (V-shaped); crowns of inner upper incisors bilobed (bifid) and not pointed; P4 lingual cusp moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 not separated as distinct lobes from rest of tooth; M3 small (peg-like and practically uncusped) or absent; m3 small (peg-like) but still cusped.

The karyotype is 2n = 30-31, FN = 56, with a Y_1, Y_2 chromosome system (X-autosome fusion); X and Y_1 chromosomes are subtelocentric, and Y_2 chromosome is acrocentric (Baker 1979).

Subspecies

Artibeus inopinatus is monotypic.

Distribution

Artibeus inopinatus has been recorded from the Pacific versant of Middle America from El Salvador (Divisidero) to Nicaragua (Boaco and León) (Baker & Jones 1975; Davis & Carter 1964).

Natural History

The lesser hairy Artibeus is restricted to thorn-scrub habitat; from 50 m to 1,100 m in Honduras, Morazán (Dolan & Carter 1979). Davis and Carter (1964) found this bat roosting in unoccupied houses. The diet of *A. inopinatus* probably is fruits (Garder 1977b).

Pregnant females have been collected in March and May and lactating females in July in Honduras; females with enlarged nipples were collected in May and July in El Salvador and Honduras; and juveniles were collected in August in Honduras and Nicaragua (Baker & Jones 1975; Davis & Carter 1964; Dolan & Carter 1979; Webster & Jones 1983, USNM collection). No information is available on parasites and diseases.

Material examined: 3 specimens

HONDURAS. El Paraíso: 4-5 km NE Soledad, Aldea La Paz (USNM 564898 ♂, USNM 564899 ♀). Valle: 10 km N Nacaome, Coray, Aldea Las Mesas (USNM 564900 ♀).

Artibeus jamaicensis Leach, 1821
Common fruit bat
(Figures 3, 5, 7, 9)

Synonyms

Artibeus jamaicensis Leach, 1821: 75; type locality "Jamaica."
Madataeus lewisii Leach, 1821: 81; type locality "Jamaica."
Phyllostoma planirostre Spix, 1823: 66; type locality "suburbiis Bahiae;" identified as Salvador, Estado da Bahia, Brazil, by Carvalho (1965: 61).
Arctibeus planirostris: Gray, 1838: 487 (part, name combination).
? *Arctibeus lobatus* Gray 1838: 487; type locality unknown.
Artibeus carpolegus Gosse, 1851: 271; type locality "Content," Jamaica.
Artibeus fallax Peters, 1865: 355; type locality "Guiana . . . Surinam;" subsequently restricted to Cayenne, French Guiana, by Cabrera (1958: 89) whose restriction was invalidated when Husson (1962: 175) designated a lectotype and fixed the type locality as Suriname.

Artibeus macleayii Dobson, 1878: 520 (*nomen nudum*).

Dermanura eva Cope, 1889: 130; type locality "Island of Saint Martins, West Indies."

Artibeus coryi Allen, 1890: 173; type locality "St. Andrew's Island, Caribbean Sea."

[Artibeus (Uroderma)] planirostre: Trouessart, 1897: 159 (name combination).

[Artibeus (Artibeus)] Coryi: Trouessart, 1897: 160 (name combination).

[Artibeus (Dermanura)] eva: Trouessart, 1897: 160 (name combination).

Uroderma planirostris: Bangs, 1900b: 101 (name combination).

Artibeus hercules Rehn, 1902: 638; type locality "Eastern Peru."

Artibeus parvipes Rehn, 1902: 639; type locality "Santiago de Cuba, Cuba."

Artibeus insularis Allen, 1904: 231; type locality "Island of St. Kitts, W.I."

Artibeus yucatanicus Allen, 1904: 232; type locality "Chichenitza, Yucatan," Mexico.

[Artibeus (Uroderma)] hercules: Trouessart, 1904: 116 (name combination).

[Artibeus (Artibeus)] jamaicensis: Trouessart, 1904: 116 (name combination).

[Artibeus (Artibeus)] parvipes: Trouessart, 1904: 116 (name combination).

Artibeus planirostris trinitatis Andersen, 1906: 420; type locality "St. Anns, Trinidad," Trinidad and Tobago.

Artibeus planirostris grenadensis Andersen, 1906: 420; type locality "Grenada, W.I."

Artibeus jamaicensis aequatorialis Andersen, 1906: 421; type locality "Zaruma, Loja, S. Ecuador, 1000 m."

Artibeus jamaicensis praeceps Andersen, 1906: 421; type locality "Guadeloupe, W.I.."

Uroderma validum Elliot, 1907: 537; type locality "Cayenne, French Guiana, South America."

Artibeus planirostris fallax: Andersen, 1908: 242 (name combination).

Artibeus jamaicensis parvipes: Andersen, 1908: 261 (name combination).

Artibeus jamaicensis yucatanicus: Andersen, 1908: 263 (name combination).

Artibeus jamaicensis richardsoni Allen, 1908: 669; type locality "Matagalpa, Nicaragua."

A[rtibeus. j[amaicensis. trinitatis: Hershkovitz, 1949: 447 (name combination).

A[rtibeus]. j[amaicensis]. planirostris: Hershkovitz, 1949: 447 (name combination).

A[rtibeus]. l[ituratus]. fallax: Hershkovitz, 1949: 447 (name combination).

A[rtibeus]. l[ituratus]. praeceps: Hershkovitz, 1949: 447 (name combination).

A[rtibeus]. l[ituratus]. aequatorialis: Hershkovitz, 1949: 447 (name combination).

Artibeus lituratus hercules: Cabrera, 1958: 89 (name combination).

Artibeus hercules literatus Tamsitt and Valdivieso, 1963a: 263 (name combination, and incorrect subsequent spelling of *lituratus* Olfers, 1818).

Artibeus jamaicensis triomylus Handley, 1965: 299; type locality "Papayo, Guerrero, México."

Artibeus jamaicensis paulus W. B. Davis, 1970a: 119; type locality "7½ km WNW La Libertad, elevation ca. 500 feet, Department of La Libertad, El Salvador."

Artibeus jamaicensis schwartzi Jones, 1978: 2; type locality "Mesopotamia, 350 ft., Charlotte Parish, St. Vincent."

[A[rtibeus]. planirostris] fallax: Koopman, 1982: 275 (name combination).

[A[rtibeus]. planirostris] hercules: Koopman, 1982: 275 (name combination).

A[rtibeus]. j[amaicensis]. fallax: Handley, 1987: 164 (name combination).

A[rtibeus]. j[amaicensis]. hercules: Handley, 1987: 164 (name combination).

A[rtibeus]. j[amaicensis]. aequatorialis: Handley, 1987: 164 (First modern use of *Artibeus jamaicensis aequatorialis* Andersen, 1906).

Type material

Holotype - British Museum (Natural History), not numbered, adult of undetermined sex, probably female, skin, collected by J. S. Redman, date of collection unknown. The type locality is not specified in the specimen label, but Leach stated that it came from Jamaica (Carter & Dolan 1978).

Diagnosis

Base of forearm (dorsal side) practically naked, with only scattered hair, is unique for *Artibeus jamaicensis*. This species may be further distinguished from other *Artibeus* species by the following combination of character states: horseshoe of noseleaf free; preorbital, and postorbital processes moderately developed; supraorbital ridges nearly parallel to each other; maxillary toothrows converge anteriorly (V-shaped).

Description

Total length (head and body) 85.8 mm (77 - 93); forearm length 63.1 mm (59.0-69.4); skull greatest length 29.3 mm (27.1 - 31.9); maxillary toothrow length 10.7 mm (9.8 - 11.6). Coloration of dorsal fur varies from pale brown or grayish brown to dark brownish or blackish, sometimes slightly tinged with gray; underparts slightly paler, and conspicuously frosted with white; fur on the back (mid-dorsum) short (equal to or less than 8.0 mm); base of forearm hairy on ventral side, but practically naked (scattered hair) on dorsal side; facial stripes moderately developed, obscure, or indistinct; interfemoral membrane broad (equal to or more than 10.0 mm), practically naked, and not fringed medially; wing membrane attached at side of foot; wingtips whitish, grayish, or undifferentiated. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf usually free (lower edge rarely fused). Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29), rostral shield not developed, and rostrum arched; preorbital and postorbital processes moderately developed; supraorbital ridges nearly parallel to each other; postorbital constriction broad and well behind postorbital process; zygomatic arches subparallel; paraoccipital process moderately developed. Mesopterygoid fossa not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch), resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 2-3/3 x 2 = 30-32; maxillary toothrows converge anteriorly (V-shaped); crowns of inner upper incisors bilobed (bifid) and not pointed; P4 lingual cusp moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 set apart as a distinct lobe from rest of tooth by a deep fissure; M3 small (peg-like and practically uncusped) or absent; m3 small (peg-like, but still cusped).

The karyotype is 2n = 30-31, FN = 56, with a Y_1, Y_2 chromosome system (X-autosome fusion; Baker 1967, 1973). X chromosome large subtelocentric; Y_1 and Y_2 small acrocentrics, one about half the size of the other.

Subspecies

Hall (1981) recognized seven subspecies in tropical North America (México, Central America, and the West Indies): *A. j. jamaicensis*, *A. j. parvipes*, *A. j. paulus*, *A. j. richardsoni*, *A. j. triomylus*, *A. j. yucatanicus*, and *A. j. schwartzi*. Handley (1987) additionally recognized five subspecies in South America: *A. j. aequatorialis*, *A. j. fallax*, *A. j. hercules*, *A. j. planirostris*, and *A. j. trinitatis*.

Distribution

Artibeus jamaicensis is found from central Mexico (Sinaloa and Tamaulipas) south throughout Central and South America to southern Brazil (Santa Catarina), northern Argentina (Salta, and Tucumán), and Paraguay (Central). It occurs also on the Bahamas, the Greater and Lesser Antilles, and has been reported (probably erroneously, see remarks) from the lower Florida Keys, USA (for a summary see Hall 1981; Honacki et al. 1982; Koopman 1982; Marques in press; Nowak 1991).

Natural History

The common fruit bat occupies a variety of habitats, such as forest, swamp, savanna (including cerrado, cerradão, and caatinga), pasture, yards, orchard, and cropland. In South America, it occurs on both sides of the Andes, except in the highest and driest places. Its altitudinal range is from sea level to 2,300 m at Hacienda Moyobamba, Peru (Albuja 1983; Brosset & Charles-Dominique 1990;

Emmons & Feer 1990; Hall 1981; Handley 1976; Mares et al. 1981; Marques in press; Villa-R. 1967). However, it is most common at lower elevations (e.g., 83% of specimens reported by Handley (1976) from Venezuela were collected below 500 m).

This species roosts in tunnels, hollow logs, culverts, houses, the dark foliage of trees (e.g. mango and bread fruit), and occasionally in shallow, well-illuminated caves, under bridges, tree roots, and palm leaves (Goodwin & Greenhall 1961; Handley 1976; Husson 1978; Kunz 1982; Morrison & Handley 1991; Tuttle 1968, 1976; Villa-R. 1967). Morrison and Handley (1991), working on Barro Colorado Island, Panama, commented that foliage roots were used primarily by males, and tree hollows by harems, including females, their nursing young, and a single male. According to Kunz (1982), this bat makes opportunistic use of available roost sites.

Villa-R. (1967) reported that *A. jamaicensis* usually shares the same roost sites with *Mormoops megalophylla*, *Macrotus waterhousii*, *Anoura geoffroyii*, *Glossophaga soricina*, *G. leachii* (identified as *G. morenoi*), *Leptonycteris nivalis* (identified as *L. nivalis*), *L. curasoae* (identified as *L. yerbabuenae*), and *Desmodus rotundus*. Goodwin and Greenhall (1961) reported the common fruit bat in Trinidad and Tobago roosting in association with *Saccopteryx leptura*, *Noctilio leporinus*, *Carollia perspicillata*, *Uroderma bilobatum*, *Artibeus lituratus*, and *A. glaucus* (identified as *A. cinereus*). Handley (1967) found the species most common near the forest floor in the vicinity of Belém, Pará, Brazil, where it was replaced by *A. lituratus* in the canopy.

