

*Artibeus jamaicensis*. By Jorge Ortega and Iván Castro-Arellano

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***Artibeus jamaicensis* Leach, 1821**

Jamaican Fruit-eating Bat

*Artibeus Jamaicensis* Leach, 1821:75. Type from “Jamaica.”

*Madataeus Lewisii* Leach, 1821:81. Type from “Jamaica.”

*Artibeus carpolegus* Gosse, 1851:271. Type locality “Content, Jamaica.”

*Dermanura eva* Cope, 1889:130. Type locality “St. Martins, Lesser Antilles.”

*Artibeus coryi* Allen, 1890:181. Type locality “St. Andrews, Caribbean Sea.”

*Artibeus parvipes* Rehn, 1902:639. Type locality “Santiago de Cuba, Oriente, Cuba.”

*Artibeus insularis* Allen, 1904:231. Type locality “St. Kitts, Lesser Antilles.”

*Artibeus yucatanicus* Allen, 1904:232. Type locality “Chichén-Itza, Yucatán.”

*Artibeus planirostris trinitatis* Andersen, 1906:420. Type locality “St. Anns, Trinidad.”

**CONTEXT AND CONTENT.** Order Chiroptera, suborder Microchiroptera, family Phyllostomidae, subfamily Stenodermatinae, tribe Stenodermatini (Baker et al. 1989). *A. fraterculus* and *A. planirostris* were considered either as subspecies of *A. jamaicensis* (Handley 1987; Jones and Carter 1976) or as species (Koopman 1993). *A. obscurus* (= *A. fuliginosus*) was separated from *A. jamaicensis* by Handley (1989). Seven subspecies are recognized.

*A. j. jamaicensis* Leach, 1821:75, see above (*praeceps* Andersen is a synonym).

*A. j. parvipes* Andersen, 1908:261, see above.

*A. j. paulus* Davis, 1970:119. Type locality “7.5 km WNW La Libertad, ca. 500 ft., Dept. of La Libertad, El Salvador.”

*A. j. richardsoni* Allen, 1908:669. Type locality “Matagalpa, Matagalpa, Nicaragua.”

*A. j. trinitatis* Hershkovitz, 1949:447, see above (*grenadensis* Andersen is a synonym).

*A. j. tryomylus* Handley, 1966:299. Type locality “Pápayo, Guerrero.”

*A. j. yucatanicus* Andersen, 1908:263, see above.

**DIAGNOSIS.** *Artibeus jamaicensis* (Fig. 1) is easily distinguished from members of the subfamily Carollinae because it has a complete zygomatic arch. It can be separated from other stenodermatines by absence of a tail and a narrower interfemoral membrane (Jones and Carter 1976). Large fruit bats (subgenus *Artibeus*; length of forearm, >48 mm) differ from small fruit bats (subgenera *Dermanura*, *Enchistenes*, and *Koopmania*; length of forearm, <48 mm) by size. *A. jamaicensis* has an unfurred uropatagium and is larger (length of forearm, 52.0–67.4 mm) than *A. hirsutus* (length of forearm, 52.0–59.7 mm) and *A. inopinatus* (length of forearm, 48–53 mm) that possess fringed to densely furred uropatagia (Davis and Carter 1964; Hall 1981; Handley 1966). *A. lituratus* differs most notably from *A. jamaicensis* in having a larger and more massive skull and a rostrum that is wider at base of canines; it also has distinct supraorbital stripes and brownish fur (Jones 1978). *A. planirostris* is similar to *A. jamaicensis*, but forearm (length of forearm, 56.5–63.1 mm) and tibia are consistently smaller, feet are narrower and lightly built, postorbital processes are poorly developed, and a reduced M3 occurs on both sides (*A. j. tryomylus* has a reduced M3 on one side—Handley 1991). *A. fraterculus* is smaller in overall size and paler than *A. jamaicensis* but is located only on the Pacific slope of Peru and Ecuador (Koopman 1978).

Taxonomic status of *A. obscurus* is uncertain because it has been considered a subspecies of *A. jamaicensis* (Koopman 1978). Compared with *A. jamaicensis*, *A. obscurus* has a dorsum that is

mostly dark brown, a darker membrane between fingers 2 and 3, facial stripes that are always faded, poorly developed supraorbital ridges and postorbital processes, a longer and broader noseleaf, a chin with fewer and smaller ornamental warts, and m3 present in almost all specimens (Handley 1989). The fringed-lipped bat (*A. fimbriatus*) differs from *A. jamaicensis* by having bicolored and longer fur; internally fringed noseleaf and lips; a shorter, shallower, and less arched rostrum; and less-developed supraorbital and postorbital ridges and processes (Handley 1989). Finally, *A. amplus* is distinct from *A. jamaicensis* by having the lower edge of noseleaf horseshoe attached, interfemoral membrane slightly hairy and fringed medially, longer and narrower skull, less arched nasals, thinner and more fragile zygomata, and longer and narrower post-palatal extensions (Handley 1987).

**GENERAL CHARACTERS.** *Artibeus jamaicensis* is a medium-sized bat with considerable morphological variation. Northern subspecies are largest in the Atlantic versant of Middle America and smallest in the Atlantic versant of the Mexican Gulf, Yucatan Peninsula, Pacific versant (Davis 1970). Other subspecies are larger in the Amazon Basin and on St. Vincent Island and smaller in the southern and northern part of South America, including other Caribbean Islands (Handley 1987). In general, ears are broad, triangular, pointed, and separated. Tragus is short with 4–5 relatively small serrations on outer margin. Noseleaf is well developed with a cluster of sebaceous glands (Dalquest et al. 1952). Whitish facial stripes are not sharply defined and are less developed in dark compared with light populations (Andersen 1908). Lower lip has a central wart with smaller warts surrounding. Upper and lower lips have sebaceous holocrine glands (Dalquest et al. 1952). Dorsal fur varies from ashy gray to ashy brown with white hair bases showing through (Davis 1970). Wings are broad and dark gray in color. External tail is absent. Interfemoral membrane is narrow and naked with a brief calcar.

Ranges of measurements (in mm) are: total length, 78–89; length of hind foot, 16–18; length of ear, 20–27; length of forearm, 52.0–67.4; length of lancet, 8.6–9.0; width of lancet, 6.3–6.5; width of horseshoe, 8.7–9.0; greatest length of skull, 26.2–31.6; condylobasal length, 27.8–30.0; zygomatic breadth, 16.2–20.6; postorbital constriction, 6.7–7.3; breadth of braincase, 12.0–12.9; depth



FIG. 1. Marked adult female *Artibeus jamaicensis* roosting in Los Murciélagos Cave in Yucatán, México. Photograph by Jorge Ortega.

