Phyllostomus hastatus.

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Phyllostomus Lacépède, 1799

- Vespertilio: Pallas, 1767:7. In part, not Vespertilio Linnaeus, 1758. Phyllostomus Lacépède, 1799:16. Type species Vespertilio hastatus Pallas, 1767, by monotypy, although ruled to be by subsequent selection by Miller and Rehn (1901), according to Hemming (1955).
- Phyllostoma Cuvier, 1800. Table end of volume 1. Unjustified emendation of Phyllostomus Lacépède (ICZN Direction 24, Hemming 1955).
- Phyllostoma: É. Geoffroy St.-Hilaire, 1810:182. Part; incorrect subsequent spelling of Phyllostomus Lacépède, 1799.
- Alectops Gray, 1866:114. Type species Alectops ater Gray, 1866, by monotypy.

CONTEXT AND CONTENT. Order Chiroptera, suborder Microchiroptera, family Phyllostomidae, subfamily Phyllostominae, tribe Phyllostomini (Baker et al. 1989). The genus *Phyllostomus* contains 4 living species (Jones and Carter 1976; Koopman 1993). A key to the species, modified from Anderson (1997), Eisenberg (1989), Hall (1981), and Muñóz (1995) follows (measurements in mm):

- 2 Total length ≤100; mass ≤39 g; length of forearm ≤65; dorsal hair brown with white tips; white venter ... P. discolor Total length >100; mass >39 g; length of forearm >65; uniform color of pelage ______ 3
- 3 Total length ≤105; mass ≤42 g, length of forearm ≤68; tips of wings usually white; present only in South America ... P. elongatus

Phyllostomus hastatus (Pallas, 1767)

Spear-nosed Bat

- V(espertilio). hastatus Pallas, 1767:7. Type locality "Amérique," restricted to Surinam by Allen (1904:233); based on la chauvesouris fer-de-lance of Buffon (1765).
- *Phyllostomus hastatus*: Lacépède, 1799:16. First use of current name combination.
- Phyllostoma emarginata É. Geoffroy St.-Hilaire, 1803:60. Type locality "La Buiane."
- Phyllostoma hastatum: É. Geoffroy St.-Hilaire, 1810:177. Name combination.
- Phyllostomus maximus Wied-Neuwied, 1821:242, footnote. Type locality "Die Wälder an den Ufern de Rio das Contas," Bahia, Brazil.
- *Phyllostomus hastatus caurae* Allen, 1904:234. Type locality "Cali, upper Cauca Valley, [Valle del Cauca] Columbia," an incorrect original spelling for *caucae*.
- Phyllostomus hastatus caucae Allen, 1916:225. Corrected spelling of Phyllostomus hastatus caurae Allen, 1904.
- Phyllostomus hastatus curaca Cabrera, 1917:12. Type locality "Archidona, sobre el río Napo," Napo, Ecuador.
- Phyllostomus hastatus paeze Thomas, 1924:235. Type locality "Bogatá," Cundinamarca, Colombia.
- Phyllostomus hastatus aruma Thomas, 1924:236. Type locality "Taguatinga," Goiás, Brazil.

CONTEXT AND CONTENT. Context as above. *P. hastatus* has 2 subspecies (Allen 1904; Hall 1981; Koopman 1994):

- P. h. hastatus (Pallas, 1767:7) see above (aruma Thomas, curaca Cabrera, emarginatus (É Geoffroy St.-Hilaire), and maximus Wied-Neuwied are synonyms).
- P. h. panamensis Allen, 1904:233. Type locality "Boqueron, Chiriqui" Panamá (caucae Allen and paeze Thomas are synonyms).

DIAGNOSIS. Phyllostomus hastatus (Fig. 1) is the second largest American bat. Only Vampyrum spectrum is larger; Phylloderma stenops and Chrotopterus auritus are comparable in size (Medellín 1989; Nowark 1991). Venter and dorsum are colored similarly, ranging from dark brown to reddish brown; some individuals are golden throughout. P. hastatus is the largest species of the genus (length of forearm, $\bar{X} = 83.17 \text{ mm} \pm 2.02 \text{ SD}$, n = 80; mass, $\bar{X} = 100.96 \text{ g} \pm 9.25 \text{ SD}$, n = 38) and is easily distinguishable from other Phyllostomus species that occur in its range. P. elongatus is smaller, having a forearm 10 mm shorter, and has white tips on the wings. P. discolor is smaller, with forearm 55–68 mm (n = 163), and white tips of the hairs convey mottled effect (Eisenberg 1989).