Artibeus jamaicensis eats the fruits of canopy trees and, less commonly, flowers, leaves, and insects (e.g., Albuja 1983; Fleming et al. 1972; Goodwin & Greenhall 1961; Greenhall 1956; Handley & Leigh 1991; Handley et al. 1991; Heithaus et al. 1975; Howell & Burch 1974; Sazima & Sazima 1975; Tuttle 1968; for a summary see Gardner 1977b). Fleming et al. (1972) reported 4 species of fruits, of which *Ficus insipida* was the favorite of *A. jamaicensis*, in central Panama. Handley et al. (1991) also found the fruit of *Ficus insipida* to be favored by *A. jamaicensis* among the 17 species of fruits they recorded as eaten by this species on Barro Colorado Island, Panama. Goodwin and Greenhall (1961) recorded, in Trinidad and Tobago, 51 species of fruits, including a number of economically important species, consumed by the common fruit bat. Willig (1983) added the fruits of *Vismia* sp. which he found to be the predominant food consumed in Ceará, Brazil. Throughout most of its range, in terms of quantity, figs are probably the most important food consumed by the common fruit bat because of abundance and year-round availability.

Heithaus et al (1975) suggested that in Costa Rica, *A. jamaicensis*, although it is primarily frugivorous, apparently feeds heavily on nectar in the dry season. Gardner's (1977b) summary of feeding habits listed at least 92 species of plants consumed by the common fruit bat. Handley and Morrison (1991) reported group foraging at fruiting trees by *A. jamaicensis*.

Eisenberg (1989) suggested that owls, snakes, and the bat falcon, *Falco rufigularis*, may be significant predators. Howler monkeys (*Alouatta palliata*) and kinkajous (*Potos flavus*) compete with *A. jamaicensis* for figs (Handley and Leigh 1991), along with other bats, opossums, and a wide array of frugivorous birds.

In Panama *Artibeus jamaicensis* is seasonally polyestrous, has a postpartum estrus, and presents alternate periods of normal and delayed embryonic development (Fleming 1971; Wilson et al. 1991). Wilson (1979) summarized reproductive data and categorized the reproductive cycle as one of bimodal polyestry. The peaks of reproduction, however, seem to vary temporally according to latitude and longitude, and may reflect rain cycles and, ultimately, food abundance (Fleming et al. 1972; Handley & Leigh 1991; Heithaus et al. 1975; Wilson 1979; Wilson et al. 1991). In addition, the persistence of the pattern in captive animals suggests some measure of genetic control, as stressed by Wilson et al. (1991).

In Mexico (Sinaloa), pregnant females were collected in January, February, and April through July (Jones et al. 1972). On Barro Colorado Island, Panama, two peaks of pregnancy are recorded, one from January to March, and the other, from May to July; after the second cycle of births, a period of delayed embryonic growth of approximately three months, is followed by a period of normal development (Wilson et al. 1991). The same pattern was found in two other Panamanian communities by Fleming (1971), and Fleming et al. (1972). In western Costa Rica, pregnancy peaks are recorded about a month earlier than in Panama, probably because the dry season begins earlier as well (Fleming et al. 1972).

From west to east across South America, there is an apparent delay in breeding with pregnancy peaks in November for Ecuador, December-January for Colombia, January-February for Venezuela, and February for Brazil (eastern Pará). Pregnancy occurs even later (March-April) on Trinidad and Tobago. There is a second pregnancy peak in June for Ecuador, June-July for Venezuela, and July for Trinidad and Tobago (pregnancy data from Albuja 1983; Goodwin & Greenhall 1961; Wilson 1979; Handley, personal communication; and USNM collection).

A continuous or lack of a well defined breeding period has been reported in *A. jamaicensis* in Isla Providencia (Tamsitt & Mejia 1962), in Yucatan (Jones et al. 1973), in Colombia (Tamsitt 1966; Thomas 1972), and in southern Brazil (Taddei 1976).

Morrison (1979) described a harem mating system in Panamanian and Mexican populations of *A. jamaicensis*, with harems composed of 3 to 14 adult females, their young, and a single adult male. Morrison (1979) and Morrison and Handley (1991) determined that the system is based on male defense of tree hole roosts used by females. In Puerto Rico, however, harem groups occupy caves, suggesting that environmental factors promoting harem social organization in this species varies between populations and is influenced by the availability of roost sites (Kunz et al. 1983, Morrison 1979). Bachelor males and juveniles roost in foliage (Emmons & Feer 1990; Morrison & Handley 1991). Goodwin and Greenhall (1961) found colonies of up to 25 individuals of both sexes roosting in foliage on Trinidad and Tobago. Willig (1983) found evidence of sexual dimorphism with males larger than females in northeastern Brazil.

Villa-R. (1967) reported *A. jamaicensis* in Mexico infected with rabies at high rates. Goodwin and Greenhall (1961) also reported rabies in the species on Trinidad but not on Tobago. Antibodies to six arboviruses, three of which infect humans, were found in Brazilian *A. jamaicensis*: Catu, Eastern equine encephalitis, and Mucambo virus (Woodall *in* Constantine 1970). Other infections in *A. jamaicensis* include yeasts and yeastlike fungi (Mok et al. 1982); one species of acanthocephala, eight species of nematodes, four species of protozoans, and two species of trematodes (see Ubelaker et al. 1977). Webb and Loomis' (1977) summary of ectoparasites listed six species of ticks (Ixodidae, Argasidae), 17 species of mites (Ereynetidae, Gastronyssidae, Labidocarpidae, Macronyssidae, Myobiidae, Sarcoptidae, Spelaeorhynchidae, Spinturnicidae, Trombiculidae), and 23 species of batflies (Nycteribiidae, Streblidae) found on *A. jamaicensis*. Other recent reports and summaries (Brennan & Reed 1975; Furman 1972; Herrin & Tipton 1975; Reed & Breenan 1975; Saunders 1975; Tipton & Machado-Allison 1972; Villa-R. 1967; Wenzel 1976) have added 15 species of mites (Laelapidae, Macronyssidae, Spinturnicidae, Trombiculidae), 14 of batflies (Streblidae), and 2 of fleas (Hystrichopsyllidae, Rhopalopsyllidae) to the known ectoparasite fauna hosted by *A. jamaicensis*.

Remarks

Artibeus jamaicensis shows unusually high geographical variation in morphology. Due to their larger size, most authors have considered *A. j. fallax* and *A. j. hercules* to be synonyms of *A. lituratus*. However, they share *A. jamaicensis* apomorphies of weakly developed facial stripes, naked interfemoral membrane, and broad postorbital, and lack the *A. lituratus* apomorphies of strongly developed postorbital processes, and flattened rostrum. In addition, Koopman (1968) transferred *A. l. praeceps* back to *A. jamaicensis*, and invalidated even the subspecific status of *A. praeceps* because of the extent of its overlap with *A. jamaicensis*; therefore, *A. j. praeceps* joins the long list of synonyms of *A. j. jamaicensis*.

Many authors in the past 20 years have considered *Artibeus planirostris* a species distinct from *A. jamaicensis* (e.g., Albuja 1983; Bárquez 1988; Bárquez et al. 1991; Davis & Dixon 1976; Koepcke & Kraft 1984; Koopman 1982; Owen 1987, 1988; Redford & Eisenberg 1992; Smith & Genoways 1974). Handley (1991: 16), however, treated *A. planirostris* as a subspecies of *A. jamaicensis* "intergrading with *A. j. fallax* Peters, but still recognizable as *A. j. planirostris* south to Mato Grosso [Brazil] and eastern Paraguay." *A. j. fallax* in turn intergrades with *A. j. trinitatis* in central Venezuela. *Artibeus jamaicensis planirostris* is a small *A. jamaicensis* (forearm 56.0 - 63.1 mm) with a pale brown coloration, instead of larger and darker. However, there is no morphological character to place *A. planirostris* as a species separate from *A. jamaicensis*.

Koopman (1982) considered *Artibeus obscurus* (called either *A. fuliginosus* or *A. davisi* in the recent literature) to be a synonym of *A. jamaicensis*. Handley (1990), however showed that *A. obscurus* is distinct from *A. jamaicensis*. *Artibeus obscurus* has the following apomorphies not shared by *A. jamaicensis*: much darker coloration; much longer, softer fur; postorbital constriction immediately behind postorbital process, instead of well behind postorbital process; zygomatic arches diverge markedly posteriorly, and not subparallel.

The lectotype of *Phyllostoma planirostre* Spix was designated by Andersen (1908: 239) as the no. 65 (1903/9437) in the Zoologische Staatssammlung Munich (ZSM). Later, Kraft (1982: 315) designated another bat ([66]/1903/9438, ZSM) instead as the lectotype of *P. planirostre* Spix "because the corresponding one 1903/9437 is possibly juvenile or subadult"; he placed no. 65 (1903/9437) as the paralectotype of that species. Handley (1991: 14), however, invalidated Kraft's designation of the lectotype because of its prior selection by Andersen (1908). In addition, the specimen no. 66 (1903/9438) cannot be considered even as a paralectotype of *P. planirostre* Spix, because that bat actually represents the species *Artibeus fimbriatus* Gray, and not *P. planirostre* Spix as understood today.

Handley (1990) and Patten (1971) considered *Artibeus lobatus* Gray (1838) to be unrecognizable *nomen dubium*. *Artibeus macleayii*, listed by Dobson (1878), is one of Gray's manuscript names and, therefore, a *nomen nudum*. Carter and Dolan (1978) provided information and measurements on types of *Artibeus carpolegus* Gosse, *Artibeus fallax* Peters, *Artibeus jamaicensis* Leach, *Artibeus jamaicensis aequatorialis* Andersen, *Artibeus planirostris trinitatis* Andersen, *Madataeus lewisii* Leach, and *Phyllostoma planirostre* Spix. Lazell and Koopman (1985) reported *Artibeus jamaicensis* from the Lower Florida Keys, USA, based on a picture taken by L. Page Brown; they stated the presence of this species seems anomalous. Humphrey and Brown (1986), however, pointed out the record of *A. jamaicensis* in the Florida Keys is erroneous for two reasons: first, the species is misidentified, and second, there is no substantial evidence of a resident population.

Material examined: 51 specimens

ANGUILLA. 0.5 km S South Hill Village (USNM 544817 ♀, USNM 544819 ♀, USNM 544821 ♂, USNM 544824 ♂).

BAHAMA ISLANDS. Great Inagua: Inagua (USNM 289123 ♂); no specific locality (USNM 255657 ♂, USNM 255661 ♀, USNM 255671 ♂). Mariguana (=Mayaguana) Island: Abrams Hill (USNM 255582 ♀; USNM 255584 ♀).

BELIZE. Toledo: Columbia Forest Station (USNM 506504 ♂). Locality unknown (USNM 37888/5208 ♀).

BRAZIL. Pará: Belém, Fazenda Velha (USNM 361755 ♀, USNM 361756 ♂, USNM 361757 ♀, USNM 361759 ♂).

ECUADOR. Guayas: 20 km ESE Balao, Huerta Negra Tenguel (USNM 498942 ♂, USNM 498944 ♂, USNM 498947 ♀, USNM 498948 ♀).