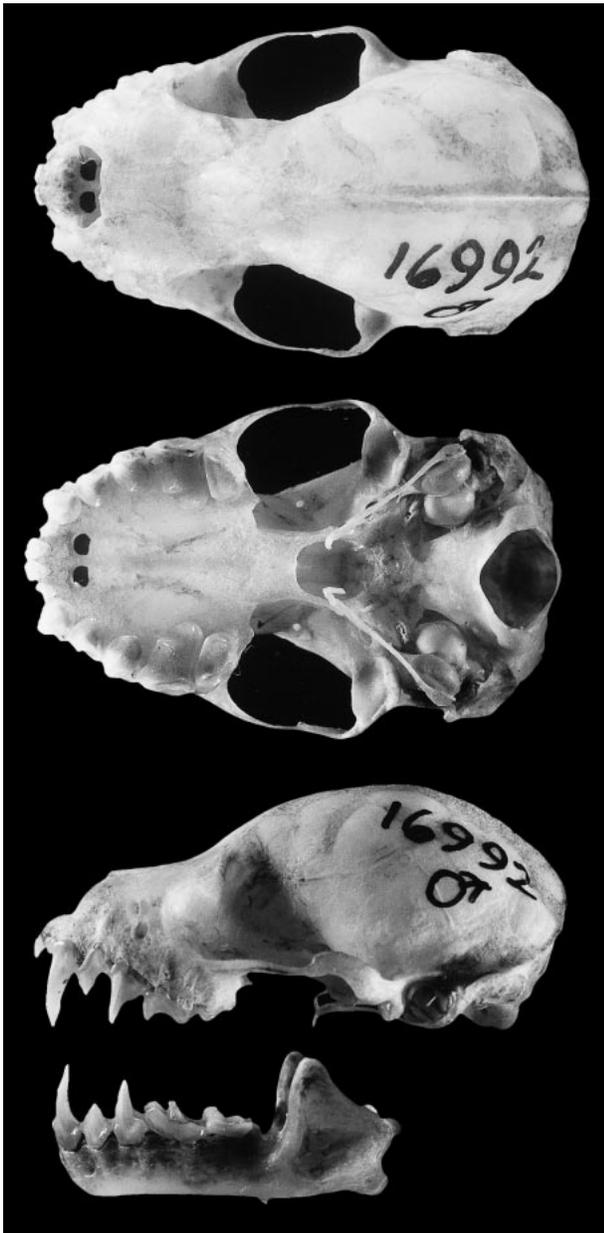


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a male *Artibeus jamaicensis yucatanicus* from Yucatán (Instituto de Biología, Universidad Nacional Autónoma de México [IBUNAM 16992]). Greatest length of the skull = 28.4 mm.

of braincase, 9.1–10.3; mastoid breadth, 13.9–14.7; length of maxillary tooththrow, 9.8–11.5; length of mandibular tooththrow, 4.8–9.6; postpalatal length, 7.7–8.7; length of palate, 8.8–11.0; breadth across upper molars, 7.9–13.2; and body mass, 36–48 g. Cochlea (with 6 half-turns) is 2.5 mm high (Hall 1981; Handley 1966; Hershkovitz 1949; Jones 1978; Swanepoel and Genoways 1979). Most variable cranial character is breadth across upper molars (range, 12.1–13.0 mm), and least variable is length of skull (range, 27.8–29.4 mm). Wing measurements (in mm) are: length of metacarpal III, 10.5–19.2; length of metacarpal IV, 52–56; length of metacarpal V, 57.0–58.8; length of phalanx 2, digit III, 9.4–18.6; and length of phalanx 1, digit III, 12.5–17.9 (Davis 1970). Most variable wing character is length of phalanx I, digit III (coefficient of variation 7.22), and least variable is length of forearm (Smith and Starrett 1979; Swanepoel and Genoways 1979).

Skull of *A. jamaicensis* is short and robust with prominent preorbital and postorbital processes (Fig. 2); anterior portion is depressed; sagittal crest is moderately developed; posterior portion of

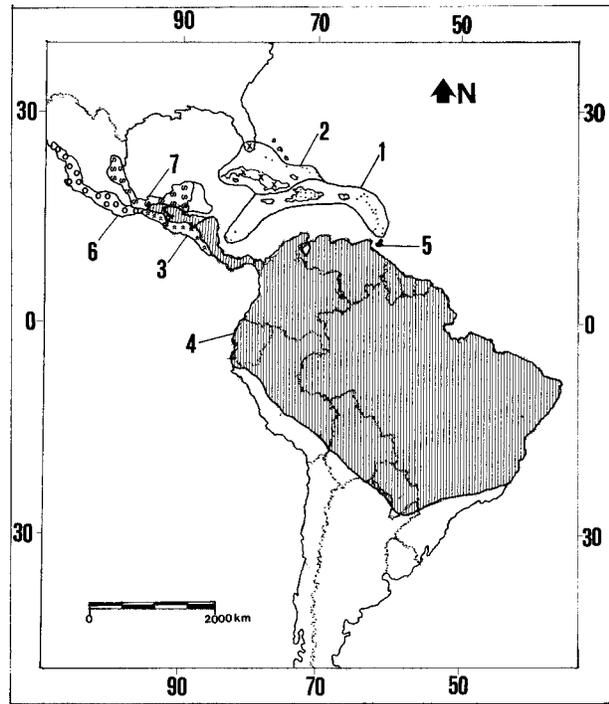


FIG. 3. Distribution of *Artibeus jamaicensis*: 1. *A. j. jamaicensis*. 2. *A. j. parvipes*. 3. *A. j. paulus*. 4. *A. j. richardsoni*. 5. *A. j. trinitatis*. 6. *A. j. triomylus*. 7. *A. j. yucatanicus*. Modified from Eisenberg (1989), Hall (1981), and Koopman (1982).

temporal bone has concave muscular impressions; infraorbital foramen is doubled; rostrum is short and wide; basisphenoidal pits are absent; inner upper incisor is small with a distinctly bilobed cutting edge; molar teeth are strong with large crushing surfaces (Davis 1970; Goodwin and Greenhall 1961).