GENERAL CHARACTERS. Phyllostomus hastatus has short, velvety fur and a robust form (Nowark 1991). Nose leaf of P. hastatus is simple and well developed, and the horseshoe is not fused to the upper lip. Lower lip has a V-shaped groove edged with wartlike protuberances. Ears are triangular, with tips pointed and widely separated. Glandular throat sac is well developed in males but rudimentary in females. Tail is short. Membranes, ears, and facial skin are black. Calcar is as long as hind foot. Ranges of external and cranial measurements (in mm) are: total length, 124-131 (n = 78—Cunha Vieira 1942; Dobson 1878; Eisenberg 1989; Miller 1912); length of ear, 28-34 (n = 78—Cunha Vieira 1942; Dobson 1878; Eisenberg 1989; Miller 1912); mass, 78–112 g (n = 78-Cunha Vieira 1942; Dobson 1878; Eisenberg 1989; Miller 1912); length of forearm, 79–94 (n = 94—Cunha Vieira 1942; Dalquest 1951; Dobson 1878; Eisenberg 1989; Goodwin and Greenhall 1961; Miller 1912); greatest length of skull, 28.2-31.9 (n = 18—Allen 1904; Cunha Vieira 1942; Dalquest 1951; Goodwin and Greenhall 1961; Miller 1912); zygomatic breadth, 14.6-16.3 (n = 18—Allen 1904; Cunha Vieira 1942; Dalquest 1951;



FIG. 1. *Phyllostomus hastatus* from "Guanapo Cave, Trinidad West Indies." Photograph by Gary MacCraken.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Phyllostomus hastatus* (Instituto de Biología, Universidad Nacional Autónoma de México 9809, male, from Brazil, Rio, 3 km W + 1 km S Univ. Rural). Greatest length of skull is 41.72 mm.

Goodwin and Greenhall 1961; Miller 1912); interorbital breadth, 6.7–7.4 (n = 18—Allen 1904; Cunha Vieira 1942; Dalquest 1951; Goodwin and Greenhall 1961; Miller 1912); and length of maxillary toothrow, 9.2–10.4 (n = 18—Allen 1904; Cunha Vieira 1942; Dalquest 1951; Goodwin and Greenhall 1961; Miller 1912). Skull of *P. hastatus* (Fig. 2) is heavy and robust.

DISTRIBUTION. *Phyllostomus hastatus* occupies the lowlands (600 m) and several habitats, including deciduous forests, antropic clearings, and multistratal tropical evergreen forests from southern Belize, eastern Guatemala, and northern Honduras to Peru, Brazil, Paraguay, Bolivia, and northern Argentina (Fig. 3). The spear-nosed bat also is found in Trinidad and Tobago Islands and Margarita Island, Venezuela (Eisenberg 1989; Jones and Carter 1976; Koopman 1993; Marinho-Filho and Sazima 1998; Nowak 1991; Reid 1998). *P. h. hastatus* occurs from eastern Venezuela south to northern Bolivia and southeastern Brazil, whereas *P. h. panamensis* occurs from Honduras to Peru and east to western Venezuela (Koopman 1994; Simmons and Voss 1998).

FOSSIL RECORD. Some skulls, 1 rostrum, and dentaries of *P. hastatus* were found in Gruta do túnel de Santana and Gruta



FIG. 3. Geographic distribution of *Phyllostomus hastatus* in Central and South America: 1, *P. h. hastatus*; 2, *P. h. panamensis* (subspecies boundary is approximate).

dos Brejöes caves, in Minas Gerais, Brazil. The age of these caves is late Pleistocene (Czaplewski and Cartelle 1998). Subfossil remains of the species were reported from caves in Venezuela (Linares 1968).