MEXICO. Chiapas: 10 mi. E Chiapa del Corzo, Mountains (USNM 554281 ♀); Upio Ocosingo, Ejido La Gloria, Río Lagartos (USNM 554857 ♀). Jalisco: 1 km N Chamela, Arroyo Chamela (USNM 559633 ♀); 10 mi. S Chamela, Rancho Cuitzmala (USNM 559634 ♂, USNM 559635 ♂, USNM 559638 ♀). Yucatan: Izmal (USNM 172082 ♂, USNM 172083 ♀); 7 km N Pibtuch, Rancho XChancal (USNM 564570 ♂, USNM 564571 ♂); 70 km N Tizimin, Rancho Santa Pilar (USNM 564572 ♀).

NICARAGUA. Managua: 3 km N Sabana Grande (USNM 337670 ♂). Río San Juan: Greytown (= San Juan del Norte) (USNM 16362/23360 ♀). Zelaya: Bonanza (USNM 337671 ♂, USNM 338768 ♀).

PANAMA. Darien: Tacarcuna Casita Camp (USNM 310012 ♀, USNM 310014 ♀); Tacarcuna Village Camp (USNM 310015 ♂, USNM 310016 ♂).

PARAGUAY. Central: Asunción (MVZ 144440 ♀, MVZ 144433 ♂, MVZ 144439 ♀).

PERU. Ucayali: 59 km SW Pucallpa (USNM 499114 ♂, USNM 499115 ♀, USNM 499118 ♂, USNM 499119 ♀).

ST. VINCENT (Lesser Antilles). St. George Parish: Ratho Mill (USNM 395029 ♀).

TRINIDAD AND TOBAGO. Trinidad: Barataria (USNM 536907 ♂, USNM 536910 ♀, USNM 536917 ♀, USNM 536921 ♂).

Artibeus lituratus (Olfers, 1818)
Striped large Artibeus
(Figures 1, 3, 5, 7, 9)

Synonyms

Phyllostoma perspicillatum: Geoffroy St. Hilaire, 1810: 176 (not *Vespertilio perspicillatus* Linnaeus, 1758).

[Phyllostomus] lituratus Illiger, 1815: 109 (*nomen nudum*).

[Phyllostomus] frenatus Illiger, 1815: 109 (*nomen nudum*).

Ph[yllostomus]. lituratus Olfers, 1818: 224; type locality "Paraguay;" restricted to Asunción by Cabrera (1958: 90), which may be incorrect (see remarks).

Ph[yllostomus]. frenatus Olfers, 1818: 224; type locality "Brasilien."

Phyll[ostoma]. superciliatum Schinz, 1821: 163; type locality "Ostküste von Brasilien;" identified as "Fazenda von Tapebuçú aufgehängt, welche etwas nördlich von Cabo Frio zwischen den Flüssen S. Joao und Macaché gelegen ist," Rio de Janeiro, Brazil, by Wied-Neuwied (1826: 200).

Arctibeus perspicillatus: Gray, 1838: 487 (part; not *Vespertilio perspicillatus* Linnaeus, 1758; name combination).

Stenoderma perspicillatum: D'Orbigny and Gervais, 1847: 41 (not *Vespertilio perspicillatus* Linnaeus, 1758; name combination).

Pteroderma perspicillatum: Gervais, 1856: 34 (not *Vespertilio perspicillatus* Linnaeus, 1758; name combination).

Artibeus intermedius Allen, 1897: 33; type locality "San José, Costa Rica."

Artibeus palmarum Allen and Chapman, 1897: 16; type locality "Port-of-Spain, Trinidad," Trinidad and Tobago; restricted to Royal Botanic Gardens, Port-of-Spain, by Goodwin and Greenhall (1961: 261).

[Artibeus (Artibeus)] perspicillatus: Trouessart, 1897: 160 (name combination).

Artibeus femurvillosum Bangs, 1900a: 73; type locality "La Concepcion, Colombia, 3000 feet altitude."

Artibeus lituratus: Thomas, 1900: 547 (name combination).

Artibeus rusbyi Allen, 1904: 230; type locality "Yungas, Peru (alt. 6000 ft.);" identified as 18°S in southeastern Cochabamba, Bolivia by Anderson et al. (1982: 9).

[Artibeus (Artibeus)] lituratus: Trouessart, 1904: 116 (name combination).

[Artibeus (Artibeus) lituratus] superciliatus: Trouessart, 1904: 116 (name combination).

[Artibeus (Artibeus)] intermedius: Trouessart, 1904: 116 (name combination).

[Artibeus (Artibeus)] palmarum: Trouessart, 1904: 116 (name combination).

A[rtibeus]. j[amaicensis]. dominicanus Andersen, 1908: 249 (*nomen nudum*).

Artibeus jamaicensis lituratus: Andersen, 1908: 272 (part; name combination).

Artibeus jamaicensis palmarum: Andersen, 1908: 278 (part; name combination).

Artibeus lituratus palmarum: Hershkovitz, 1949: 445 (part; name combination).

Artibeus lituratus: Hershkovitz, 1949: 447 (first modern use of name combination).

Artibeus lituratus intermedius: Goodwin, 1969: 87 (name combination).

Artibeus intermedius koopmani Wilson, 1991: 230; type locality "María Cleofas, Tres Marías Islands, Nayarit, México."

Type material

Unknown (see Remarks for the species)

Diagnosis

Unique character states for *Artibeus lituratus* are: rostrum flat, shield developed; preorbital and postorbital processes well developed; postorbital constriction narrow; angular process broad. Lack of conspicuous white frosting on underparts is unique in *Artibeus*, but is also present in *Enchisthenes* and *Koopmania*. Paraoccipital process well developed is also unique among species of *Artibeus*, but is present also in *Enchisthenes*.

Description

Total length (head and body) 94.3 mm (83 - 103); forearm length 69.2 mm (62.8 - 74.2); skull greatest length 30.3 mm (27.3 - 32.6); maxillary toothrow length 11.0 mm (10.1 - 11.8). Coloration of fur usually chocolate brown, occasionally tinged with gray; underparts slightly paler, and not conspicuously frosted with white (some Mexican specimens show more evident frosting); fur on the back (mid-dorsum) short (equal to or less than 8.0 mm); base of forearm hairy on dorsal and ventral surfaces; facial stripes prominent and well defined or moderately developed; interfemoral membrane usually broad, and moderately hairy; wing membrane attached at side of foot; wingtips whitish, grayish, or undifferentiated. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf free, although in some specimens the lower edge is fused medially. Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral index equal to or more than 0.29); rostral shield developed and rostrum flat; preorbital and postorbital processes well developed (some specimens in Central America have preorbital processes less developed); supraorbital ridges nearly parallel to each other; postorbital constriction narrow and immediately behind postorbital process; zygomatic arches subparallel; paraoccipital process well developed, with exception of some Mexican specimens. Mesopterygoid fossa not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch) resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process broad. Dental formula 2/2 1/1 2/2 2/3 x 2 = 30; maxillary toothrows converge anteriorly (V-shaped); crowns of inner upper incisors bilobed (bifid) and not pointed; P4 lingual cusp moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not set apart as distinct lobes from the rest of tooth; metaconid of m2 set apart as a distinct lobe from the rest of tooth by a deep fissure; M3 absent; m3 small (peg-like), and cusped.

The karyotype is 2n = 30-31, FN = 56, with a Y_1, Y_2 sex chromosome system (X-autosome fusion; Baker 1967). Baker et al. (1979) described the sex chromosomes as subtelocentric or submetacentric X, subtelocentric or acrocentric Y_1, and submetacentric or acrocentric Y_2 chromosome. The differences they described may reflect normal variation, be an artifact of technique, or result from misidentification of taxa.

Subspecies

There are two subspecies of *A. lituratus* in South America (*A. l. lituratus* and *A. l. palmarum*). A third subspecies (*A. lituratus intermedius*, considered a distinct species by Davis 1984), apparently is confined to Central America and México (Hall 1981). A fourth subspecies (*A. l. koopmani*, described under *A. intermedius*) is present only in Tres Marías Islands, Mexico (Wilson 1991).

Distribution

Artibeus lituratus occurs from central Mexico (Sinaloa) south through Central and South America to southern Brazil (Rio Grande do Sul), northern Argentina (Misiones), and Paraguay (Central, and Presidente Ayes); Lesser Antilles, and Trinidad and Tobago (for a summary see Hall 1981; Honacki et al. 1982; Marques in press; Nowak 1991).

Natural History

Artibeus lituratus, like *A. jamaicensis*, is present in a variety of habitats, such as forest, swamp, marsh, savanna (including cerrado, cerradão, caatinga), palm groves, pasture, yards, orchard, and cropland at elevations from sea level to 2,620 m (Santa Elena, Colombia; Muñoz Arango 1990); although both species seem to be more abundant at elevations below 500 m (Brosset & Charles-Dominique 1990; Handley 1976; Mares et al. 1981; Reis & Peracchi 1987). Both species also are common in humid forest habitats; however, *A. lituratus* seems better able to tolerate more arid habitats (e.g., 34% versus 16% *A. jamaicensis* were caught in Venezuelan dry uplands; Handley 1976). Handley (1967) found that *A. lituratus* was the most abundant *Artibeus* in the forest canopy in the vicinity of Belém, Brazil, whereas at ground level *A. jamaicensis* was more common.

Several authors claimed that *A. lituratus* and *A. jamaicensis* use similar roost sites (Goodwin & Greenhall 1961; Handley 1976; Villa-R. 1967; for a summary see Tuttle 1976). Morrison and Handley (1991), working in Panama, listed a variety of roost sites that include foliage, cave-like recesses of canopy-height trees, and branches overhanging the water along the lake shore. A study of *A. lituratus* from Barro Colorado Island, Panama, shows that it roosts in sheltered sites in the foliage of trees and vines, rather than in the tree holes, as *A. jamaicensis* does (Morrison 1980).

Villa-R. (1967) reported *A. lituratus* in Mexico in association with *Pteronotus parnellii* (identified as *P. rubiginosus*), *P. personatus* (identified as *P. psilotis*), *Mormoops megalophylla*, *Macrotus waterhousii*, and *Desmodus rotundus*. Goodwin and Greenhall (1961) reported the species on Trinidad and Tobago roosting in association with *Saccopteryx bilineata*, *S. leptura*, *Uroderma bilobatum*, *A.*

jamaicensis, and *Desmodus rotundus*. In southern Brazil, Trajano (1985) reported *A. lituratus* roosting in association with *Peropteryx macrotis*, *Chrotopterus auritus*, *Phylloderma stenops*, *Trachops cirrhosus*, *Anoura caudifer*, *Carollia perspicillata*, *Sturnira lilium*, *Diphylla ecaudata*, *Desmodus rotundus*, and *Furipterus horrens*.

The diet of *A. lituratus* is mainly the fruits of canopy trees and, less commonly, flowers, leaves, and insects (e.g., Fleming et al. 1972; Goodwin & Greenhall 1961; Greenhall 1956; Heithaus et al. 1975; Muller & Reis 1992; for a summary see Gardner 1977b). Villa-R. (1967) mentioned that Mexican *A. lituratus* and *A. jamaicensis* have similar food habits. Handley et al., (1991) found the fruits of *Ficus insipida* to be favored by *A. lituratus* among at least five species of fruits they recorded as eaten by this species at Barro Colorado Island, Panama. In addition, Bonaccorso et al. (1980) reported in the same island *A. lituratus* dispersing large numbers of seeds of *Dipteryx panamensis*. Reis and Peracchi (1987) said that *A. lituratus* is an important seed disperser of at least 10 species of rainforest trees. Willig (1983) found the diet of populations in Ceará, Brazil, to be mainly *Vismia* spp. Figs (*Ficus* spp.) are an important food throughout the range of this species. Gardner's (1977b) summary of feeding habits listed at least 67 species of plants consumed by the striped large Artibeus. In French Guiana, Brosset and Charles-Dominique (1990) found that *A. lituratus* has a larger home-range than either *A. jamaicensis* or *A. obscurus*. They suggested this was linked to their ability to exploit the fruit crops of large trees in flocks (also see Handley & Morrison 1991).