**DISTRIBUTION.** *Artibeus jamaicensis* occurs from Sinaloa and Tamaulipas, México (Fig. 3), southward to Ecuador, Venezuela, Trinidad, Tobago, Greater and Lesser Antilles, Florida Keys, and Amazonian Brazil to northwestern Argentina (Mares et al. 1981; Myers and Wetzel 1983; Redford and Eisenberg 1992). It occurs from sea level to 2,135 m (Eisenberg 1989; Tamsitt 1966).

**FOSSIL RECORD.** Three fossil jaws and 1 isolated fossil molar were found in Abra Cave in Tamaulipas, México (Dalquest and Roth 1970). *A. jamaicensis* subfossil bones were recovered from Spukil, Lara, Has, Coyok, and Chacaljas caves and the Chichen-Itza sacred Mayan natural water well, Yucatán, México (Alvarez 1976). Archeological excavation of Loltún Cave resulted in 1,522 subfossil bones, illustrating the great abundance of the Jamaican fruit bat in this sediment of the late Pleistocene and Holocene (Arroyo-Cabrales 1992).

Thirteen partial skulls and 28 mandibles represent the fossil record of *A. jamaicensis* in the Daiquiri and Camaguey caves of Cuba (Koopman and Ruibal 1955). Additional subfossil records from the Caribbean Islands are: Clara and Perro caves and Culebra Island in Puerto Rico; Aguas Buenas, Cayey, Comerio, Corazal, and Monte Grande caves in Puerto Rico; a cave near St. Michel, and Diquini cave in Haiti (Choate and Birney 1968).

In South America a fragmented bone was discovered in Laguna Santa, Brazil, but the taxonomic assignment is unclear (named as *Artibeus jamaicensis lituratus*—Paula-Couto 1946). Additional fossil records for Brazil are Toca da Boa Vista and Gruta dos Brejões (Czaplewski and Cartelle 1998). No significant morphological differences were found between 74 subfossil skulls recovered from the Quebrada Honda cave in Venezuela and extant specimens (Linares 1968). The subfossil record shows that *A. jamaicensis* has invaded the Antillean islands from the continent (Koopman and Williams 1951).

**FORM AND FUNCTION.** The Jamaican fruit-eating bat has sebaceous holocrine glands in upper and lower lips and noseleaf.

Salivary mucous glands occur on extreme lateral borders of lower lips (Dalquest et al. 1952). Dental formula is i 2/2, c 2/2, p 2/3, m 2/3, total 36, in Middle and South America, and m 3/3 in western Mexico (Davis 1970).

Milk is rich in glucose, galactose, and proteins (Jenness and Studier 1976). Composition (per 100 g) of milk of *A. jamaicensis* is 18.6 g fat, 7.3 g lactose, 1.1 g casein, 3.6 g whey protein, and 0.11 g citrate. Calculated energy content was 2.3 kcal/g in dry weight (Jenness and Studier 1976). A 45-g *A. jamaicensis* produces milk at a rate of 12.3 g/day. Milk of *A. jamaicensis* is 70% water, consequently, production of milk demands an additional daily intake of 8.6 ml of water for lactating females compared with water intake of nonlactating bats (Studier and Wilson 1991).

Mean diameter of erythrocytes of *A. jamaicensis* is 5.6  $\mu\text{m}$  (range, 4.3–7.0—Riedesel 1977). Mean density of red blood cells is 6.95 million cells/ $\text{mm}^3$  (6.13–7.76). Mean and range (in parentheses,  $\mu\text{g}$  leukocytes) are: lymphocytes, 7.86 (6.97–8.75); monocytes, 15.37 (13.89–16.85); basophils, 11.82; eosinophils, 12.82 (11.08–14.56); neutrophils, 9.60 (8.91–10.30). Leukocytes have a density of 7,920 cells/ $\text{mm}^3$  (7,282–8,558—Martinez 1941). Total protein present in serum of *A. jamaicensis* ranges from 5.19 to 6.55 g/100 ml and relative proportions of protein (g %) of some serum fractions are: albumin, 2.62–3.70; beta globulin, 0.87–1.45; gamma globulin, 0.36–1.00 (Valdivieso and Tamsitt 1974).

Externally, the brain of *A. jamaicensis* has relatively well-convoluted cerebral hemispheres and well-developed major sulci. "The pseudotemporal lobes project ventrally in an angular fashion, and the inferior colliculi are not dorsally exposed. The cerebellum is well crested and has a small secondary foliation at the lateral edges of the vermiform body" (McDaniel 1976:155). Internally, the brain of *A. jamaicensis* has an interhemispheric sulcus containing a shallow cingulate sulcus and a shallow callosal sulcus just dorsal to the corpus callosum. Callosal sulcus deepens as it courses caudally, and it is deeper than the cingulate sulcus near the habenular nuclei. Lateral olfactory tracts are generally ventral, but anteriorly they are more lateral than in phyllostomatines. Anterior thalamic nuclei project dorsally to level of habenular nuclei. Pons is shallow, well nucleated, and ventrally flattened. Dorsal nucleus contains fusiform cells, and ventral nucleus has small, dark, "spherical cells" (McDaniel 1976). Free amino acids (mg/100 g  $\pm$  SD of tissue) occur in encephalon of *A. jamaicensis*: aspartic acid, 49.9  $\pm$  3.5; glutamic acid, 227.1  $\pm$  15.2; glutamine, 71.9  $\pm$  7.2;  $\gamma$ -aminobutyric acid, 27  $\pm$  1.46; alanine, 1.12  $\pm$  0.17 (Ortega and Massieu 1963).

The Jamaican fruit-eating bat has a group of unusual papillae extending from the posterior middle region of the tongue to the base. These papillae are rounded and flattened, with 2 points directed anteriorly (Park and Hall 1951). Submandibular saliva of *A. jamaicensis* has a low level of amylase activity: 0.25% the activity of the highest rated frugivorous bat (*Sturnira lilium*) and ca. 0.03% the activity in humans (Tandler et al. 1986). Parotid salivary glands are exceptionally large and have secretory cells morphologically similar to the seromucoid type. The large size of salivary glands and increased production of saliva may be related to regulation of mineral and water balance, neutralization of alkaloids present in figs (*Ficus*), bonding of pellets rejected during feeding, and buffering of gastric secretions (Phillips et al. 1977; Studier and Wilson 1991; Wimsatt 1956). Secretory salivary granules are large, pale, and contain twisted fibers (Phillips et al. 1987).

