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Artibeus obscurus.

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Artibeus Leach, 1821

Phyllostoma: É. Geoffroy St.-Hilaire, 1810:176. Part, not *Phyllostoma* Cuvier, 1800.
Phyllostomus: Olfers, 1818:224. Part, not *Phyllostomus* Lacépède, 1799.
Phyllostoma: Schinz, 1821:164. Part, not *Phyllostoma* Cuvier, 1800.
Artibeus Leach, 1821:75. Type species *Artibeus jamaicensis* Leach, 1821, by monotypy.
Madataeus Leach, 1821:81. Type species *Madataeus lewisii* Leach, 1821 (= *Artibeus jamaicensis*), by monotypy.
Phyllostoma: Spix, 1823:66. Not *Phyllostoma* Cuvier, 1800.
Medateus Gray, 1827:74. Incorrect subsequent spelling of *Madataeus* Leach.
Arctibeus Gray, 1838:486. Incorrect subsequent spelling of *Artibeus* Leach.
Arctibius Bonaparte, 1847:115. Incorrect subsequent spelling of *Artibeus* Leach.
Pteroderma Gervais, 1855:34. Type species *Pteroderma perspicillatum* Gervais, 1856 (= *Phyllostoma perspicillatum* É. Geoffroy St.-Hilaire, 1810; not *Vespertilio perspicillatus* Linnaeus, 1758), by monotypy.
Artibaeus Gervais, 1856:34. Incorrect subsequent spelling of *Artibeus* Leach.
Dermanura Gervais, 1856:36. Type species *Dermanura cinereum* Gervais, 1856, by monotypy.
Artibacus Saussure, 1860:429. Incorrect subsequent spelling of *Artibeus* Leach.
Artibaeus Saussure, 1860:429. Incorrect subsequent spelling of *Artibeus* Leach.
Artiboeus Trouessart, 1878:214. Incorrect subsequent spelling of *Artibeus* Leach.
Desmanura Kappler, 1881:163. Incorrect subsequent spelling of *Dermanura* Gervais.
Artobius Winge, 1892:10. Incorrect subsequent spelling of *Artibeus* Leach.
Koopmania Owen, 1991:21. Type species *Artibeus concolor* Peters, 1865, by original designation.

CONTEXT AND CONTENT. Order Chiroptera, suborder Microchiroptera, family Phyllostomidae, subfamily Stenodermatinae. The genus *Artibeus* includes 17 extant species (Koopman 1993). The synonymy is modified from Hall (1981) and Miller (1907). A key to the large *Artibeus* from northern South America is below (modified from Anderson 1997; Lim and Wilson 1993; Ortega and Castro 2001).

1 Fur on dorsum >8 mm and dark; blackish dorsum; canine breadth <8.4 mm ..... *A. obscurus*
Fur on dorsum <8 mm and paler; brownish or grayish dorsum; canine breadth >8.4 mm 2
2 Facial stripes distinct; fur on ventrum unicolor pale brown; M3 absent; supraorbital rim elevated and postorbital process conspicuous ..... *A. lituratus*
Facial stripes less distinct; fur on ventrum with frosted tips; M3 present or absent; supraorbital rim not noticeably elevated and postorbital process less conspicuous 3
3 Base of noseleaf continuous with upper lip; wing tips brown ..... *A. amplus*
Base of noseleaf with free flap above upper lip; wing tips white 4
4 Distributed north of the Orinoco River; smaller, greatest length of skull <29.5 mm ..... *A. jamaicensis*
Distributed south of the Orinoco River; larger, greatest length of skull >29.5 mm ..... *A. planirostris*

Artibeus obscurus (Schinz, 1821)

Dark Fruit-eating Bat

Phyllost[*oma*] *obscurum* Schinz, 1821:164. Type locality "Ostküste von Brasilien;" identified by Wied-Neuwied (1826:206) as "Villa Vicosa [= Marobá according to Bokermann, 1957:223] am Flusse Peruhype, Bahia, Brazil."
?*Arctibeus fuliginosus* Gray, 1838:487. Type locality "S. America."
Artibeus davisi Patten, 1971:12. Nomen nudem.
Artibeus fuliginosus: Tuttle, 1974:142. Name combination.
Artibeus j(*amaicensis*) *fuliginosus*: Anderson et al., 1982:9. Name combination.
Artibeus obscurus: Handley, 1989:449. First use of current name combination.