Wilson (1979) classified the reproductive cycle of *A. lituratus* as one of bimodal polyestry. He suggested, however, that in the northern part of its distribution, *A. lituratus* produces only one young per year. Tamsitt and Valdivieso (1963b, 1965), on the other hand, claimed that reproduction in *A. lituratus* occurs throughout the year in Colombia. Taddei (1976) reported also lack of a well defined breeding period in southern Brazil. Pregnant females were reported for Mexico (Sinaloa) in February, April, June, and July (Jones et al. 1972). In Costa Rica, pregnant females were collected in January, February, May, and July suggesting a bimodal cycle; and in Panama, pregnant females were found in January, March through May, and August (Fleming et al. 1972). Peaks of pregnancy occur in October-November in Ecuador and Colombia, in February in Venezuela and Brazil (Pará), and in April-May in Trinidad and Tobago. There is a second pregnancy peak in June-July in Venezuela, July in Minas Gerais, Brazil, and August in Amazonas, Brazil (Goodwin & Greenhall 1961; Mumford & Knudson 1978; Reis & Peracchi 1987; Wilson 1979; Handley, personal communication; USNM collection).

Morrison (1980), observing only one adult male in each group of Panamanian *A. lituratus*, concluded that the species has a harem-based mating system. Willig (1983) found limited secondary sexual variation in populations in northeastern Brazil.

Villa-R. (1967) reported *A. lituratus* infected with rabies in Mexico. Goodwin and Greenhall (1961) also found this bat infected with rabies in Trinidad but not in

Tobago. Woodall (*in* Constantine 1970) reported the antibodies to five arboviruses isolated from Brazilian *A. lituratus*; three (Catu, Carapuru, and Utinga viruses) are infectious to humans. *Salmonella sandiego* (see Arata et al. 1968), *Blastomyces (Paracoccidioides) brasiliensis* (Grose & Tamsitt 1965), and *Scopulariopsis* sp. (Marinkelle & Grose 1966) have been found in Colombian populations. Mok et al. (1982a) reported on 11 fungal species of the genera *Candida* and *Kluyveromyces* isolated from populations in Amazonian Brazil. Endoparasites listed by Ubelaker et al. (1977) from *A. lituratus* include one species of cestode, one species of nematode, and five species of protozoans. Webb and Loomis' (1977) summary of ectoparasites listed four species of ticks (Argasidae, Ixodidae), seven species of mites (Gastronyssidae, Labidocarpidae, Macronyssidae, Psorergatidae, Spinturnicidae, Trombiculidae), and 12 species of batflies (Streblidae). Other reports (Brennan & Reed 1975; Herrin & Tipton 1975; E. K. Jones et al. 1972; Tipton & Machado-Allison 1972; Wenzel, 1976) have added a species of argasid tick, four spinturnicid and trombiculid mites, seven species of streblid batflies, and one species of pulicid flea to the known ectoparasite fauna hosted by *A. lituratus*.

Remarks

Olfers based *Phyllostomus lituratus* on Azara's (1801: 269) "chauve-souris obscure et rayée," which Azara did not collect. The bat came from "Pueblo mi amigo Don Pedro Blas Noseda" (Azara 1802: 291), which Azara said was near 27°S, more closely approximating the latitude of San Ignacio than that of Asunción. Therefore, Cabrera's (1958: 90) restriction of the type locality to Asunción is not appropriate.

Patten (1971: 48), in his Ph.D. dissertation, proposed a neotype for *Artibeus lituratus*, an adult male from Goiás, Brazil. The neotype locality is very far from the locality given by Azara(1802b) as Paraguay. Furthermore, since the neotype was never published, the designation is invalid.

Davis (1984: 10) considered *A. intermedius* to be a species distinct from *A. lituratus*. Earlier authors, on the other hand, had considered *A. intermedius* to be a subspecies of *A. lituratus* (Cabrera 1958; Goodwin 1969; Jones & Carter 1976). Davis (1984) listed size and facial stripe development as characters to separate the species. He considered intermediate individuals in the zone of sympatry to be "probable hybrids" of *A. lituratus* and *A. intermedius*, and not variations within a single species. He recorded *A. lituratus* in Central America mainly on the Gulf-Caribbean side, with a preference for tropical rainforest habitat, and *A. intermedius* in Central America mainly on the Pacific side, with a preference for drier tropical and subtropical habitats. I studied specimens of *A. lituratus* and *A. intermedius*, collected in Guatemala (El Petén) and Panama (Darien and Bocas del Toro). The two groups overlap in measurements, as well in development of facial stripes and other qualitative characters. It seems that *A. lituratus* and *A. intermedius* are ecologically more distinct than geographically, although with an intergradation zone. I found no morphological character to place *A. intermedius* as a species separate from *A. lituratus*. Therefore, until additional studies are made, e.g., molecular analysis, *A. intermedius* should be regarded as a subspecies of *Artibeus lituratus*.

Material examined: 173 specimens

BELIZE. Toledo District: San Anthony (USNM 506505 ♀, USNM 506506 ♂, USNM 506507 ♂, USNM 506508 ♂, USNM 506509 ♂, USNM 506510 ♀, USNM 506511 ♂, USNM 506512 ♀).

BOLIVIA. Beni: Reserva Beni, Río Cureraba, Biolat Zone 1 (USNM 564327 ♂, USNM 564328 ♀).

BRAZIL. Amapá: Serra do Navio (USNM 460494 ♂). Mato Grosso: 264 km N (by road) Xavantina (USNM 393749 ♂, USNM 393750 ♀). Minas Gerais: Viçosa (USNM 391091 ♀, USNM 391092 ♂, USNM 391093 ♂, USNM 391094 ♀). Pará: 50 km SSW Altamira, Island in Rio Xingu (Ilha Jabuti), 03°38'S, 52°22'W (USNM 549476 ♀, USNM 549478 ♂); Belém, Fazenda Velha (USNM 361764 ♂, USNM 361765 ♀).

COLOMBIA. Magdalena: El Salado (USNM 281017 ♂); Sierra Negra, Villanueva, Valledupar (USNM 281018 ♀, USNM 281019 ♀, USNM 281020 ♀, USNM 281021 ♂, USNM 281022 ♀). Valle: 2 km S Pance, ca. 20 km S and SW Cali (USNM 483847 ♀; USNM 483848 ♂; USNM 483850 ♂; USNM 483852 ♀).

COSTA RICA. San José: Fuentes (USNM 250313 ♀). Puntarenas Monteverde (USNM 565814 ♂).

ECUADOR. Guayas: 20 km ESE Balao, Huerta Negra, Tenguel (USNM 498964 ♂); 7 km S Balao, San Rafael (USNM 498965 ♀).

GUATEMALA. Baja Verapaz: Santa Barbara, Km 138.5 on road to Coban, Finca Raxija (USNM 564990 ♂). Petén: 60 km N Flores, Parque Nacional Tikal (USNM 564973 ♀, USNM 564974 ♂, USNM 564976 ♀, USNM 564978 ♀, USNM 564979 ♀, USNM 564980 ♂, USNM 564981 ♀, USNM 564982 ♀, USNM 564983 ♂, USNM 564986 ♀, USNM 564987 ♀, USNM 564988 ♂, USNM 564991 ♂); La Libertad (USNM 245138 ♀, USNM 245139 ♀). El Progreso: San Agustin Acasaguastlan, 4.5 km N San Agustin, Aldea Puerto Golpe, along river (USNM 564993 ♀, USNM 564994 ♂; USNM 564996 ♀, USNM 564997 ♂; USNM 564998 ♀; USNM 564999 ♀); San Agustin Acasaguastlan, 4.5 km N San Agustin, El Jute (USNM 565000 ♀, USNM 565001 ♀. Escuintla: Brito, 33 km SE Escuintla, Finca Las Mercedes (USNM 565007 ♀, USNM 565008 ♀). San Marcos: 10 km N Nuevo Progreso, Finca Eden (USNM 565002 ♂, USNM 565003 ♂, USNM 565004 ♂, USNM 565005 ♂, USNM 565006 ♂). Santa Rosa, Chiquimolilla (USNM 502267 ♂, USNM 502268 ♂, USNM 502269 ♂, USNM 502270 ♀). Zacapa: Río Hondo, Km 146 on road to CA-9, Jesus Maria (USNM 564992 ♂).

HONDURAS. El Paraíso: Soledad, Aldea La Paz (USNM 565009 ♀). Valle: 10 km N Nacaome, Coray, Las Mesas (USNM 565010 ♀); 13-14 km NE Nacaome, Mapachin, (USNM 565011 ♀, USNM 565013 ♂, USNM 565014 ♂, USNM 565015 ♂, USNM 565016 ♂).

MEXICO. Nayarit: Tres Marias Islands, Maria Cleofas (USNM 512351 ♀, USNM 512352 ♀, USNM 512353 ♀, USNM 512396 ♂, USNM 512397 ♂, USNM 512398 ♀, USNM 512400 ♀); Tres Marias Islands, Maria Madre (USNM 512316 ♂, USNM 512317 ♂, USNM 512318 ♂, USNM 512320 ♂, USNM 512321 ♂, USNM 512324 ♀); Tres Marias Islands, Maria Magdalena (USNM 512329 ♀, USNM 512334 ♂, USNM 512335 ♂, USNM 512336 ♂, USNM 512337 ♂, USNM 512339 ♂, USNM 512340 ♂); Tres Marias Islands, San Juanito (USNM 512402 ♀, USNM 512403 ♂); Playa Novillero (USNM 553895 ♀). Sinaloa: 2 km E Santa Lucia, Chirimollos (USNM 559669 ♀); 1 km N San Ignacio (USNM 553796 ♂, USNM 553797 ♂).

NICARAGUA. Zelaya: Bonanza (USNM 338769 ♂, USNM 338700 ♂).

PANAMA. Colón: Barro Colorado Island (BCI) (USNM 304927 ♂). Darien: Tacarcuna Village Camp (USNM 310130 ♂, USNM 310131 ♀, USNM 310132 ♀, USNM 310133 ♂, USNM 310134 ♀, USNM 310135 ♂, USNM 310136 ♀, USNM 310137 ♀, USNM 310138 ♂, USNM 310139 ♀, USNM 310140 ♀, USNM 310141 ♂, USNM 310142 ♂, USNM 310143 ♀, USNM 310144 ♀, USNM 310145 ♀, 310146 ♀, USNM 310147 ♀, USNM 310148 ♀, USNM 310149 ♂, USNM 310150 ♀, USNM 310151 ♀, USNM 310152 ♀, USNM 310153 ♂, USNM 310154 ♀, USNM 310155 ♀, USNM 310156 ♀, USNM 310157 ♀, USNM 310158 ♀, USNM 310159 ♀, USNM 310160 ♂, USNM 310161 ♀, USNM 310162 ♀, USNM 310163 ♀, USNM 310164 ♀, USNM 310165 ♀, USNM 310166 ♀, USNM 310169 ♀, USNM 310170 ♀, USNM 310171 ♀, USNM 310174 ♂, USNM 310175 ♀, USNM 310176 ♂, USNM 310177 ♂, USNM 310178 ♂, USNM 310179 ♂, USNM 310180 ♀, USNM 310181 ♀, USNM 310182 ♀, USNM 310183 ♂, USNM 310184 ♂, USNM 310185 ♂, USNM 310186 ♂, USNM 310187 ♂, USNM 310188 ♂, USNM 310189 ♂, USNM 310190 ♂, USNM 310191 ♂). San Blas: Mandinga (USNM 305551 ♂, USNM 305556 ♀). Panamá: Cerro Azul (USNM 305557 ♂, USNM 305558 ♀).