The esophagus of the Jamaican fruit-eating bat is 41.05 mm long with gross internal folds arranged longitudinally. The cardia sphincter is almost on the same plane as the pyloric sphincter and the cardiac vestibule is enlarged (Forman et al. 1979). The stomach averages 18.7 mm from the gastroesophageal junction to the apex of greatest curvature of the stomach and 27.64 mm from the right to left side. The fundic caecum is big and rounded with a well-developed apex. The gastric mucosa has narrow transition zones because the pyloric glands are closer to the gastric zone. Pyloric glands are large (ca. 80% longer than fundic glands—Forman et al. 1979). Pyloric glands react to Hale's colloidal iron by secreting acid mucopolysaccharides. Folds of stomach are complex (Forman et al. 1979). The pylorus is longer and wider than the esophagus, and the pyloric sphincter is symmetrical with a well-developed musculature. Internally, the stomach has a septum that separates the cardiac vestibule from the fundic caecum. The total length of the intestine ranges from 337 to 587.9 mm, with a diameter 2.8–3.3 mm; large and small intestine do not differ, and the caecum is absent (Park and Hall 1951). Brunner's glands are sparse in the

1st portion of the duodenum. Paneth cells of the intestine are acidophiles by secretion of mucopolysaccharides (Forman et al. 1979). Free amino acids (mg/100 g  $\pm$  SD of tissue) occur in the liver as: aspartic acid, 12  $\pm$  0.82; glutamic acid, 51  $\pm$  4.9; glutamine, 39.7  $\pm$  4.24; alanine, 7.1  $\pm$  1.35; serine + glycine, 17.8  $\pm$  0.83 (Ortega and Massieu 1963).

Food passage is rapid, ca. 30 min, so digestive efficiency of the Jamaican fruit-eating bat is low (Studier et al. 1983). Only 25–30% of whole metabolizable energy present in *Ficus insipida* fruits is extracted, but large quantities of this fruit are processed. Eighty-five grams of figs would provide a 50-g Jamaican fruit-eating bat 14.3 kcal (Morrison 1980b). *A. jamaicensis* extracts only the juices of *F. insipida*, allowing the bat to process large quantities of fruit (2 times their body weight) without flying with more than a few grams of food in the gut. Swallowed juice contains 40% of nonfiber carbohydrates found in whole figs and is digested almost completely (Morrison 1980b). This strategy increases the dietary sodium level and decreases potassium compared to ingestion of whole pulp or whole fruit (Studier et al. 1983). Based on body mass or daily energy expenditure, daily protein requirements for the Jamaican fruit-eating bat are 122 or 128 mg, respectively (Studier and Wilson 1991). Leaves high in protein are consumed selectively by *A. jamaicensis* (Kunz and Díaz 1995). The Jamaican fruit-eating bat may obtain enough water from pulp juices of figs because free drinking water is not required (Studier et al. 1983; Studier and Wilson 1991).

The Jamaican fruit-eating bat has a tubular simplex uterus with a fundic end covered by the oviducts. Oviducts enter the uterine body near the midsagittal line. Internally, the uterus has a single common lumen without an intramural uterine cornua (Hood and Smith 1983).

Spermatozoa of *A. jamaicensis* resemble those of *Glossophaga soricina* in morphology and size. Each sperm has a short, rounded, nearly circular head; a marked basal concavity; and lacks a neck. Head dimensions range from 4.28 to 4.65  $\mu\text{m}$  in length and 3.16–3.44  $\mu\text{m}$  in width. Measurements are (in  $\mu\text{m}$ ): acrosome length, 2.51–2.98; nuclear length, 3.35–4.00. Morphology of head is similar to *Artibeus* and *Ardops*, but a portion of the acrosome anterior to the nucleus is smaller. The midpiece is relatively short and narrow and tapers gradually to a junction with the tail; its length ranges from 8.23 to 8.32  $\mu\text{m}$  (Forman and Genoways 1979). The Jamaican fruit-eating bat has accessory cavernous tissue in the penis that is restricted to the glans region. The preputial area includes a globular mass in the middorsal portion (Smith and Madkour 1980).

The kidney has an outer cortex (C) and an undivided inner medulla (M) whose thickness ratio (M/C) is 2.4. This ratio does not vary with aridity of habitat and is comparable to other frugivores, but low compared with insectivores (Studier et al. 1983). Mean maximum urine concentration in the Jamaican fruit-eating bat is 972 mOsm/kg (Studier and Wilson 1983). Because of poor renal water conservation and the primarily liquid diet, urinary output is high and varies from 209 to 262 ml  $\text{kg}^{-1} \text{day}^{-1}$  (Studier and Wilson 1991).

A natural urine concentration cycle was determined at Barro Colorado Island, Panamá. Upon emergence from day roosts (900 h), urine osmotic pressure was uniform and relatively high, averaging 699 mOsm/kg. After 0.5–1.5 h of leaving roosts, urine osmotic pressure fell to a mean of 539 mOsm/kg, associated with rehydration due to ingestion of pulp juices of fruit. Subsequently, dehydration occurred, with a peak osmotic pressure by 0200 h, and remained constant until the following sunset, unaffected by subsequent feeding sessions (Studier and Wilson 1991).

Although the Jamaican fruit-eating bat has a mean body temperature of 38.7°C, it has daily fluctuations in body temperature reaching a mean minimum of 36.4°C between 1130 and 1430 h and a mean maximum of 39.1°C at 2100 h. A difference of 5°C in body temperature exists between resting bats and those after vigorous flight (Morrison and McNab 1967). *A. jamaicensis* is intolerant of low ambient temperatures; lethal upper and lower ambient temperatures are 41.5 and 10°C, respectively (McManus 1977).

Thermoregulatory capabilities are variable; *A. jamaicensis* has been reported to be a homeothermic and a heterothermic endotherm (McNab 1969; Studier and Wilson 1991). These differences are attributed to a "captivity effect," in which the bats pass from being a heterotherm at capture to a homeotherm after some period in captivity (Studier and Wilson 1979, 1991). *A. jamaicensis* tested soon after capture may represent the natural thermoregulatory per-

formance, or the Jamaican fruit-eating bat may be a homeothermic endotherm during periods of flight and feeding activity and a heterothermic endotherm during periods of rest (Studier and Wilson 1991).