CONTEXT AND CONTENT. Context as for genus. *A. obscurus* is monotypic.

DIAGNOSIS. *Artibeus obscurus* (Fig. 1) is most similar in size to *A. jamaicensis*: they are allopatric in Central America and northwestern South America. *A. obscurus* is darker than *A. jamai-*

FIG. 1. Adult *Artibeus obscurus* from Poaro-Siparuni, Iwokrama Reserve, 25 km SSW Kurupukari, Guyana, 4°28′N, 58°47′W. Photograph by Thomas E. Lee, Jr., Silvia Armitano, and Burton K. Lim.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a male *Artibeus obscurus* from Poaro-Siparuni, Iwokrama Reserve, 25 km SSW Kurupukari, Guyana, 4°28′N, 58°47′W (ACUNHC 203/ROM 104677). Greatest length of skull is 28.52 mm. Photographs by Steve Butman.

censis and has longer, softer fur; longer, broader noseleaf; furrier forearms; darker membrane between fingers 2 and 3; fewer and smaller ornamental warts on chin; relatively longer, shallower rostrum; postorbital constriction more parallel-sided and narrowest anteriorly, immediately behind postorbital processes; and crests and processes not well developed (Handley 1989). Vibrissae surrounding base of noseleaf are more numerous and longer than in *A. jamaicensis*.

Artibeus obscurus is cranially and externally smaller than *A. fimbriatus*, *A. lituratus*, and *A. planirostris*. Skull (Fig. 2) of *A. obscurus* resembles that of *A. planirostris* but has even more obscured pre- and postorbital processes. These contrast with the well-developed pre- and postorbital processes of *A. lituratus* (Koepcke and Kraft 1984). Ornamental chin warts do not effectively distinguish between *A. obscurus* and *A. planirostris* because most individuals of both species in Paracou show 9 small papillae arranged in a 'U' around a larger central papilla, with considerable variation in papillary size (Simmons and Voss 1998).

Differences between *A. lituratus* and *A. obscurus* include blackish color with frosted ventral fur in *A. obscurus* rather than chocolate brown and unfrosted ventral fur of *A. lituratus*. In *A. obscurus*, the supraorbital ridge and facial shield is poorly developed; the rostrum is not as shallow and flattened; M3 is usually present. M3 occurs in 94% of *A. obscurus* north and at the head of the Amazon (n = 224) and in 77% of *A. obscurus* south of the Amazon (n = 26).

Artibeus obscurus can be distinguished from *A. fimbriatus* by smaller length of forearm, blacker color, less distinct facial stripes, lower rim of horseshoe of noseleaf free from lip, and nearly naked interfemoral membrane and legs (Handley 1989). Compared to *A. fraterculus*, *A. obscurus* is overall larger and darker and has less distinct facial stripes, 3 upper molars versus 2 in *A. fraterculus*, greater spacing between M1 and M2, shorter coronoid process, more massive condyloid process, and poorly developed accessory lingual cusps of M1 (Patten 1971).

GENERAL CHARACTERS. *Artibeus obscurus* has pelage that is sooty to dark blackish-brown to dark brown on dorsum, is paler on underparts, and has a white frosting. Facial stripes are indistinct; forearm is furry; tibia, foot, and interfemoral membrane are almost naked. Lips, noseleaf, ears, tragus, and wings are blackish in museum specimens. Fresh specimens have blackish-brown ears; tragus is blackish-brown basally, shading to sooty cream at tip; interfemoral membrane, fingers, legs, and feet are fuscous; claws are horn-colored. Iris in fresh specimens is dark brown. Noseleaf is long and broad; lower rim of horseshoe is not bound down to lip; chin ornaments are small (Handley 1989). Calcars are longer than metatarsals, averaging 7.3 mm in length. Tragus has sharp tip; nasals are not tubular; condyloid processes are extremely prominent; M3 is usually present (Patten 1971). Length of skull is up to 29.5 mm for specimens from Ecuador and up to 29.3 mm for specimens from Peru (Koepcke and Kraft 1984). Skull is relatively gracile for its size; rostrum is relatively long, arched, and inflated anterodorsally behind canine; supraorbital and postorbital processes are usually not accentuated; postorbital constriction is narrowest close to the postorbital processes and its walls subparallel medially; zygomata flare posteriorly; sagittal, lambdoidal, and mastoidal crests are not well developed (Handley 1989).