TRINIDAD AND TOBAGO. Tobago: St. John Parish, 3 km W Charlotteville, Hermitage Estate, 25 m (11°19'N, 60°35'W) (USNM 540686 ♀); St. John Parish, Charlotteville (11°19'N, 60°33'W) (USNM 540687 ♂); St. Paul Parish, 4.5 km N Roxborough, Roxborough Valley and Ranch (USNM 540688 ♀, USNM 540690 ♂).

Artibeus obscurus (Schinz, 1821)
Black Artibeus
(Figures 2, 4, 6, 8)

Synonyms

Phyllost[oma]. obscurum Schinz, 1821: 164; type locality "Ostküste von Brasilien;" identified as "Villa Viçosa [= Marobá; according to Bokerman, 1957: 223] am Flusse Peruhype," Bahia, Brazil, by Wied-Neuwied (1826: 206). (17°55'S, 39°25'W).

?*Arctibeus fuliginosus* Gray, 1838: 487; type locality "S. America."

Artibeus davisi Patten, 1971: 12 (*nomen nudum*).

[A(rtibeus). jamaicensis] fuliginosus: Koopman, 1982: 275 (name combination).

A[rtibeus]. obscurus: Handley, 1990: 449 (first modern use of current name combination).

Type material

Holotype - American Museum of Natural History (AMNH 1334), adult male, skin with wings spread, skull inside, collected early in 1816 (Bokermann 1957) by Prince Maximilian zu Wied-Neuwied (Handley 1990).

Diagnosis

Artibeus obscurus may be distinguished from other *Artibeus* species by the following combination of character states: fur on the back (mid-dorsum) long, black; preorbital process poorly developed; postorbital process moderately developed; supraorbital ridges converge posteriorly; postorbital constriction immediately behind postorbital process; zygomatic arches diverge markedly posteriorly.

Description

Total length (head and body) 78.5 mm (73 - 84); forearm length 60.0 mm (56.9 - 63.9); skull greatest length 27.8 mm (26.9-29.1); maxillary toothrow length 9.7 mm (8.2 - 10.6). Coloration of fur varies from blackish brown to dark brown on dorsum; underparts slightly paler, and conspicuously frosted with white; fur on back (mid-dorsum) long (more than 8.0 mm); base of forearm on dorsal and ventral sides hairy; facial stripes obscure or indistinct; interfemoral membrane broad (equal to or more than 10.0 mm), practically naked, and not fringed medially; wing membrane attached at side of foot; wingtips whitish, grayish, or undifferentiated. Noseleaf longer than wide by an index of about 1.57; horseshoe of noseleaf free. Tragus without a pointed projection on inner margin near tip. Rostrum relatively long (rostral shield equal to or more than 0.29); rostral shield not developed and rostrum arched; preorbital process poorly developed; supraorbital ridges converge posteriorly; postorbital process moderately developed; postorbital constriction relatively broad and immediately behind postorbital process; zygomatic arches diverge markedly posteriorly; paraoccipital process moderately developed. Mesopterygoid fossa not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); anterior shape of mesopterygoid fossa U-shaped (no distinct medial notch), resulting in curved lateral borders. Condylar (articular) process not prominent, projecting slightly from ramus; angular process narrow. Dental formula 2/2 1/1 2/2 2-3/3 x 2 = 30-32; maxillary toothrows converge anteriorly (V-shaped); crowns of inner upper incisors bilobed (bifid) and not pointed; P4 moderately to well developed; hypocone of M1 moderately developed; metacone and metaconule of M2 not separated as distinct lobes from rest of tooth; metaconid of m2 set apart as a distinct lobe from the rest of tooth by a deep fissure; M3 small (peg-like and practically uncusped) or absent; m3 small (peg-like, but cusped).

The karyotype is 2n = 30-31, FN = 56, with a Y_1, Y_2 chromosome system (X-autosome fusion); X subtelocentric and Y_1 and Y_2 both acrocentric (Gardner 1977a).

Subspecies

Artibeus obscurus is monotypic.

Distribution

Artibeus obscurus occurs from Venezuela (Bolívar and Territorio Federal del Amazonas) south and east through the Guianas, and Brazil (to São Paulo and Mato Grosso), and west to the eastern lowlands of Colombia (Antioquia, Meta, and Vichada), Ecuador (Pastaza), Peru (Huánuco, Madre de Dios, Piura, and San Martin), and Bolivia (Santa Cruz de La Paz) (Handley 1990; Marques in press).

Natural History

Artibeus obscurus is found mainly in tropical humid forests and modified habitats, centered in the greater Amazon Basin, including palm groves, orchards, croplands, pastures, and yards (Handley 1990). The black *Artibeus* seems to be irregularly distributed in arid northeastern Brazil where Mares et al. (1981) reported the species in palm groves, but not from caatinga and cerrado (kind of savanna) habitats. The altitudinal range is sea level to 1,350 m (Bolivia); although in Venezuela 97% of specimens captured came from below 500 m (Handley 1976, 1990; Koopman 1978; Mares et al. 1981).

Little is known about the diet of *A. obscurus*. A. L. Gardner (personal communication) caught individuals in Colombia and Perú carrying figs (*Ficus* spp.)

as did C. O. Handley, Jr. (personal communication) at Belém, Pará, Brazil. Brosset and Charles-Dominique (1990) found a complete toothrow of an *A. obscurus* in the nest of the falcon *Falco deiroleucus* in French Guiana. The sparse information on reproduction suggests a pattern of bimodal polyestry. Pregnant females have been collected from February to May in Venezuela and Brazil (Pará), and from July to November in Perú, Venezuela, and Brazil (Mato Grosso); a lactating/pregnant female was collected in February in Ecuador (based on reproductive data from C. O. Handley, Jr., personal communication, and the USNM collection).

Antibodies to the Catu virus have been isolated from Brazilian *A. obscurus* (Woodall *in* Constantine 1970). Ectoparasites of *A. obscurus* include four species of mites (Macronyssidae and Spinturnicidae) and nine species of streblid batflies (Herrin & Tipton 1975; Saunders 1975; Wenzel 1976). Ueshima (1972: 17) recorded *Hesperoctenes* sp. (Hemiptera: Polyctenidae) in Venezuelan *A. obscurus* (= *A. fuliginosus*), but cautioned that the record "should be regarded as a possible contamination."

Remarks

Patten (1971) considered *Phyllostoma obscurum* Schinz and *Arctibeus fuliginosus* Gray as *nomena dubia* because the types were not known to exist. Cited as "in press," Patten (1971: 12) redescribed the black Artibeus in his Ph.D. dissertation under the name *Artibeus davisi*. However, *Artibeus davisi* is a *nomen nudum* because the name was never published.

Handley (1976: 31) began using *Arctibeus fuliginosus* Gray for the black Artibeus and other authors followed (e.g., Davis & Dixon 1976: 748; Eisenberg 1989: 171; Koopman 1978: 14; Koepcke & Kraft 1984: 76; Taddei & Reis 1980: 365). Later, Handley (1990: 447), like Patten (1971: 24), regarded *Arctibeus fuliginosus* Gray as a *nomen dubium*. Handley (1990: 448) resurrected *Phyllostoma obscurum* Schinz after concluding that a specimen (AMNH 1334) of the black *Artibeus* in the Wied-Neuwied collection in the American Museum of Natural History "must be the holotype of *Phyllostoma obscurum* Schinz."

In addition, Koopman (1982: 275) treated *Artibeus obscurus* (called either *A. fuliginosus* or *A. davisi* in the recent literature) as a subspecies of *A. jamaicensis*. Handley (1990), however, showed that *A. obscurus* is distinct from *A. jamaicensis*. *Artibeus obscurus* has the following apomorphies not shared by *A. jamaicensis*: much darker coloration; much longer, softer fur; postorbital constriction immediately behind postorbital process, instead of well behind postorbital process; zygomatic arches diverge markedly posteriorly, and not subparallel.

Material examined: 22 specimens

BOLIVIA. Beni: Reserva Beni, Río Cureraba, Biolat Zone 2 (USNM 564324 ♂, USNM 564325 ♀).

BRAZIL. Amapá: Serra do Navio, Rio Amapari, Terezinha (USNM 460485 ♂, USNM 460489 ♀). Mato Grosso: Serra do Roncador, 264 km N (by road) Xavantina, ca. 1,750 ft. (12°51'S, 51°46'W) (USNM 393734 ♂, USNM 393737 ♀, USNM 393740 ♀, USNM 393741 ♂). Pará: 52 km SSW Altamira, E bank Rio Xingu (03°39'S, 52°22'W) (USNM 549450 ♀, USNM 549451 ♂); Belém, IAN, Station A (USNM 361728 ♀, USNM 361729 ♂). São Paulo: São Sebastião (USNM 141389 ♂).

COLOMBIA. Vaupés: 50 km W Mitú, near mouth Caño Cubiyu, Río Vaupés (USNM 483809 ♂).

ECUADOR. Pastaza: Mera (USNM 548246 ♂, USNM 548249 ♀).

PERU. Pasco: Prov. Oxapampa, San Juan (USNM 364439 ♀, USNM 364440 ♂).

VENEZUELA. Bolívar: 28 km SE El Manteco, Los Patos (USNM 387547 ♀); 56 km SE El Manteco, Río Supamo (USNM 387544 ♂). Territorio Federal del Amazonas: Belén, Río Cunucunuma, 150 m (USNM 405505 ♂, USNM 405506 ♀).

PHYLOGENETIC ANALYSIS

Cladogram

Two equally parsimonious cladograms were obtained for the 31 characters given in Appendix 4. Each had a length of 55 steps, a consistency index (C.I.) of 0.70, and a retention index (R.I.) of 0.56. The two sets of commands used with "Hennig86" (ie; and mhennig*;bb*;) gave the same cladograms. Successive weighting did not reduce the number of trees. The only difference between the cladograms is the relative positions of *Artibeus fraterculus* and *A. obscurus* (Figures 10 & 11). In cladogram 1, *A. fraterculus* is the sister taxon of *A. hirsutus* and *A. inopinatus*; in the cladogram 2, however, *A. obscurus* is the sister taxon of *A. hirsutus* and *A. inopinatus*. Cladogram 1 is preferred on biogeographic grounds (see Phylogeny of *Artibeus (Artibeus)* Leach section).

Artibeus (Artibeus) is considered a monophyletic group because of the following synapomorphies:

Character 6 - fur on the venter conspicuously frosted with white (Char. 6-1). This condition is a convergent feature in *Dermanura.*

Character 25 - fourth upper premolar (P4) lingual cusp moderately to well developed (Char. 25-1).

Character 29 - third lower molar small (peg-like). This condition is a convergent feature in three species of *Dermanura* (Char. 29-2).

Character 30 - condylar (articular) process not prominent, projecting slightly from ramus (Char. 30-1). This state is a convergent feature in *Koopmania.*

In addition, rostrum relatively long (rostral index equal or greater than 0.29) (Char. 12-1), is present only in *Artibeus*; this character, however, was not polarized because it varied within the outgroups and the primitive condition could not be determined.

Each clade in the subgenus *Artibeus* is treated separately below:

Artibeus fimbriatus has one autapomorphy: horsehoe of noseleaf bound down and rimmed on lower edge (Char. 10-1). In addition, it shares one convergence with *A. obscurus*: fur on the back (mid-dorsum) long (Char. 3-1).

The clade formed by all the remaining *Artibeus (Artibeus)* species is defined by two synapomorphies: preorbital and postorbital processes moderately developed (Char. 14-1, Char. 15-1). However, these synapomorphies reverse to the primitive condition in the clade formed by *A. fraterculus*, *A. hirsutus*, *A. inopinatus*, and *A. obscurus*.