Body temperature of *A. jamaicensis* depends on ambient temperature but is tightly regulated over a middle range of ambient temperatures. From 8 to 33.2°C, *A. jamaicensis* maintains a relatively constant body temperature differential between 8.3 and 6.6°C higher than ambient temperature (Studier and Wilson 1979). Some individuals can tolerate temperatures of 40°C for 5 h, and a few have a body temperature >35°C after 6 h at 10°C (McManus 1977).

Fat content, expressed as a ratio (g fat/g fat-free dry weight), was 0.188 for males in December (dry season) and 0.0126 in July (wet season). Females had a ratio of 0.279 in December and 0.0115 in July (McNab 1976). Based on mass, daily energy requirements for a 45-g Jamaican fruit-eating bat are estimated at 10.3 kcal (43.3 kJ). The average daily energy budget for a reproductively inactive homeothermic *A. jamaicensis* is based on time partitioning distributed among 2 expenditures: basal metabolism, 8.77 kcal (36.7 kJ) and flight costs, 1.8–3.2 kcal (7.63–13.4 kJ—McNab 1969; Morrison 1978d).

Nitrogen and mineral concentrations ( $\pm SD$ , parts per thousand dry mass) from feces of *A. jamaicensis* are: Ca, 31.47  $\pm$  6.24; Mg, 9.07  $\pm$  0.88; K, 35.76  $\pm$  5.50; Na, 0.67  $\pm$  0.09; Fe, 0.74  $\pm$  0.07; N, 55.7  $\pm$  5.4. A low concentration of sodium in plant parts is reflected in feces, suggesting that *A. jamaicensis* experiences at least periodic dietary sodium deficiencies (Studier et al. 1994).

*Artibeus jamaicensis* has a higher aspect ratio (2.27  $\pm$  0.03 SE) in the plagiopatagial region as result of a large forearm. The metacarpal of the third digit is long, but phalangeal elements are short (Smith and Starret 1979). Selected measurements ( $\pm SE$ ) of morphological traits for *A. jamaicensis* are: depth of forearm/width of forearm, 0.85  $\pm$  0.01; tip index, 2.03  $\pm$  0.02; flap of leading edge/width of wing for forearm, 0.106  $\pm$  0.004; flap of leading edge/width of wing for wrist, 0.034  $\pm$  0.002; flap of leading edge/width of wing for metacarpal, 0.072  $\pm$  0.001; area index, 257.3  $\pm$  5.1 cm<sup>2</sup> (Vaughan and Bateman 1980).

**ONTOGENY AND REPRODUCTION.** The Jamaican fruit-eating bat has a bimodal polyestrous breeding pattern, with peaks of offspring production probably related to fruit availability (Heithaus et al. 1975). Each female has 2 periods of postpartum estrus annually and produces a single young or, rarely, twins (Barlow and Tamsitt 1968) at each parturition. Peak breeding occurs at the end of the wet season and parturition occurs during dry months. In the second breeding season, females can show delayed embryonic development (2.5-month period), and young are born in the next breeding period (Fleming 1971).

*Artibeus jamaicensis* breeds year-round in México; many females have been captured with embryos or lactating at different times of the year (Hall and Dalquest 1963; Jones et al. 1972, 1973). In Central America and the Caribbean Islands, parturition takes place all year (Tamsitt and Mejía 1962; Wilson 1979), and *A. jamaicensis* is seasonally polyestrous in tropical habitats of Central America (Fleming et al. 1972; Wilson et al. 1991). A few records show an acyclic polyestrous breeding pattern for *A. jamaicensis* in South America (Tuttle 1970).

Testes size of adult males is correlated with spermatogenesis production and testes become enlarged during postpartum estrus of females (Fleming et al. 1972). Harem males have slightly larger testes and show a greater amount of wear on canine teeth than bachelor males (Kunz et al. 1983). Length of testes for adult males is 3.5–10.0 mm (Forman and Genoways 1979). First copulation does not occur until day 2 postpartum, and the last can occur 25 days later. During copulation, the vaginal rim of the vulva becomes dark and extensive (Keast and Handley 1991).

Normal gestation is 3.5–4 months, but can extend to 7 months with delayed embryonic development (Wilson et al. 1991). Embryos reach the blastocyst stage before entering the uterus. Implantation is interstitial and cytolytic, and the placenta is discoidal and hemochorial (Bleier 1979; Wislocki and Fawcett 1941). At the end of gestation, the mass of a pregnant female is 35% more than of a nonpregnant female (Keast and Handley 1991).

The average crown-rump length of full-term embryos is 26 mm (Ramírez-P. et al. 1977). Dental laminae are evident at the 9-mm crown-rump length when tooth buds can be distinguished. The bell stage primordial, only in anterior teeth, was identified in 13.5-

mm embryos. Deciduous teeth in late bell stage were found in a 20.5-mm embryo. Well-formed deciduous incisors in bell stage and canines in cap stage were found in a 31.5-mm embryo (Phillips et al. 1977).

Parturition begins with the female hanging head-down. The neonate presents head first, without the aid of the mother, and is expelled after a few contractions. The placenta is expelled, and the mother consumes it (Bhatnagar 1978; Jones 1946). During the 1st days after birth, young are carried by the mother but later remain in the day-roosting area. During nursing, nipples become enlarged and pigmented, and surrounding hair is lost. Young nurse for 15 days (Novick 1960). Lactation occurred for 2 months in a captive colony (Keast and Handley 1991).

Young have a complete, permanent dentition at 40 days of age, and at 50 days, forearm growth is complete and young start to fly. Adult body mass is reached at 80 days of age, and >104-day-old individuals show complete epiphyseal fusion. Wing loading increases geometrically with age and is exponentially correlated with body mass. Sexual maturity is attained in 8 months for females and 12 months for males (Keast and Handley 1991; McManus and Nelis 1972).

**ECOLOGY.** *Artibeus jamaicensis* is the most widespread species of the genus and occurs in a wide range of habitats. It is found mainly in humid tropical habitats, such as tropical evergreen forest, but it even penetrates cloud forest and drier tropical habitats, such as seasonal dry forest and human-modified habitats (Eisenberg 1989; Morrison 1979). It uses caves, hollow trees, dense foliage, buildings, and leaf tents as roost sites (Kunz and McCracken 1995; Morrison and Handley 1991; Timm 1987).