No geographic variation in external measures has been reported. Females are slightly larger than males (Brosset and Charles-Dominique 1990; Eisenberg and Redford 1999; Simmons and Voss 1998). Mean (*SD*) measurements (in mm) of 25 specimens from Guyana and Venezuela (Lim and Wilson 1993) are: length of cranium, 28.2 (0.5); length of palatal, 11.4 (0.2); length of maxillary toothrow, 10.2 (0.2); zygomatic breadth, 16.9 (0.4); mastoid breadth, 14.9 (0.5); breadth across upper molars, 12.5 (0.4); postorbital constriction, 6.6 (0.2); length of rostral, 10.9 (0.3); width of interorbital, 7.3 (0.3); width across upper molars, 8.1 (0.2); height of coronoid, 8.0 (0.2); length of forearm, 59.0 (2.0). Mean cranial and external measurements (in mm, range in parentheses) of 5 males and 8 females from Amazonian Peru (Koepcke and Kraft 1984) are: greatest length of skull, 27.31 ± 0.45 *SD* (26.4–28.1); upper toothrow (C–M2 distance), 9.62 ± 0.25 (9.0–10.0); postorbital width, 6.62 (5.9–7.0); width across cingula of upper canines, 7.78 ± 0.23 (7.4–8.1); width across alveolar border of upper M2, 11.93 ± 0.31 (11.2–12.3); zygomatic breadth, 16.79 ± 0.44 (15.9–17.5); breadth of braincase, 12.0 ± 0.33 (11.5–12.5); height of braincase, 11.69 ± 0.32 (11.0–12.1); length of dentary, 18.84 ± 0.30 (18.3–19.2); lower toothrow (c–m2 distance), 10.05 ± 0.24 (9.6–10.5); height of mandible at coronoid process, 7.47 ± 0.31 (7.0–8.1); length of forearm, 60.2 ± 2.10 (56.7–63.4); 3rd metacarpal, 57.91 ± 1.89 (54.4–61.3). Additional skull measurements (in mm) for a male and a female, respectively, from Peru (Tuttle 1970) are: greatest length, 28.0, 27.5; depth of brain case, 10.8, 10.6; zygomatic breadth, 17.3, 16.9; breadth of brain case, 12.5, 12.1; interorbital breadth, 12.9, 12.5; length of maxillary toothrow, 10.2, 9.9; palatal breadth, 12.9, 12.5; length of postpalatal, 8.4, 8.5.

Body mass (in g) and mean cranial and external measurements (in mm, range in parentheses) of 25 females and 9 males, respectively, from Paracou (Simmons and Voss 1998) are: body mass, 37.7 (28.0–52.2), 33.9 (30.5–39.2); total length, 80.8 (74.0–87.0), 79.1

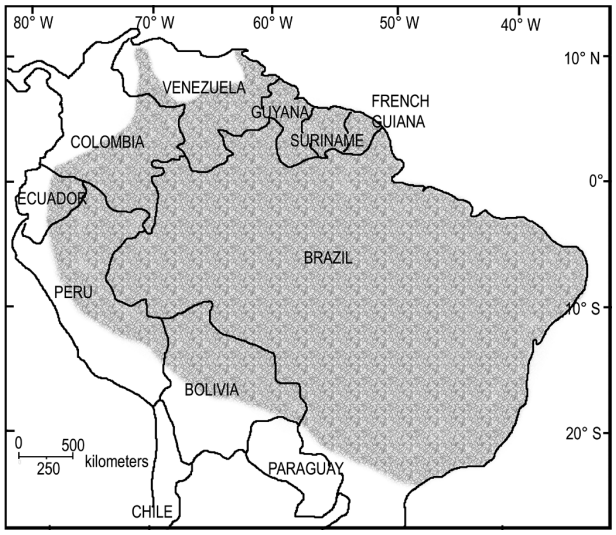

FIG. 3. Geographic distribution of *Artibeus obscurus* based on Eisenberg (1989), Eisenberg and Redford (1999), Handley (1989), Koopman (1993), Lim and Engstrom (2001), Linares (1998), Patten (1971), and Simmons and Voss (1998).