Artibeus amplus has two synapomorphies, but both are convergent with the outgroups: horseshoe of noseleaf bound down and not rimmed on lower edge (Char. 10-2) is shared with *Enchisthenes*; maxillary toothrows nearly parallel to each other (Char. 23-1) is shared with *Dermanura* and *Koopmania.*

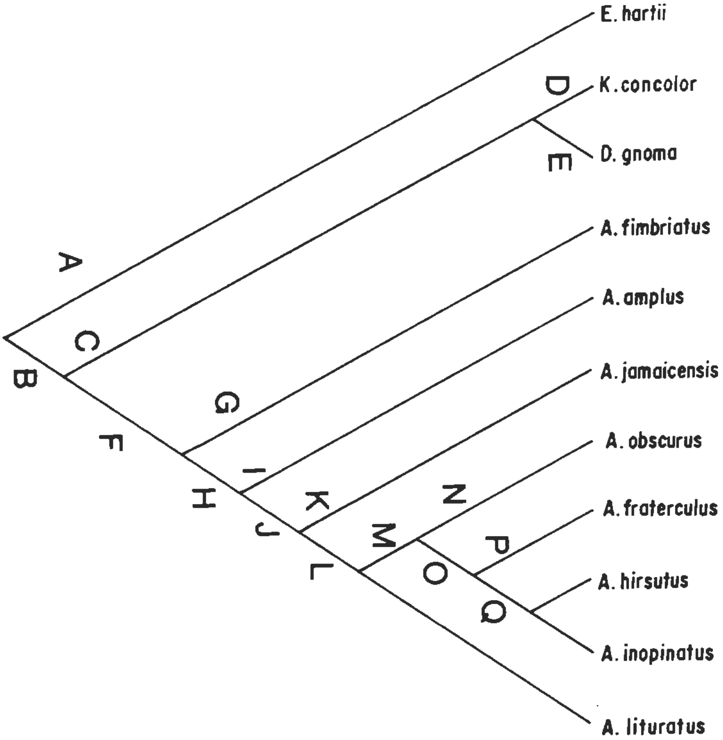

Figure 10 — Cladogram 1 of *Artibeus (Artibeus)*. Letters indicate branchs, * convergence, and ¯ reversal. Character-states are given below:

A - 7-1, 9-2, 10-2*, 11-1, 21-1, 24-1, 27-1
B - 8-1, 9-0, 20-1, 29-1
C - 20-2, 23-1*
D - 4-1, 7-2, 20-3, 30-1*
E - 6-1*, 9-1, 20-2, 21-1, 22-1*, 29-2*, 26-0
F - 6-1*, 12-1, 25-1, 29-2*, 30-1*
G - 3-1*, 10-1
H - 14-1, 15-1
I - 10-2*, 23-1*
J - 10-0¯
K - 2-1
L - 17-1
M - 14-0¯, 16-1
N - 3-1*, 19-1*
O - 5-1
P - 26-2
Q - 8-0, 15-0¯, 17-0¯, 19-1*, 22-1*, 28-1
R - 6-0¯, 13-1, 14-2, 15-2, 18-1, 20-0¯, 31-1

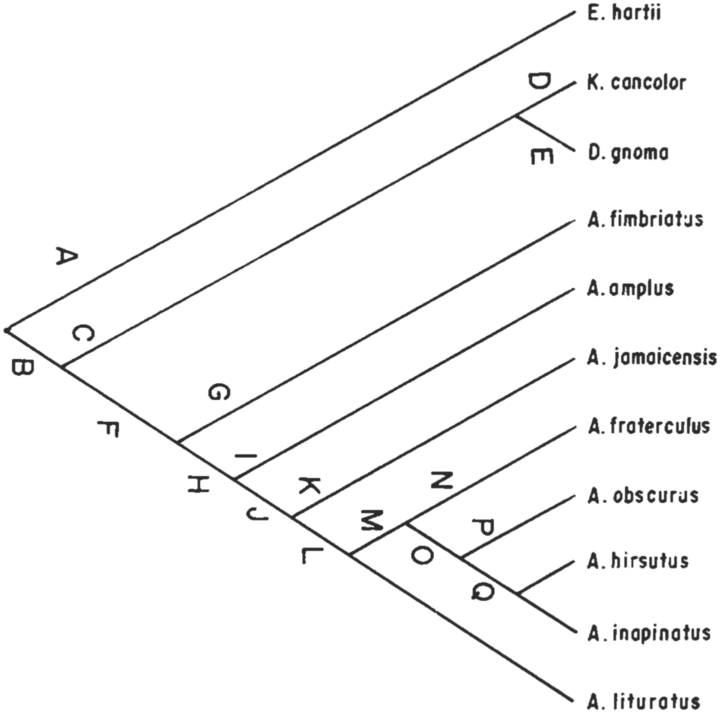

Figure 11 — Cladogram 2 of *Artibeus (Artibeus)*. Letters indicate branchs, * convergence, and $^{-}$ reversal Character-states are given below:

A - 7-1, 9-2, 10-2*, 11-1, 21-1, 24-1, 27-1
B - 8-1, 9-0, 20-1, 29-1
C - 20-2, 23-1*
D- 4-1, 7-2, 20-3, 30-1*
E - 6-1*, 9-1, 20-2, 21-1, 22-1*, 29-2*, 26-0
F - 6-1*, 12-1, 25-1, 29-2*, 30-1*
G - 3-1*, 10-1
H - 14-1, 15-1
I - 10-2*, 23-1*
J - 10-0^{-}
K - 2-1
L - 17-1
M - 14-0^{-}, 16-1
N - 5-1*, 26-2
O - 19-1
P - 3-1*
Q - 5-1*, 8-0, 15-0^{-}, 17-0^{-}, 22-1*, 28-1
R - 6-0^{-}, 13-1, 14-2, 15-2, 18-1, 20-0^{-}, 31-1

The clade formed by *A. jamaicensis*, *A. obscurus*, *A. fraterculus*, *A. hirsutus*, *A. inopinatus*, and *A. lituratus* is defined by a synapomorphy which is convergent with the outgroups: horseshoe of noseleaf becomes free again, as in *Dermanura* and *Koopmania* (Char. 10-0).

Artibeus jamaicensis has one autapomorphy: forearm (proximal, dorsal side) with scattered hair, practically naked (Char. 2-1).

The clade formed by *A. lituratus*, *A. obscurus*, *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* has one synapomorphy: postorbital constriction immediately behind postorbital process (Char. 17-1). This apomorphy, however seems to revert to the primitive condition in *A. hirsutus* and *A. inopinatus*.

Artibeus lituratus is the most distinctive species, having five autapomorphies: rostral shield developed with a flat rostrum (Char. 13-1); preorbital process well developed (Char. 14-2); postorbital process well developed (Char. 15-2); postorbital constriction narrow (Char. 18-1); angular process broad (Char. 31-1). In addition, this bat has many reversals to the plesiomorphic state: fur on the ventral surface without a conspicuous frosting of white (Char. 6-0) is shared only with *Enchisthenes* and *Koopmania*; paraoccipital process well developed (Char. 20-0) is shared only with *Enchisthenes*.

The clade formed by *A. fraterculus*, *A. hirsutus*, *A. inopinatus*, and *A. obscurus* has one synapomorphy: supraorbital ridges converge posteriorly (Char. 16-1); and one reversal: preorbital process poorly developed (Char. 14-0).

Because cladograms 1 and 2 differ in the position of *A. fraterculus* and *A. obscurus* in relation to the clade formed by *A. hirsutus* and *A. inopinatus*, the following clades will be treated separately for each cladogram.

In cladogram 1 (Figure 10), *A. obscurus* is not part of the clade formed by *A. fraterculus*, *A. hirsutus*, and *A. inopinatus*. *Artibeus obscurus* has two convergences: fur on the back (mid-dorsum) long (Char. 3-1) is convergent with *A. fimbriatus*; zygomatic arches diverge markedly posteriorly Char. 19-1) is convergent with the clade *A. hirsutus*, and *A. inopinatus*. The clade formed by *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* has one synapomorphy: fur on the back (upper parts) with a conspicuous silvery tinge (Char. 5-1). *Artibeus fraterculus* presents one autapomorphy: hypocone of first upper molar (M1) well developed (Char. 26-2). The clade formed by *A. hirsutus* and *A. inopinatus* has one synapomorphy: metaconid of m2 not set apart from the rest of tooth by a deep fissure (Char. 28-1); two convergences: mesopterygoid fossa constricted posteriorly on basicranium (Char. 22-1, convergent in *Dermanura*), and zygomatic arches diverge markedly posteriorly (Char. 19-1, convergent in *A. obscurus*; and two reversals: postorbital process poorly developed (Char. 15-0), and postorbital constriction well behind postorbital process (Char. 17-0). Interfemoral membrane narrow is present in this clade and *Enchisthenes*; this character is not polarized (Char. 8-0).

In cladogram 2 (Figure 11) *A. fraterculus* is not part of the clade formed by *A. obscurus*, *A. hirsutus*, and *A. inopinatus*. *Artibeus fraterculus* has one autapomorphy: hypocone of first upper molar (M1) well developed (Char. 26-2); and one convergence with *A. hirsutus*, and *A. inopinatus*: fur on the back (upper parts) with a conspicuous silvery tinge (Char. 5-1). The clade formed by *A. obscurus*, *A. hirsutus*, and *A. inopinatus* has one apomorphy: zygomatic arches diverge markedly posteriorly (Char. 19-1). *Artibeus obscurus* has one convergence with *A. fimbriatus*: fur on the back (mid-dorsum) long (Char. 3-1). The clade formed by *A. hirsutus* and *A. inopinatus* has one apomorphy: metaconid of m2 not set apart from the rest of tooth by a deep fissure (Char. 28-1); one convergence: mesopterygoid fossa constricted posteriorly on basicranium (Char. 22-1, convergent with *Dermanura*); and two reversals: postorbital process poorly developed (Char. 15-0), and postorbital constriction well behind postorbital process (Char. 17-0). Interfemoral membrane narrow is present in this clade and *Enchisthenes*; this character is not polarized because it varied within the outgroups, and the primitive condition could not be determined (Char. 8-0).

In both cladograms, *Artibeus hirsutus* has the interfemoral membrane (dorsal side) conspicuously hairy, and facial stripes moderately developed. These two characters were not included in the phylogenetic analysis because they vary among the individuals in some of the other species. *Artibeus inopinatus* has the interfemoral membrane (dorsal side) moderately hairy and facial stripes obscure or indistinct. As in *A. hirsutus*, these two characters were not included in the phylogenetic analysis because they vary among the individuals in some of the other species (see Methods and Materials).

*Phylogeny of **Artibeus (Artibeus)** Leach*

Owen (1987) commented that *Artibeus* is only distantly related to *Dermanura* (including *Enchisthenes*, and *Koopmania*). A recent paper by Lim (1993), however, suggested that *Artibeus*, *Dermanura*, *Enchisthenes*, and *Koopmania* are closely related, forming a monophyletic group, and therefore supporting the idea of *Artibeus* (*sensu lato*) as a single genus. With the present research, any inference of relatedeness of *Artibeus* with the outgroups can not be made because the outgroups were used only to polarize the character states in the ingroup (*Artibeus*).