*Artibeus jamaicensis* can modify broad leaves of various plants to produce a day roosting "tent" (Timm 1987). These tents are temporary, and bats abandon them in 3–5 days (Handley and Morrison 1991). At least 8 different plant species (*Philodendron fragrantissimum*, *Coccolobos barbadensis*, *Sabal mauritiformis*, *Scheelea rostrata*, *Pentagonia donnel-smithii*, *Geonoma congesta*, *Bactris wendlandiana*, and *Asterogyne martiana*) with 3 distinct tent architectures are used for refuge (Foster and Timm 1976; Timm 1987). Tent making is critical, and tents are an easily defendable resource with a relatively short life span compared with tree hollows (Kunz and McCracken 1995).

The Jamaican fruit-eating bat is a frugivore, a fruit generalist (Gardner 1977), and a fig specialist (August 1981). *A. jamaicensis* will eat the following plants—plant part coded as: entire fruit (E); skin only (S); pulp only (P); flowers, pollen, or nectar (F); leaves (L), and parts unknown (fruit): *Achras sapota* (S, P), *Acrocomia aculeata* (P), *Anacardium excelsum* (fruit), *Ananias umbellulifera* (P), *Andira inermis* (S, P), *Annona muricata* (P), *A. squamosa* (P), *Anthurium* (fruit), *Bactris* (S, P), *Birsononima crasifolia* (fruit), *Bombax* (F), *Brosium alicastrum* (fruit), *Byrsonima spicata* (S, P), *Calocarpum mammosum* (P), *Calophyllum brasiliense* (fruit), *C. calaba* (L), *C. longifolium* (fruit), *Carica papaya* (E), *Casimiroa edulis* (P), *Cecropia bureaniana* (E), *C. obtusifolia* (E), *C. peltata* (E, F), *Cecropia* (E, F), *Ceiba pentandra* (F), *Cereus hexagonus* (S, P), *Cerocarpus disticus* (E), *Chlorophora tinctoria* (E), *Chrysobalanus icaco* (P), *Chrysophyllum cainito* (S, P), *Clusia rosea* (fruit), *Coccoloba wifera* (P), *Coccolobos* (S, P), *Coffea* (S, P), *Cordia bicolor* (S), *C. collococca* (P), *C. dodecandra* (fruit), *Crescentia cujete* (F), *Cynometra retusa* (fruit), *Dendropanax arboreum* (fruit), *Diospyros digyna* (P), *D. mabola* (P), *Dipteryx odorata* (S, P), *D. panamensis* (fruit), *Elaeodendron xylocarpum* (fruit), *Epiphyllum hookeri* (P), *Erhetia tiliifolia* (fruit), *Erythrina poeppigiana* (L), *Eugenia jambos* (S, P), *E. malaccensis* (S, P), *Ficus benjamina comosa* (E), *F. citrifolia* (fruit), *F. dugandii* (fruit), *F. glabrata* (E), *F. hartwegii* (fruit), *F. insipida* (fruit), *F. obtusifolia* (E), *F. popenoi* (fruit), *F. radula* (E), *F. religiosa* (E, L), *F. retusa* (E), *F. trigonata* (fruit), *F. yoponensis* (fruit), *Ficus* (E, L), *Flacourtia indica* (E), *Genipa* (fruit), *Guazuma ulmifolia* (fruit), *Guettarda foliacea* (fruit), *Hura crepitans* (F), *Hylocereus lemairei* (P), *Hymenaea courbaril* (F), *Iriartea exorrhiza* (E), *Jambosa vulgaris* (S, P), *Lemaireocereus* (fruit), *Licania* (fruit), *Madhuca latifolia* (F), *Malpighia glabra* (S, P), *Mammea americana* (P), *Mangifera indica* (S, P), *Manilkara achras* (fruit), *M. bidentata* (S, P), *M. zapota* (F), *Mastichodendron capiri* (fruit), *Melicocca bijuga* (P), *Mimusops elengi* (S, P), *Muntingia calabura* (fruit), *Musa* (E), *Nectandra ambigens* (fruit), *Ochroma lagopus* (F), *Passiflora quadrangularis* (P), *Persea americana* (P), *Pilocarpus racemosus*

(fruit), *Pimenta racemosa* (E), *Piper aduncum* (fruit), *P. amalago* (E), *P. auritum* (E), *P. hispidum* (E), *P. lapathifolium* (fruit), *P. sanctum* (E), *P. tuberculatum* (E), *Piper* (E), *Poulsenia armata* (fruit), *Pouteria campechiana* (fruit), *P. multiflora* (S, P), *P. unilocularis* (fruit), *Pseudobombax septinatum* (F), *Pseudolmedia oxyphyllaria* (fruit), *Psidium guajava* (E), *Putranjiva roxburghii* (S, P), *Quararibea asterolepis* (fruit), *Q. funebris* (fruit), *Rheedia edulis* (fruit), *Roystonea oleracea* (E), *Sabal mexicana* (fruit), *Sapindus saponaria* (P), *Sideroxylon quadrilaterale* (S, P), *Solanum torvum* (fruit), *Solanum* (fruit), *Spondias cytherea* (P), *S. mombin* (S, P), *S. purpurea* (fruit), *S. radlkoferi* (fruit), *Spondias* (S, P), *Thebetia gaumeri* (fruit), *Terminalia catappa* (S, P), *Trema micratha* (fruit), *Turpinia pinnata* (fruit), *Vitex gaumeri* (fruit), and *Vitis vinifera* (E—Gardner 1977; Greenhall 1956; Handley et al. 1991a; Kunz and Díaz 1995).

Figs (*Ficus*) are an important part of the diet; for example at Barro Colorado Island, Panamá, they form  $\geq 78\%$  of the annual fruit consumed by this bat. At this site, Jamaican fruit-eating bats remove  $\geq 7\%$  of the annual production of 250 kg figs/ha (Handley and Leigh 1991). Figs are consumed like leaves; animals ingest only the pulp juices (Studier et al. 1983). Leaves of plants with high concentrations of protein are selected by *A. jamaicensis* as a protein supplement (e.g., *E. poeppigiana*, *Ficus*, *C. calaba*—Kunz and Díaz 1995).