(75.0–84.0); length of hind foot, 16.1 (13.0–19.0), 17.0 (15.0–19.0); length of ear, 22.6 (21.0–24.0), 22.6 (22.0–24.0); length of forearm, 61.0 (55.4–64.0), 62.3 (60.0–65.0); greatest length of skull, 27.6 (26.7–28.3), 28.0 (27.9–28.0); length of condyloincisive, 24.7 (23.8–25.2), 25.4 (25.2–25.7); postorbital breadth, 6.6 (6.3–7.1), 6.4 (6.4–6.5); braincase breadth, 12.1 (11.3–12.7), 12.3 (12.2–12.5); mastoid breadth, 14.6 (14.2–15.2), 14.7 (14.7–14.7); zygomatic breadth, 17.0 (16.4–17.7), 17.0 (16.9–17.0); length of maxillary toothrow, 9.9 (9.7–10.3), 10.1 (10.1–10.1); breadth across molars, 12.6 (12.3–13.1), 12.4 (12.3–12.4).

Ranges of body mass (in g) and external measurements (in mm) of 8 males and 2 females collected in Río Nareuda, Bolivia (Anderson 1997), are: body mass, 34–50; total length, 72–90; length of hind foot, 14–17; length of ear, 20–23; and length of forearm, 59–69. Ranges of cranial measurements (in mm) of 4 females and 2 males collected at Caranavi and Río Madidi, Bolivia (Anderson 1997), are: length of condylobasal, 24.8–25.6; length of maxillary, 9.3–10.9; breadth at canines, 7.8–8.6; dental span, 11.6–13.8; molar width, 3.2–4.0; zygomatic breadth, 16.6–19.1; lambdoidal breadth, 14.7–16.7; breadth of braincase, 12.2–13.3; and depth of skull, 10.2–11.6. Average (range) measurements (in mm) of 14 females and 5 males from Bolivia (Webster and Jones 1980), are: length of forearm, 59.8 (55.7–61.6); greatest length of skull, 27.9 (27.1–28.9); zygomatic breadth, 16.7 (15.8–17.2); maxillary toothrow, 9.8 (9.4–10.2); and length of dorsal fur, 8–12. Mean, variance, and range (in mm), respectively, of forearm measurements of 10 males and 5 females from Bolivia are as follows: 59.5, 2.24, 55.4–63.3 (Anderson et al. 1982).

Average measurements (in mm) for 105 males and 50 females, respectively, from unspecified localities (Eisenberg and Redford 1999) are: length of forearm, 58.94, 60.16; total length, 75.00, 77.24; length of hind foot, 16.53, 17.26; and length of ear, 23.01, 23.48. Mean body masses (g) of the same individuals are 35.34 and 36.61, respectively (Eisenberg and Redford 1999).

DISTRIBUTION. The Amazon Basin is the core range of *A. obscurus* (Fig. 3). It is found throughout Brazil except in the extreme south (Eisenberg and Redford 1999) and is found approximately south of the Llanos in Venezuela and Colombia and in the Amazonian regions of Guyana, French Guiana, Suriname, Ecuador, Peru, and Bolivia (Albuja 1999; Engstrom and Lim 2002; Handley 1989; Koopman 1993; Lim and Engstrom 2001; Linares 1998; Ochoa 1995; Patten 1971; Simmons and Voss 1998; Webster and Jones 1980). One location in northwestern Venezuela is outside the remaining range (Eisenberg 1989) and is probably a misidentification (B. K. Lim, in litt). *A. obscurus* has been reported from the southern portion of the Atlantic coastal forests of Brazil (Geraldes 1995). No fossils are known.

FORM AND FUNCTION. Dental formula is i 2/2, c 1/1, p 2/2, m 3/3 or 2/3, total 30 or 32 (Patten 1971). Some of the serous cell mitochondria of *A. obscurus* are modified into megamitochondria, which have short peripheral cristae and a laminar inclusion in the matrix compartment. Megamitochondria of *A. obscurus*, under lower magnifications, contain ≥1 packets of parallel filaments in the matrix compartment (Tandler et al. 1997).