FORM AND FUNCTION. Massive cerebral hemispheres of *P. hastatus* are elongated and blunt anteriorly. The brain has very well-developed sulci anterior and pseudocentral sulci. Small secondary fissures radiating from larger sulci are in the cerebral hemispheres. *P. hastatus* presents inferior colliculli completely covered with cerebral and cerebellar tissues. A pronounced medial create in the cerebellum is in the form of a secondary foliation at lateral edges. Internally, the brain has one of the best-developed cingulate sulcus and the largest inferior culliculi within the family, with the lateral olfactory tracts located ventrally (McDaniel 1976).

Phyllostomus hastatus has small, simple deciduous teeth, but the permanent teeth are robust and relatively primitive (Phillips et al. 1977). A high incidence of dental caries, fissures in the enamel of the teeth, and a flap of tissue covering labial coronal and cervical surfaces of upper molars occur in *P. hastatus* (Phillips and Jones 1970). Also, posterointernal part of crown of molars has sharp cusps due to the omnivorous diet of the spear-nosed bat (Glass 1970). Tongue is broad and usually rounded at apex, having an abundance of conical papillae (Phillips et al. 1977). Dental formula is i 2/2, c 1/1, p 2/2, m 3/3, total 32 (Eisenberg 1989; Hall 1981; Nowak 1991; Reid 1998).

Phyllostomus hastatus is unable to completely close its pupils in bright light and has a refractive error ranging from 3.50 to 4.50. Pupil diameter is 0.3 mm when constricted and 2.4 mm when dilated; the diffraction limit of the constricted pupil is 7.1 min. Number of cells in outer nuclear layer of retina is 416,000 cells/mm². When flying in subdued daylight (with ears plugged to prevent acoustic orientation), *P. hastatus* can visually detect and avoid 30cm-wide strips of white cloth hung across their flight path (Suthers 1970).

Males of *P. hastatus* have a chest gland at the base of the neck; it is rudimentary in females (Müller-Schwarze 1983). The olfactory receptor in *P. hastatus* is a somewhat prominent bulb. A vomeronasal organ is present (Mann 1961).

Peyer's patches (gut-associated lymphoid tissue related to the immune system) in *P. hastatus* are not abundant. They are structurally specialized for improved contact with intestinal contents (Forman 1974).

Uterus of *P. hastatus* is externally simple, with a tubular to

pear-shaped form. Fundus of uterus is prominent and rounded. Internally, uterine anatomy consists of a large common lumen and narrow tubular segments that are extremely short uterine lumina and constitute the intramural uterine cornua. Oviducts enter uterine body on the lateral (mesometrial) border, whereas oviducts in all other simplex forms enter on the fundic border (Hood and Smith 1983).

Compared with other phyllostomatids, *P. hastatus* has relatively long wings (Lawlor 1973; Smith and Starret 1979). The average $(\pm SD)$ wing measurement for adult females was greater than for adult males: wingspan, females, 54.6 ± 1.6 cm, males, 53.7 ± 2.2 cm, n = 112 both sexes; wing area, females, 434 ± 25.1 cm², males, 428.2 ± 26.8 cm², n = 349 both sexes; aspect ratio, females, 6.9 ± 0.3 , males, 6.7 ± 0.4 , n = 112 both sexes. However, average $(\pm SD)$ wing loading of females is significantly lower than in males (females, 17.4 ± 1.8 , males, 20.4 ± 2.0 N/m², n = 156 both sexes). Wing area, wingspan, and aspect ratio increase until volancy, whereas wing loading reaches its lowest values at and after weaning (Stern et al. 1997). Wing beat frequency is ca. 10/s (Suthers et al. 1971).

Phyllostomus hastatus has 3 sesamoid bones on the wrist: 1 on radial side of the radiocarpal joint, another covering the carpometacarpal joint of the thumb, and a third that lies over the articulation of the magnum (Dobson 1878).