In spite of the diversity of plant species eaten by the Jamaican fruit-eating bat, only a few compose the bulk of the diet at any given locality, with other species appearing in much lower quantities (Humphrey and Bonaccorso 1979). In southern Veracruz, México, the most common fruit species consumed by Jamaican fruit-eating bats were *Cecropia obtusifolia*, *Spondias mombin*, and *Brosium alicastrum*, but if the 4 species of *Ficus* were combined, their prominence in the diet was comparable to these 3 (Humphrey and Bonaccorso 1979). Pollen from *Anacardium occidentale*, *Bauhinia pauletia*, *Ceiba pentandra*, *Crescentia*, *Hymenaea courbaril*, *Manilkara zapota*, *Ochroma lagopus*, and *Pseudobombax septinatum* was recovered from the fur of Jamaican fruit-eating bats in Brazil and Costa Rica (Gardner 1977).

The Jamaican fruit-eating bat usually carries fruits and leaves by mouth, carrying food from the source to a feeding roost, which can be close or several hundred meters away; thus, *A. jamaicensis* is a good seed disperser (Fleming and Heithaus 1981; Janzen et al. 1976). At Barro Colorado Island, Panamá, *A. jamaicensis* carried fruits weighing from 3 to 14 g, representing 20–40% of their body mass (Humphrey and Bonaccorso 1979). However, Jamaican fruit-eating bats may carry fruits up to 50 g (Gardner 1977). *A. jamaicensis* uses vision and olfaction to find fruits with brilliant colors and strong odors (Bhatnagar 1975).

Reports of insects as food items are scarce, although Jamaican fruit-eating bats were observed actively hunting black flies at a roost in a rain forest in Chiapas, México (Tuttle 1968). Insect remains were present in 2.5% of digestive tracts examined from different areas (Fleming et al. 1972), accounting for 25% by volume of contents of the tracts. About 0.86 g of insects would meet the daily protein requirements of a 46-g bat (Morrison 1979), implying active pursuit of this prey (Gardner 1977), but the role of insects as a complementary or alternative food item has not been addressed (Heithaus et al. 1975).

The Jamaican fruit-eating bat is often a common and abundant bat throughout most of its range, where it composed ca. 66% of the nightly catch at mist nets year-round and was the dominant element in the frugivorous bat community (Gardner et al. 1991). Population size at any one time was estimated at 3,800–4,500 individuals on the 20 km<sup>2</sup> of Barro Colorado Island and adjoining regions, translating to a density of 200 *A. jamaicensis*/km<sup>2</sup> (Leigh and Handley 1991). The ecological importance of this species is greater in wet habitats than in dry forest, and its abundance in the latter habitat is an artifact of the presence of fig trees grown as crops and of riparian forest (Humphrey and Bonaccorso 1979).

*Artibeus jamaicensis* had a feeding niche breadth of 1.61 at Barro Colorado Island, Panamá. A high niche overlap in food species was found between bats of the same frugivorous guild. However, fruit size and bat body mass were correlated for the 3 largest bat species of the frugivorous guild (*Vampyroides caraccioli*, *A. jamaicensis*, and *A. lituratus*); thus, resources are divided among species with different nocturnal peaks of activity (Humphrey and Bonaccorso 1979).

Known predators of Jamaican fruit-eating bats are barn owls

(*Tyto alba*) and boas (*Boa constrictor*). Other potential predators are arboreal snakes, large opossums (*Didelphis marsupialis*, *Phyllorhynchus opossum*), coati-mundi (*Nasua narica*), false vampire bat (*Vampyrus spectrum*), owls (*Pulsatrix perspicillata*, *Ciccaba virgata*, *Otus guatemalae*), and the bat falcon (*Falco rufigularis*—Gardner et al. 1991).

*Histoplasma capsulatum* has been isolated from Jamaican fruit-eating bats from several sites. In addition, individuals of *A. jamaicensis* may be infected with rabies (Constantine 1988). Several arboviruses occur in the Jamaican fruit-eating bat: Eastern equine encephalitis, Mucambo, Jurona, Tacaribe, Catu, Itapora, and Tacaiuma (Jones 1976).

Parasitic protozoa from the Jamaican fruit-eating bat include: *Trypanosoma pessoai*, *T. cruzi*, *T. evansi*, and *T. hippicum* (Ubelaker et al. 1977). Round worms (Nematoda) hosted by *A. jamaicensis* include: *Bidigiticauda vivipara*, *Capillaria cubana*, *Cheiropteronema globocephala*, *Histiostromylos octacantha*, *Litomoides*, *L. chandleri*, *L. colombiensis*, and *L. guiterasi*; and the acantocephalean worm *Neonicola novellae*. Platyhelminthes (flatworms) found in the Jamaican fruit-eating bat were *Athesmia parkeri* and *Lecithodendrium pricei* (Trematoda—Ubelaker et al. 1977).

Ectoparasites recorded from *A. jamaicensis* include the following mites, ticks, and chiggers (Acarina): *Ablyomma*, *Ixodes* (Ixodidae); *Ornithodoros azteci*, *O. brody*, *O. dusbabeki*, *O. hasei* (Argasidae); *Macronyssoides kochi* (Macronyssidae); *Eudusbabekia viguerasi* (Myobiidae); *Spelaeorhynchus praecursor* (Spelaeorhynchidae); *Periglyphichurus acutisternus*, *P. iheringi*, *P. vargasi* (Spinturnicidae); *Chiroptella myops*, *Eutrombicula alfreddugesi*, *E. webbi*, *Hooperella saccopteryx*, *H. vesperuginis*, *Leptotrombidum hamaxiaium*, *Microtrombicula carmenae*, *Whartonia nudosetosa* (Trombiculidae); *Phyllostomonyssus conradyunker* (Gastronyssidae); *Speleochir brasiliensis* (Speleognathidae = Erynetidae); *Chirnyssoides caparti*, *Teinocoptes* (Sarcoptidae); *Paralabidocarpus foxi* (Labiocarpidae), as well as batflies (Diptera): *Aspidoptera buschi*, *Megistopoda aranea*, *Neotrochobius delicatus*, *Nycterophilina coxata*, *Paratrichobius dunnii*, *P. longicrus*, *Srebla carollinae*, *S. hertigi*, *S. wiedemanni*, *Trichobius cernyi*, *T. dugesii*, *T. frequens*, *T. intermedius*, *T. joblingi*, *T. longipes*, *T. pseudotruncatus*, *T. robynae*, *T. truncatus*, *T. uniformis* (Streblidae) and Nycteribiidae (*Basilisa bellardii*, *B. rondanii*, *B. wenzeli*—Webb and Loomis 1977).