Mean (*SE*) concentrations (parts per thousand dry mass) of elements in feces of 1 male and 1 female (Studier et al. 1994) were: Ca, 16.07 (7.16); Mg, 7.72 (0.04); K, 40.47 (15.01); Na, 0.45 (0.10); Fe, 0.62 (0.18); and N, 49.8 (10.7).

ONTOGENY AND REPRODUCTION. Mating occurs from September to November. Embryonic development in Ecuador occurs until around March, and in April lactation is initiated (Albuja 1999). Two pregnant females (1 embryo each) from Bolivia were recorded in May and July; 6 nonpregnant females were recorded in March (1), April (1), June (2), July (1), and December (1—Anderson 1997). At San Juan, Peru (Tuttle 1970), 1 nonpregnant female was captured 16 August, and 1 pregnant female (crown–rump length of the single embryo =9 mm) on 26 August; testes of 3 males captured 25 July–2 August measured 8 by 6, 8 by 5, and 6 by 4 mm.

ECOLOGY. *Artibeus obscurus* is found throughout the wet South American lowlands east of the Andes (Simmons and Voss 1998). In Ecuador, it inhabits the eastern tropical floor and the adjacent lower floor subtropics (Albuja 1999). Habitats range from the lowland and upland rain forests of the Amazon valley to the savanna and semideciduous forests of eastern Bolivia and southern Brazil (Patten 1971). Patchy distribution was reported in the arid portions of northeastern Brazil (Mares et al. 1981b). Specimens occur in the extreme northwest of the Caatingas, a forest of palm groves in the predominantly mesic areas in Brazil (Mares et al. 1981a). *A. obscurus* occurs up to 1,032 m in Venezuela (Handley 1976), up to 1,330 m in Peru, and 1,350 m in Bolivia (Anderson et al. 1982). *A. obscurus* is found principally between 200 and 1,400 m in the Amazon Basin, in areas that consist of an herbaceous ground layer, lowland rain forest, montane rain forest, and the lower cloud forest (Graham 1983; Patterson et al. 1996). The locations of 321 *A. obscurus* captured in Venezuela were: 59% evergreen forest, 41% yards and openings, and <1% cloud forest; in these habitats, 91% were near streams, 9% were in other moist areas, and <1% were in dry areas (Handley 1976). The life zones in which the same 321 Venezuelan *A. obscurus* were captured included: tropical dry forests, 2%; tropical humid forests, 73%; tropical very humid forests, 19%; premontane humid forest, 3%; premontane very humid forests, 3%; and lower montane humid forests, <1% (Handley 1989). *A. obscurus* occurred in 4 of the 5 major Brazilian biomes, including Amazonia, Atlantic Forest, Caatingas, and Pantanal (Marinho-Filho and Sazima 1998). In collections made in Brazil during August, 3 times more *A. obscurus* were captured in bat nets set at ground level than in the canopy; thus, *A. obscurus* travels through the lower strata of the forest, at least during August (Handley 1967). Similar results from 117 captures in Paracou (Simmons and Voss 1998) were: 89% in ground-level mistnets, 6% in elevated mistnets, and 5% at roosts. Three collections were found roosting under exfoliating pieces of bark 6–7 m above the ground on the trunks of grignon trees, *Octea rubra* (Lauracae); the 1st consisted of an adult female with a nursing juvenile; the 2nd consisted of an adult female, a nursing juvenile, and an escaped adult of unknown sex; and the 3rd was a solitary near-term pregnant female. A solitary adult male was found roosting beneath an unmodified leaf of *Phenakospermum guyannense* (Strelitziaceae) ca. 4 m above the ground.

In Amazonian Peru, *A. obscurus* was netted along with *A. planirostris* in a primary rain forest and an adjacent cattle farm, at low-level strata (Koepcke and Kraft 1984). Near Iquitos, Peru, *A. lituratus*, *A. obscurus*, and *A. planirostris* were caught at the low-level strata in a flyway between a pig wallow and village house and near fruit trees. The bats appeared to feed on several trees, including *Ficus*, *Inga marginata*, and *Pourouma cecropiaefolia* (Davis and Dixon 1976). *A. obscurus* was netted with *A. cinereus*, *A. lituratus* and *A. planirostris* over tapir trails and a stream in mature evergreen forest in Peru, but *A. obscurus* was not found around fruit trees (Tuttle 1970). *A. obscurus* was caught in the late

evening hours, but none were caught in the early morning hours near Iquitos, Peru (Davis and Dixon 1976).