For orientation, P. hastatus uses short-duration, harmonically structurated, frequency modulation (FM) signals of moderately low intensity. Signals have a bandwidth of ca. 35 kHz, with the predominant frequency near 40 kHz. Spear-nosed bats use sounds that cover a broad bandwidth with several narrower, overlapping frequency sweeps (Simmons 1973). Calls of an adult P. hastatus are loud vocal sounds when feeding in groups, and for infants (with a length of forearm of ca. 37 mm) sounds are at 12 kHz (Gould 1970, 1975). P. hastatus gives audible vocalizations at feeding sites without evidence of territorial behavior (Wilkinson 1995). Audiograms of P. hastatus usually show peaks at 30-35 kHz and 50-55 kHz, principal harmonic sweeps from 42-50 kHz to 25-30 kHz, and a peak sensitivity about 20 dB (Gould 1977; Novick 1970). In experimental situations P. hastatus is able to distinguish targets separated by 4-6°C and is able to detected range differences as low as 12 mm (Peff and Simmons 1972; Simmons and Vernon 1971).

Heart of P. hastatus weighs almost 1% (0.94 g) of body mass, and minimum stroke volume is ca. 1.9-2.2 ml/kg (Thomas and Suthers 1972). P. hastatus maintains a rigid 1:1 synchronization between ventilation and the wing beat cycle. Breathing rate ranges from ca. 7 cm³ of O² g⁻¹ h⁻¹ before flight to ca. 27 cm³ g⁻¹ h⁻¹ during flight (Hill and Smith 1984). At an environmental temperature of 24°C, P. hastatus has a mean resting heart rate of ca. 420 beats/min and during flight, a mean rate of 780 beats/min (maximum = 828 beats/min, n = 4—Kallen 1970). Minimum stroke volume (cardiac output) of P. hastatus is 1.9-2.2 cm3/kg body mass. P. hastatus has a blood oxygen capacity that is 40-50% higher than that of a bird or nonflying mammal and could, theoretically, transport 1.5 times as much oxygen per unit of blood flow as a bird or rodent. P. hastatus has an average speed of 8.6 m/s \pm 0.5 SD (n = 9) and a maximum speed of 12.3 m/s (n = 1— Morrison 1980).

With a metabolic rate in flight of 130.4 W/kg, *P. hastatus* requires only one-sixth the energy needed by a terrestrial mammal of the same size to cover an equivalent distance (Thomas 1975). The lowest mean rate of energy use to sustain level flight was 94.2 W/kg (n = 2). Basal rate of metabolism was ca. 0.84 cm³ O² g⁻¹ h⁻¹, whereas minimal thermal conductance was 0.116 cm³ O² g⁻¹ h⁻¹ \pm 0.093 *SD* (n = 7—McNab 1969). Fourteen percent of the total metabolic heat load generated in flight is lost through the respiratory tract (Hill and Smith 1984).

Average total blood cholesterol is 108 mg/100 ml \pm 43.1 SD (n = 2) with 160 \pm 103.9 mg/100 ml (n = 2) of phospholipids (Riedesel 1970).

ONTOGENY AND REPRODUCTION. Reproductive patterns of the spear-nosed bat vary geographically; it is monoestrous in Middle America and Trinidad and polyestrous in South America (Wilson 1979). In Nicaragua, pregnant females were reported in March, with lactation during the summer period (Jones et al. 1971). Lactating females were reported for Panama in the April–May interval, but in the same locality, adult females exhibit an inactive breeding pattern from June to October (Fleming et al. 1972). Pregnant and lactating females were documented in Trinidad and Tobago islands from March to September; additionally inactive females were reported in July and August (Carter et al. 1981; Goodwin and Greenhall 1961). In July, a pregnant female was caught in Colombia (Arata and Vaughn 1970). In the Cerrado habitats of Brazil, the breeding season was documented from April to October, with a lactation period from September to April (Willig 1985). Twelve pregnant females (embryos with a crown-rump length average of 27.4 mm) were reported for Peru in August (Tuttle 1970). Early spermatogenesis occurred in testes of 2 males in Costa Rica in July (Starret and de la Torre 1964). Synchronized reproduction occurs in Trinidad, with young being born during the dry season (April–May) and weaned early in the rainy season (McCracken and Bradbury 1981).

Females reach sexual maturity at ca. 16 months of age (McCracken and Bradbury 1981). Lactating females roost colonially and make nurseries with their broods (Kleiman and Davis 1979; McCracken and Bradbury 1981). Neonates are sparsely furred and active, and eyes are open. Average length of neonate forearm is 37 mm \pm 2.5 SD (n = 10—Gould 1975). From days 1 to 7 postpartum, visual cues are more important for young than the double-note vocalizations that happen at the moment of contact with the mother; subsequently, young produce FM pulses during reunions (Gould 1977). During the first 6 weeks of birth, wing area, aspect ratio, and wingspan of young increase considerably (ca. 90% of the adult values); this wing morphology maximizes the maneuverability and minimizes the energy requirements for 1st flying attempts (Stern et al. 1997).