The two cladograms produced by Hennig86 differ from each other only in the relative position of *A. obscurus*, and *A. fraterculus* with *A. hirsutus*, and *A. inopinatus* (Figures 10 & 11). Biogeographic distribution of these species can be used to argue for preferring Cladogram 1 over Cladogram 2. Based on distribution, *Artibeus fraterculus*, *A. hirsutus*, and *A. inopinatus* could be considered closely related because they are confined to dry places on the Pacific side of Central and South America (Figure 2). *Artibeus obscurus*, on the other hand, is confined to the tropical rainforest of the Amazonian region (Figure 2). An ecological approach, however, could suggest that the relationships of *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* is apparent, and not real. It could be proposed that because they occur in ecologically similar places, they share convergences, rather than homologies. This hypothesis, however, is not supported by the cladistic analysis (see Cladogram section). The choice of the Cladogram 1 over the Cladogram 2 is strengthened by additional information on the geology of Latin America, and fossil record.

Concerning the geology of Latin America, Haffer (1974) observed that the Andes, along the Pacific side of South America, were gradually lifted above sea level during the Tertiary Period, with a probable very late uplifting during the Pliocene and Lower Pleistocene for some parts of the Andes. Furthermore, a continuous land bridge between North and South America was finally established during the late Pliocene as well (see also Cerqueira 1982; Webb & Marshall 1982). The Andes seem to represent an efficient barrier for recent *Artibeus* species. *Artibeus obscurus* is on the eastern side of the Andes isolated from *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* that occur on the western side of the Andes. However, it is necessary to get additional information on the past record for these species to know if in the past they could occur together.

Within the genus, only *A. jamaicensis* has a fossil record: late Pleistocene of Puerto Rico and Cuba (Smith 1976). Based on the fossil record of *Artibeus* and the geology of Latin America, it seems that *Artibeus* evolved after the connection between North and South America was established, and the uplifting of the Andes was completed. Therefore, an exchange of *Artibeus* species between North and South America could occur, but the exchange between the Pacific side of South America, and the Amazonian region seems rare because of the Andes (see Natural History section of each species). In view of this picture, it is more parsimonious to hypothesize a common ancestor for *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* than for *A. obscurus*, *A. hirsutus*, and *A. inopinatus*. Future studies, e.g. molecular analysis, may strengthen such conclusions.

The present research suggests that *A. hirsutus* and *A. inopinatus* are sister species, joined by the possession of one apomorphy, two convergences, and two reversals (see Cladogram section). Jones and Carter (1976), in their annotated checklist of Phyllostomidae, also suggested a close relationship between *Artibeus hirsutus* and *A. inopinatus*. Owen (1987), in contrast, placed *A. hirsutus* more closely related to *A. jamaicensis* (identified as *A. planirostris*) and *A. fraterculus*, and *A inopinatus* more closely related to *A. obscurus* (identified as *A. fuliginosus*). However, when the characters used by Owen (his Table 1) are optimized onto his cladogram, no characters actually define these relationships. His results may be due to using an older and unreliable computer program (Wagner78) for cladistic analysis (Luckow & Pimentel 1985), or as suggested by Lim (1993), his analyses were not be based only on shared derived characteristics. The data presented here in this biogeographic and phylogenetic analysis, supports the close relationship between *A.*

hirsutus and *A. inopinatus* over Owen's proposed relationships. In addition, *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* form a separate clade from the remainder species of *Artibeus*.

Artibeus lituratus is the most distinctive species of *Artibeus*, having at least five autapomorphies. Handley (1987), commenting about systematics of South American *Artibeus*, suggested that *Artibeus* can be arranged in two groups: one representing only *A. lituratus*, and the other including *A. amplus* (the undescribed species mentioned in that paper), *A. fimbriatus*, *A. fraterculus*, *A. jamaicensis*, and *A. obscurus*. The divergence of the line leading to *A. lituratus* early in the history of the group is now confirmed.

Artibeus fimbriatus, and *A. amplus* are the species with the least number of advanced character states and could represent primitive species of *Artibeus*. These species occur in restricted forest areas of southern, and northern South America, respectively (Figure 3). They appear to be relicts.

Artibeus jamaicensis, and the clade formed by *A. obscurus*, *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* could represent intermediate species in terms of evolution. *A. jamaicensis* occurs in practically all of neotropical America, but with preference for the tropical rainforest (Figure 3). *Artibeus obscurus* is confined to the Amazonian region (Figure 2). *Artibeus fraterculus*, *A. hirsutus*, and *A. inopinatus* are restricted to dry areas on the Pacific side of Central and South America (Figure 2).

IMPLICATIONS FOR CONSERVATION

Because *Artibeus* species play an important role as seed dispersers in secondary sucession as well as in maintaining diversity of tropical flora, they protect and make the environmental systems available for other species as well (Bonaccorso et al. 1980; Fleming et al. 1972; Handley et al. 1991; Handley & Leigh 1991; Heithaus 1982; Heithaus et al. 1975; Jimbo & Schwassmann 1967; Morrison 1978; Reis & Guillaumet 1983; Reis & Peracchi 1987; Wilson 1989). Consequently, the conservation of these fruit-eating bats is important for the maintenance of such ecosystems.

Erwin (1991) suggested an evolutionary basis for conservation biology: the knowledge of where novelties have originated and are distributed among species can provide insights for choosing critical areas to be preserved, i.e., places where the active processes of contemporary evolution are actually occurring. According to this approach, conservation strategies should concentrate efforts on *A. lituratus*, *A. obscurus*, *A. fraterculus*, *A. hirsutus*, and *A. inopinatus*, where phylogenetic theory predicts species radiation (Figure 10). *Artibeus lituratus* occurs in practically all of neotropical America with the exception of the Greater Antilles, where *A. jamaicensis* dominates; the striped large Artibeus adapts well to a variety of habitats, but with preference for the tropical rainforest (Figure 3). *Artibeus obscurus* seems to concentrate in the Amazonian region (Figure 2). *Artibeus fraterculus*, *A. hirsutus*, and *A. inopinatus* occur in dry places on the Pacific side of Central and South America in a more restricted area than the previous species (Figure 2). The Amazonian region, and dry places on the Pacific side of Central and South America, therefore should be the focus of our efforts. Conservation of these species, according to the phylogenetic theory, will protect the evolutionary processes that ultimately will generate future biodiversity. Concerning *A. amplus* and *A. fimbriatus*, although they seem to be primitive endemic forms occupying small forest areas in South America (Figure 3), the probability of speciation at that level does exist and we should not disregard those species.

Another approach for conservation biology suggests that distantly related taxa should have priority in conservation because genetic diversity, not just species number is maximized (Mares 1992; Vane-Wright, et al. 1991; see also Dizon et al. 1992; Pielou 1975). According to this approach, conservation strategies should concentrate efforts on one of the following two groups of species: 1. *Artibeus fimbriatus*, *A. jamaicensis*, *A. lituratus*, plus one species of the clade formed by *A. fraterculus*, *A. hirsutus*, and *A. inopinatus*; 2. *Artibeus amplus*, *A. obscurus*, *A. lituratus*, plus one species of the clade formed by *A. fraterculus*, *A. hirsutus*, and *A. inopinatus* (Figure 10). The conservation of one of these groups of species could ensure the preservation of the clade as well, because those species are phylogenetically closely related, and therefore genetically closely related. It seems that choosing either group of species to protect, the tropical rainforest of South America and the dry places on the Pacific side of Central and South America should be the focus of our efforts.

Either approach taken on conservation strategies would suggest that the tropical rainforest of South America and the dry places on the Pacific side of Central and South America deserve our attention. Future research should concentrate on the geographic variation of these species, for selecting areas in those regions to be protected. Comparison with other taxonomic groups could help also in the selection of such areas.

The immense tropical rainforest therefore seems to be the place for at least five species of *Artibeus*, and these bats play a very important role as seed dispersors in the reforestation and maintenance of that ecosystem (e.g. Bonaccorso et al. 1980; Gardner 1977b; Handley 1987; Handley et al. 1991; Morrison 1978; Reis & Guillaumet 1983; Reis & Peracchi 1987; Wilson 1989). However, habitat disturbance throughout all tropical regions points toward an uncertain future for bats (Johns et al. 1985). The loss of these key links could cause unpredictable and irreversible effects in the ecosystem. Conservation programs must include the flora as well as the fauna they hold (Wilson 1989). As Tuttle (1989) stated very well: "We need bats whether we like them or not; their loss poses serious, potentially irreversible consequences to the environment that we all must share." The present study is open for future research, where systematics is the basis for conservation.

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APPENDIX 1 — Material Examined of *Artibeus (Dermanura)* (65 specimens)

1. Material examined of *A. (D.) anderseni* (6 specimens)

BOLIVIA. Beni: Río Cureraba, Beni Reserve (USNM 564322 ♀); Río Mattos, Tancho Totaizal, near Beni Reserve (USNM 564323 ♀).

COLOMBIA. Antioquia: 24 km S and 22 km W Zaragoza, near La Tirana, 520 m (USNM 499499 ♂, USNM 499500 ♂).

PERU. Madre de Dios: Tamboapa [= Tambopata ?] Explore's Inn, 260 m (USNM 562 241 ♀); Manu, Pakitza (USNM 566550 ♂).

2. Material Examined of *A. (D.) aztecus* (6 specimens)

COSTA RICA. Heredia: 5 km E Vara Blanca, Parque Nacional Braulio Carrillo, 2,050 m (USNM 562857 ♂).

MEXICO. Guerrero: 5 mi. E Omilteme, 6,200 ft. (USNM 329447 ♂); 5 mi. E Omilteme, 7,240 ft. (USNM 329448 ♂). México: 2 km E Tonatico (USNM 559617 ♀). Morelos: Teteca del Volcan (USNM 52051 ♀).

PANAMA. Chiriquí: Cerro Punta, Casa Tilley, 5,300 ft. (USNM 314770 ♀).

3. Material Examined of *A. (D.) cinereus* (6 specimens)

BRAZIL. Pará: Belém, IAN, Sta. A (USNM 361746 ♀, USNM 361747 ♀, USNM 361748 ♀, USNM 361749 ♂); 52 km SSW Altamira, Rio Xingu, east bank, 03°39'S, 52°22'W (USNM 549430 ♂, USNM 549431 ♂).

4. Material Examined of *A. (D.) glaucus* (6 specimens)

COLOMBIA. Meta: Villavicencio, Finca Buque (USNM 507200 ♀, USNM 507201 ♂).

ECUADOR. El Oro: 1 km SW Puente de Moromoro, 920 m (USNM 513472 ♀, USNM 513473 ♂).

TRINIDAD AND TOBAGO. Tobago: St. John Parish, Charlotteville, sea level, 11°19'S, 60°33'W, (USNM 540677 ♂); St. John Parish, 3 km W Charlotteville, Hermitage Estate, Hermitage Creek, 25 m, 11°19'S, 60°35'W (USNM 540678 ♀).

5. Material Examined of *A. (D.) gnomus* (23 specimens)

BRAZIL. Pará: Belém, IAN, Sta. A (USNM 361737 ♂, USNM 361738 ♀, USNM 361739 ♀, USNM 361740 ♂, USNM 361741 ♂, 361742 ♂); Belém, Utinga (USNM 361744 ♀, USNM 361745 ♂). Mato Grosso: Serra do Roncador, 264 km (by road) Xavantina, ca. 1,750 ft., 12°51'S, 51°46'W (USNM 393718 ♀, USNM 393719 ♂; USNM 393721 ♀).

VENEZUELA. Bolívar: 59 km SE El Dorado, Km 74, El Manaca (USNM 387531 ♀, USNM 387536 ♀, USNM 387538 ♀); 28 km SE El Manteco, Los Patos (USNM 387529 ♂, USNM 387530 ♀). Territorio Federal de Amazonas: 108 km SE Esmeralda, Rio Mavaca, 140 m (USNM 405488 ♀, USNM

405490 ♀); 12 km SSE Puerto Ayacucho, Las Queseras, 135 m (USNM 409134 ♂); 65 km SSW Puerto Ayacucho, Morocoy, 161 m (USNM 409143 ♂, USNM 409144 ♂); Río Manapiare, San Juan, 155 m (USNM 409129 ♂, USNM 409131 ♂).