The greatest number of captures were recorded during the Smithsonian Venezuelan Project (Handley 1976), in which *A. obscurus* was the 2nd most frequent of 1,070 specimens: *A. jamaicensis* 51.9%, *A. obscurus* 30.0%, *A. lituratus* 13.9%, and *A. amplus* 4.2%. Of 62 *Artibeus* in Amazonian Peru (Koepcke and Kraft 1984), 58.0% were *A. planirostris*, 21.0% *A. lituratus*, and 21.0% *A. obscurus*. At forested netting stations in Belém, Brazil (Handley 1989), 448 captures comprised 54.5% *A. planirostris*, 38.4% *A. lituratus*, and 7.1% *A. obscurus*. Behaviorally, *A. obscurus* has a distress call distinct from that of *A. planirostris* and resembling that of *A. lituratus* (Handley 1989).

GENETICS. The diploid number of *A. obscurus* is 30/31, the fundamental number (FN) is 56, the X chromosome is subtelocentric (Gardner 1977), and somatic chromosomes range from medium to large subtelocentrics (Baker et al. 1992). Specimens from Colombia and Peru show an XYY system, with one Y considerably larger than the other (Patten 1971). Both Y chromosomes are acrocentric (Gardner 1977). Four rDNA sites occur on telomeric short arms of chromosomes in *A. obscurus* (Baker et al. 1992).

Mitochondrial 12S rRNA sequences (Pumo et al. 1996) are highly derived compared with other *Artibeus* species (Tandler et al. 1997). Sequence divergence of 12S rRNA between *A. obscurus* and other congenerics ranged between 2.9% for *A. jamaicensis* and 5.5% for *A. phaeotis* (Pumo et al. 1996).

Cytochrome-*b* sequences of *A. obscurus* form a monophyletic clade detected in 100% of 1,000 bootstrap iterations (Lim et al. 2004). Sequence divergence of cytochrome *b* between *A. obscurus* and other large *Artibeus* ranged between 6.4% (*A. planitrostis*) and 9.1% (*A. fimbriatus*—Lim et al. 2004).

CONSERVATION STATUS. *Artibeus obscurus* was listed as stable (Wilson 1997) and as a lower risk near threatened species by the International Union for Conservation of Nature Red List (Hilton-Taylor 2000).

REMARKS. Taxonomic confusion stems from the similarity of *A. obscurus* to *A. jamaicensis*, compounded by geographic variation in morphology of the latter species (Handley 1987). Although the 2 species are almost equal in size, *A. jamaicensis* is slightly larger and has a more prominent rostrum than *A. obscurus* (Lim and Wilson 1993). Previously referred to as "*Artibeus* sp. (medium)" by Handley (1967), "*A.* species" by Tuttle (1970), and "an undescribed species" by Jones and Carter (1979), discovery of Gray's (1838) use of *Arctibeus fuliginosus* established use of the name *Artibeus fuliginosus* (Handley 1976). Patten (1971) provided evidence to doubt the application of *A. fuliginosus* to the species in question and proposed a new name, *Artibeus davisi*, a nomen nudum (Koepcke and Kraft 1984). Handley (1989) concluded that *A. fuliginosus* Gray cannot be distinctly identified because it has 5–6 warts on each side and a forearm length of 63 mm, both characteristics more common to *A. jamaicensis* than *A. obscurus*. The alternative *Phyllostoma obscurum* Schinz (1821) certainly belongs to *A. obscurus*. Discovery of the holotype *Phyllostoma obscurum* from the Wied-Neuwied collection at the American Museum of Natural History confirmed renaming the species to *A. obscurus* (Handley 1989).

Artibeus is derived from the Greek words: *arti-*, straight, exactly fitted; and *bao*, to walk (Palmer 1904). Latin derivation of *obscurus*, comes from *obscur*, which means covered or dark (Borror 1960).

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