ECOLOGY. *Phyllostomus hastatus* roosts in hollows trees, caves, termite nests, and buildings. Roosting groups are composed of several harems, each with 10–100 females and a single male grouped in a tight cluster, and aggregates of 20–50 bachelor males. Harem females form stable associations that may last several years and do not change if the harem male disappears or is replaced. Females of a harem have fixed feeding areas adjacent to each other but separate from those of other harems. They leave the roost well after sunset. Individuals forage separately (although groups may be found in fruiting trees), returning to the day roost about 2 h later. Individuals for but separate soft the forest understory. In Peru and Venezuela, *P. hastatus* commonly roosts with *C. auritus*, *Desmodus rotundus*, *Pteronotus davyi*, *Peropteryx macrotis*, and *Tonatia silvicola* (Ochoa 1985; Tuttle 1970).

The spear-nosed bat is omnivorous, feeding on insects (including swarming termites), small vertebrates (bats, mice, and birds), fruits (Psidium guajava, Cecropia, and Piper), flowers, nectar, and pollen (Emmons and Feer 1997; Gardner 1977). In the Edaphic Cerrado habitats of Brazil, the diet of P. hastatus included at least 8 orders and 28 families of insects; coleopterans were dominant (60%), followed by ants (15%) and roaches (9%), and unidentified fruit pulp composed ca. 4% of diet (Willig et al. 1993). Fruits eaten by P. hastatus in Brazil, included Achras sapota, Annona muricata, Artocarpus integrifolia, Carica papaya, Cecropia, Diospyros kaki, Eriobotrya japonica, Eugenia uniflora, Livistona chinensis, Lucuma caimito, Mangifera indica, Musa paradisiaca, Myrcia jaboticaba, Passiflora quadrangularis, Pilocarpus pinnatifolius, Psidium guajava, Rubachia glomerata, Solanum paniculatum, Terminalia catappa, and Vitis vinifera (Gardner 1977). In Belem, Brazil, P. hastatus was observed feeding on inflorescences of Ceiba pentandra, Parkia gigantocarpa, and P. pendula (Gardner 1977). Also, it eats the fleshy funiculus of the Sapucaia nut (Lecythis zabucajo-Goodwin and Greenhall 1961).

Phyllostomus hastatus is locally common and widespread in rainforests (Emmons and Feer 1997). In some areas like the savannas, the species is uncommon and depends on the forest for living (Aguirre et al. 1996; Medellín and Redford 1992). The conservation status of *P. hastatus* is stable (Wilson 1997).

BEHAVIOR. *Phyllostomus hastatus* begins foraging and is most active in the 1st hours after sunset. Later, individuals return to the daytime refuge (Fenton and Kunz 1977). During the brightest parts of full and crescent moons, activity is reduced, but there is movement in the darkest parts of the same nights (Erkert 1982). Searching flights are erratic before arrival at the feeding areas. In these areas (ca. 1–5 km from the daytime refuge), they alternate roosting periods with short flights to feed (Williams and Williams 1970). Several authors reported massive flocks in diverse flowering

trees and insect larvae mass, but the most common feature is that 1 individual maintains its feeding area during most of the year (Goodwin and Greenhall 1961; Wilkinson 1987). Females that cluster together in caves have adjacent areas (1–5 km) for feeding and are away from the roost for ca. 2 h ($\hat{X} = 152 \min \pm 35.9 SD$, n = 6). In contrast, territorial males forage in areas well apart from the females (sometimes within 1 km) and are gone from roosting caves for ca. 1 h ($\hat{X} = 99.15 \pm 26.6 \min$, n = 2). Finally, bachelor males forage 9 km away from the cave and remain for a similar length of time as territorial males ($\hat{X} = 115 \pm 10 \min$, n = 1—Fleming 1982; Kunz et al. 1998; McCracken and Bradbury 1981). Harem males have more frequent departure and return bouts (7.2) to the roosting places than other members of the colony (Kunz et al. 1998).