6. Material Examined of *A. (D.) phaeotis* (6 specimens)

ECUADOR. Guayas: 7 km S Balao, San Rafael (USNM 498932 ♀). Los Rios: 3 km N Pueblo Viejo, Beata Elvira (USNM 498933 ♂).

GUATEMALA. Santa Rosa: La Avellana (USNM 502274 ♀, USNM 502276 ♂).

MEXICO. Jalisco: 1 km N Chamela, Arroyo Chamela (USNM 559672 ♂, USNM 559674 ♀).

7. Material Examined of *A. (D.) toltecus* (6 specimens)

MEXICO. México: 2 km E Tonatico (USNM 559692 ♂, USNM 559693 ♀, USNM 559694 ♀); 10 km SE Tonatico, Grutas de La Estrella (USNM 559691 ♂).

PANAMA. Darien: Tacarcuna Village Camp, 3,200 ft. (USNM 310197 ♀, USNM 310198 ♂).

8. Material Examined of *A. (D.) watsoni* (6 specimens)

COLOMBIA. Valle: Río Raposo, Celo Pacific Coast, Virology field Sta. (USNM 334690 ♂); 20 km NE Buenaventura, road to Calima, Carton de Colombia (USNM 483880 ♀).

COSTA RICA. Heredia: 1 km S, 11.5 km E San Miguel, Parque Nacional Braulio Carrillo, 700 m (USNM 562864 ♂); 11 km S, 4.5 km W Puerto Viejo, Parque Nacional Braulio Carrillo, 300 m (USNM 562865 ♀).

PANAMA. Colón: 5.5 km NWW Frijoles, Bohio Penninsula (USNM 503662 ♀). Chiriquí: 14.5 km NW El Volcan, Santa Clara (USNM 518023 ♂).

APPENDIX 2 — Material Examined of *Artibeus (Enchisthenes) hartii* (20 specimens)

COLOMBIA. Valle: 2 km S Pance, ca. 20 km SW Cali (USNM 483909 ♂, USNM 483911 ♂; USNM 483915 ♀, USNM 483936 ♀).

ECUADOR. Mera: Pastaza (USNM 548254 ♀, USNM 548255 ♂, USNM 548258 ♂, USNM 548260 ♀).

PANAMA. Darién: Tacarcuna Village Camp (USNM 310213 ♀, USNM 310228 ♂, USNM 310230 ♂); Cerro Malí, 4,700 ft. (USNM 338049 ♀). Los Santos: Cerro Hoya (USNM 323539 ♀, USNM 323542 ♂).

PERU. Junín: 3.2 km N Vitoc, Río Tulumayo, 700 m (USNM 507202 ♀).

VENEZUELA. Distrito Federal, 4 km NNW Caracas, Los Venados, 1,498-1,556 m (USNM 370730 ♀; USNM 370733 ♂; USNM 370734 ♀; USNM 370743 ♂); Pico Ávila, 5 km NNE Caracas, Hotel Humboldt, 1,982 m (USNM 370758 ♂).

APPENDIX 3 — Material Examined of *Artibeus (Koopmania) concolor* (20 specimens)

BRAZIL. Pará: 50 km SSW Altamira, Rio Xingu, Ilha Jabuti, 03°38'S, 52°22'W (USNM 549439 ♀); 52 km SSW Altamira, Rio Xingu, east bank, 03°39'S, 52°22'W (USNM 549440 ♀, USNM 549441 ♂).

VENEZUELA. Bolívar: 59 km SE El Dorado, Km 74, El Manaca (USNM 387383 ♀, USNM 387384 ♀, USNM 387387 ♂, USNM 387388 ♂); 85 km SSE El Dorado, Km 125 (USNM 387366 ♂, 387371 ♂; USNM 387374 ♀, USNM 387375 ♀; USNM 387376 ♂, USNM 387379 ♀, USNM 387380 ♀, USNM 387382 ♂); 225 km NE Icabarú, Independencia, 824 m (USNM 440889 ♂). Territorio Federal del Amazonas: 108 km SE Esmeralda, Río Mavaca, 140 m (USNM 405203 ♀); Tamatama, Río Orinoco, 135 m (USNM 405206 ♀); Casiquiare Canal, Capibara, 130 m (USNM 408888 ♂); 9 km SE Puerto Ayacucho, Chaparito, 119 m (USNM 408901 ♂).

APPENDIX 4 — Character State Transformation Series

(0 = primitive condition, 1-3 = derived conditions. The numbers designating characters and states are the same as given in the text, but do not necessarily indicate directionality).

EXTERNAL CHARACTERS (Figure 1)

Hairiness

1. Forearm hairiness, proximal end, ventral side: (0) hairy; (1) scattered hair (practically naked). Polarized: 0-1.

2. Forearm hairiness, proximal end, dorsal side: (0) hairy; (1) scattered hair (practically naked). Polarized: 0-1.

3. Fur on the back (mid-dorsum), length: (0) short (equal or less than 8.0 mm); (1) long (more than 8.0 mm). Polarized: 0-1.

Coloration

4. Fur on the back, banding: (0) individual hairs bicolored, or inconspicuously tricolored (coloration ranges from pale brownish to blackish, fur pale at base); (1) individual hairs conspicuously tricolored (coloration brown, fur pale in the middle band). Polarized: 0-1.

5. Fur on the back, frosting (upper parts): (0) without a conspicuous silvery tinge; (1) with a conspicuous silvery tinge (tip of hairs colorless). Polarized: 0-1.

6. Fur on the venter, frosting (underparts): (0) not conspicuously frosted with white; (1) conspicuously frosted with white (tip of hairs colorless). Polarized: 0-1.

OTHER EXTERNAL CHARACTERS

7. Wing membrane (plagiopatagium) attachment: (0) at side of foot (1) at ankle; (2) at base of toes. Ordered: 0-1,2.

8. Interfemoral membrane (uropatagium) width: (0) narrow (equal or less than 7.0 mm); (1) broad (equal or more than 10.0 mm). Not polarized: 0,1.

9. Noseleaf length (noseleaf length index: length/width ratio across nares): (0) length/width ratio about 1.57 (1.41-1.75); (1) length/width ratio about 2.00 (1.92-2.13); (2) length/width ratio about 1.00 (1.00-1.10). Ordered: 0-1,2.

10. Horseshoe of noseleaf, fusion of lower margin: (0) free; (1) bound down and rimmed on lower edge (ridged); (2) bound down and not rimmed on lower edge (fused). Ordered: 0-1-2.

11. Tragus distal border: (0) without a pointed projection on inner margin near tip; (1) with a pointed projection on inner margin near tip. Polarized: 0-1.

CRANIAL CHARACTERS (Figures 4-9)

12. Rostral length (rostral index: from the most anterior part of the skull to the most anterior part of orbit/skull greatest length): (0) short (index equal or less than 0.28); (1) long (equal or more than 0.29). Not polarized: 0,1.

13. Rostral shield (orbitonasal shield): (0) not developed, rostrum arched (supraorbital area swollen); (1) developed, rostrum flat. Polarized: 0-1.

14. Preorbital process: (0) poorly developed; (1) moderately developed; (2) well developed.
Ordered: 0-1-2.

15. Postorbital process: (0) poorly developed; (1) moderately developed; (2) well developed. Ordered: 0-1-2.

16. Supraorbital ridges (between preorbital and postorbital processes): (0) nearly parallel to each other; (1) converge posteriorly. Polarized: 0-1.

17. Postorbital constriction: (0) well behind postorbital process; (1) immediately behind postorbital process. Polarized: 0-1.

18. Postorbital constriction (postorbital constriction index: postorbtial constriction / skull greatest length): (0) broad (index equal or more than 0.23); (1) narrow (index equal or less than 0.22). Polarized: 0-1.

19. Zygomatic arches: (0) subparallel; (1) diverge markedly posteriorly. Polarized: 0-1.

20. Paraoccipital process: (0) well developed; (1) moderately developed; (2) poorly developed; (3) absent. Ordered: 0-1-2-3.

21. Mesopterygoid fossa, anterior shape: (0) U-shaped (no distinct medial notch) resulting in curved lateral borders; (1) V-shaped (sharp medial notch) resulting in straight lateral borders. Polarized: 0-1.

22. Mesopterygoid fossa: (0) not constricted posteriorly on basicranium (internal pterygoid ridge obsolete); (1) constricted posteriorly on basicranium (internal margin of pterygoid with a ridge). Polarized: 0-1.

23. Maxillary toothrows: (0) converge anteriorly (V-shaped); (1) nearly parallel to each other (U-shaped). Polarized: 0-1.

24. Inner upper incisors: (0) bilobed (bifid) and not pointed; (1) simple (not bifid) and pointed. Polarized: 0-1.

25. Fourth upper premolar (P4), protocone cusp: (0) absent or poorly developed; (1) moderately to well developed. Polarized: 0-1.

26. First upper molar (M1), hypocone cusp: (0) absent or only weakly developed; (1) moderately developed; (2) well developed. Ordered: 0-1-2.

27. Second upper molar (M2), metacone and metaconule position: (0) not separated as distinct lobes from the rest of tooth; (1) set apart as distinct lobes from the rest of tooth by a deep fissure. Polarized: 0-1.

28. Second lower molar (m2), metaconid: (0) set apart as a distinct lobe from the rest of m2 by a deep fissure; (1) not set apart from the rest of m2. Polarized: 0-1.

29. Third lower molar (m3): (0) present, relatively large (about 35% the size of m2); (1) present, medium-sized (about 20% the size of m2); (2) present, small, peg-like; (3) absent. Ordered: 0-1-2-3.

30. Condylar (articular) process: (0) prominent, projecting conspicuously from ramus; (1) not prominent, projecting slightly from ramus. Polarized: 0-1.

31. Angular process: (0) narrow (less than 25% the width of ramus); (1) broad (about 50% the width of ramus). Polarized: 0-1.

APPENDIX 5 — Character Matrix of *Artibeus (Artibeus)* Leach

Character state distributions for 31 characters for species of *Artibeus*; 0 = primitive condition, 1-3 = derived conditions. The numbers designating characters and states are the same as given in the text, but do not necessarily indicate directionality.

Abbreviations are as follows:

OUT1 = Outgroup1 - *Artibeus (Enchisthenes) hartii*
OUT2 = Outgroup2 - *Artibeus (Koopmania) concolor*
OUT3 = Outgroup3 - *Artibeus (Dermanura) gnomus*
AMP = *Artibeus (Artibeus) amplus*
FIM = *A. (A.) fimbriatus*
FRA = *A. (A.) fraterculus*
HIR = *A. (A.) hirsutus*
INO = *A. (A.) inopinatus*
JAM = *A. (A.) jamaicensis*
LIT = *A. (A.) lituratus*
OBS = *A. (A.) obscurus*

TAXA	CHARACTERS AND STATES																													
	1				5					10					15					20					25					30	31
OUT1	0	0	0	0	0	0	1	0	2	2	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0
OUT2	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	1	0	0	1	1	0
OUT3	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	2	0	0
AMP	0	0	0	0	0	1	0	1	0	2	0	1	0	1	1	0	0	0	0	1	0	0	1	0	1	1	0	0	2	1	0
FIM	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	2	1	0
FRA	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	1	2	0	0	2	1	0
HIR	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	1	2	1	0
INO	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	1	2	1	0
JAM	0	1	0	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	2	1	0
LIT	0	0	0	0	0	0	0	1	0	0	0	1	1	2	2	0	1	1	0	0	0	0	0	0	1	1	0	0	2	1	1
OBS	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	1	1	0	1	1	0	0	0	0	1	1	0	0	2	1	0