Maximum longevity for the Jamaican fruit-eating bat is 9 years in the wild (Gardner et al. 1991). In addition, another *A. jamaicensis* was recaptured after being marked 7 years earlier (Wilson and Tyson 1970).

The Jamaican fruit-eating bat is not on any conservation list (Arita and Ceballos 1997). Most reports regard it as common to abundant in disturbed and undisturbed habitats throughout its distribution (Fenton et al. 1992). *Artibeus* is considered destructive for fruit crops in some regions (Goodwin 1970).

**ANIMAL HUSBANDRY.** A daily temperature range of 21–29°C and a relative humidity of 55–95% are suitable for *A. jamaicensis* in captivity (Greenhall 1976). Successful breeding in captivity has been achieved with a fruit diet, by maintaining an adequate temperature, and by avoiding frequent handling (Keast and Handley 1991; Novick 1960).

**BEHAVIOR.** A polygynous mating system defined as resource defense was determined for *A. jamaicensis* roosting by day in tree hollows (Morrison 1979). Males monopolize and defend a limited resource, and females go to the best territory for breeding, where they remain for a long time (Morrison 1980a). Juvenile males live in their natal roosts when they are subadults, and females aggregate with other females at another location (Morrison and Handley 1991). In caves where roosting space is not limiting, the mating system probably is based on resource defense with aspects of female defense polygyny (Ortega and Arita 1999). In these habitats, harem males display an active behavioral defense during the breeding seasons. Attacks are manifested toward satellite males that roost in the walls and ceiling of the caves (Ortega and Arita 2000). Average harem group size in caves and trees is ca. 6 adult females, but small and large aggregations of nonharem males and nonreproductive females also occur in caves (Kunz et al. 1983). In Yucatán, harems contain >14 females with 2 associated males (dominant

and subordinate), whereas the smallest groups contain only 1 adult male (Ortega and Arita 2000).

During foraging, the dominant male is the 1st to begin movement and the last to reenter the roost (Morrison 1978d; Morrison and Morrison 1981). At nightfall, males spend an extraordinary amount of time flying in the immediate vicinity of the tree roost to ward off potential intruders (Morrison 1980c). Emergence activity is related to light intensity and is less irregular than returning activity (Jimbo and Schwassmann 1967). Prolonged search flights occurred on nights with a dark moon; the opposite occurred on bright nights (Morrison 1978a, 1978c). *A. jamaicensis* is more active during the 1st hours after dark, with a maximum peak at midnight and sporadic activity during subsequent hours (Fenton and Kunz 1977). Jamaican fruit-eating bats make brief reconnaissance flights to assess the condition of fruit trees (Handley and Morrison 1991). In productive habitats, *A. jamaicensis* has a daily route of ca. 0.6 and 8 km in poor habitat (Morrison 1978b). *A. jamaicensis* may forage in groups, with a medium or low possibility of using the same flyway (Dalquest 1953; Handley et al. 1991b). Flying ca. 0.5 km to a feeding area, Jamaican fruit-eating bats may visit the same tree several times in a single night but do not necessarily roost there. The exception is for trees with large fruits, where the bats stay while eating (Humphrey and Bonaccorso 1979).

*Artibeus jamaicensis* produces a distress call, which consists of a long series of pulses of short duration (15 kHz), when captured by predators; it is used as a warning signal for conspecifics (August 1985). *A. jamaicensis* responds to alarm sounds of other species (e.g., *Phyllostomus hastatus*) and to recorded distress calls (August 1985). The Jamaican fruit-eating bat emits 3 low-intensity FM pulses/ $\mu$ s when flying and perching and is considered a whisper bat (Gould 1977). Initial acoustic orientation starts with a short series ranging from 49 to 56 kHz, followed by a prominent harmonic (64–104 kHz), which rises at the end to 31–33 kHz (Novick 1963).

**GENETICS.** *Artibeus jamaicensis* has a highly conservative karyotype, and no chromosome variations occurred within different populations from México, Venezuela, and Puerto Rico (Baker 1967). *A. jamaicensis* has slow rates of karyotypic evolution and differs only by a few rearrangements with another phyllostomid species (Koop and Baker 1983). The karyotype has a fundamental number of 56; 2n = 30 in females and 31 in males (Baker et al. 1981). Males have 1 X chromosome that is similar to the autosomes and 2 small Y chromosomes. One of the Y chromosomes is about half the size of the other, both are acrocentric (Baker 1967; Baker and Hsu 1970). All autosomes are biarmed, 10 are metacentric, and 4 are submetacentric (Baker 1967, 1979). *A. jamaicensis* has a heterozygosity level of 0.08, with a high grade of polymorphism in the proteins  $\alpha$ - and  $\beta$ -globulin, isocitrate dehydrogenase, Mpi, and albumin (Koop and Baker 1983).

The mtDNA of *A. jamaicensis* is ca. 16,000–16,500 base pairs long. Different forms of mtDNA were identified from Caribbean populations: J subdivided into Antillean island and Jamaican lineages, SV-1 subdivided into 2 lineages, and G with 3 lineages in the Lesser Islands (Phillips et al. 1989). Divergence between J mtDNA of *A. jamaicensis* and mtDNA of *A. lituratus* is estimated as 4.8–7.9% (Pumo et al. 1988). Parsimony and bootstrap analyses linked the mtDNA of *A. j. schwartzi*, restricted to St. Vincent, with the South American population of *A. planirostris*. Similar results were obtained with 12S rRNA sequences. Thus, *A. j. schwartzi* may be a relict population of *A. planirostris* in the Antillean Islands (Pumo et al. 1996).

**REMARKS.** In the Florida Keys, the 1st record of the Jamaican fruit-eating bat was registered by a photograph (Lazell and Koopman 1985). This identification has been rejected because the record was doubtful (Humphrey and Brown 1986), but *A. jamaicensis* was confirmed later (Genoways et al. 1998). Presence of *A. jamaicensis* in the northwestern portion of Argentina is confusing because some authors report its existence (Redford and Eisenberg 1992) and others treat the specimens as *A. lituratus* or *A. planirostris* (Barquez 1988; Koopman 1982).

The generic name, *Artibeus*, comes from two Greek words: *arti-*, meaning facial lines, and *beus*, in reference to the presence of evident facial lines (Alvarez-Castañeda and Alvarez 1996). The species name, *jamaicensis*, was derived from the island of Jamaica, where the type was collected.

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