During foraging, females produce group-specific screech calls to maintain contact with others members of the same harem (Boughman 1997b). Females can distinguish screech calls among the members of the same harem. The screech calls are more frequent when females of the same harem fly together, compared with individual flights. When the feeding resource is dispersed, harem flocks and screech calls are less common than when resources are concentrated (Boughman 1997a). Female groups structure their calls through vocal learning. Because calls are related to the dynamic membership of a group, social calls change with the incorporation of new members (Boughman and Wilkinson 1998). Vocalizations are 4-18 kHz, and those calls decrease insignificantly in frequency with the bat's age (Boughman 1997b). The spear-nosed bat depends on its vision to find the daytime roost; when they are displaced several kilometers from their caves, bats use visual orientation to find the way back (Williams and Williams 1967; Williams et al. 1966).

Phyllostomus hastatus is a typical cave-dwelling bat, with a social unit in the form of harem groups. Young females form new same-aged groups that are defended actively by a dominant male for ca. 3 years. Stability of the harem groups allows a male strategy of female defense within a polygynous mating system (McCracken and Bradbury 1981). Dominant males allocate less time for foraging than other harem members; this allows for increased time for vigilance and defense of harems (Kunz et al. 1998). Electrophoretic analysis suggests that the formation of the same-aged groups still produces sufficient heterogeneity in the whole colony because new stable female groups are formed as cohorts of yearling females are drawn from different harems and cave colonies (McCracken and Bradbury 1977, 1981). The degree of relatedness among females of the same group suggests that the clusters contain subgroups of 2-4 half-sisters, but the bulk of the group is genetically different. Social grooming is frequently observed between females of the same group. Young babies roost in harem groups and can obtain milk from different females. Kin selection and mutual benefits in reciprocity can explain all social interactions but not by kin-group selection (Wilkinson 1987).

Distress call of the Jamaican fruit-eating bat (*Artibeus jamaicensis*) can affect the alert responses of *P. hastatus* (August 1979, 1985). The spear-nosed bat is a roosting generalist species and shares roosts with at least 15 species of bats in small caves, large caves, termite nests, and hollow trees, but direct interspecific interactions are not reported (Graham 1988; Tuttle 1970).

GENETICS. *Phyllostomus hastatus* has 2n = 32, FN = 58 (Baker 1979). The X chromosome is submetacentric, and the Y chromosome is acrocentric (Baker 1979). The species also has 2 rDNA sites and 2 telomeric chromosomes (Baker et al. 1992). Within the subfamily Phyllostomatinae, *P. hastatus, P. discolor, Tonatia*, and *Mimon crenulatum* form a group with shared chromosomal characteristics, having a common ancestor with 2n = 38 and FN = 60 (Patton 1976). However, *P. hastatus, P. discolor*, and *M. crenulatum* probably had a common ancestor with a 2n = 32 or 34 (Patton 1976).

Further studies using albumin immunology (Honeycutt and Sarich 1987) showed the same relationships as those found by Patton (1976), that *P. hastatus* is closely related to *M. crenulatum* and *T. silvicola*. Later, it was proposed that the tribe Phyllostomini contained 5 genera of the Phyllostomus group: *Phyllostomus*, *Mimon, Tonatia, Lonchorhina*, and *Macrophyllum*, based on female reproductive morphology, immunological distance, and G-band chromosomal studies (Baker et al. 1989).

Several studies within and among species of the genera Phyl-

lostomus and *Phylloderma* were found to have minimal geographical differentiations, and those populations of *P. hastatus* were geographically similar to one another (Baker et al. 1988). Based on cytochrome-*b* DNA sequence, variation was found indicating that *P. hastatus* is closely related to *P. elongatus* and together with *P. latifolius*, *P. discolor*, and *P. stenops* comprises a natural assemblage (Van Den Bussch and Baker 1993).

REMARKS. The generic name *Phyllostomus* is compounded from Greek words *Phyllos* (leaf) and *stoma* (mouth) and literally means leaf nose over the mouth. The species name is from the Greek *hastatus*, which means spear tip. Phyllostome fer-de-lance is an old, French, common name.

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