# MAMMALIAN SPECIES No. 533, pp. 1-7, 4 figs.

## Diaemus youngi. By Arthur M. Greenhall and William A. Schutt, Jr.

Published 27 December 1996 by the American Society of Mammalogists

#### Diaemus Miller, 1906

Diaemus Miller, 1906:84. Type species Desmodus youngi Jentink.

**CONTEXT AND CONTENT.** Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Desmodontinae (Koopman, 1993). The genus *Diaemus* is monotypic.

### Diaemus youngi (Jentink, 1893)

White-winged Vampire Bat

Desmodus youngi Jentink, 1893:282. Type locality "upper Canje Creek, a tributary of the Berbice River, British Guiana" (=Guyana).

Diaemus youngi cypselinus Thomas, 1928:288. Type locality "Peru, Loreto; Pebas."

**CONTEXT AND CONTENT.** Context as noted above. *Diaemus* is regarded as a valid genus along with *Desmodus* and *Diphylla*. No subspecies are recognized (Koopman, 1988, 1993).

DIAGNOSIS. Diaemus resembles Desmodus and Diphylla (Fig. 1), but is recognizable from other genera of vampire bats by characters which include ear length and shape, thumb size, and wing tip coloration, as well as presence, absence, and shape of the metacarpal pads and calcar. The ears of Diaemus (and Desmodus) are longer than broad, whereas in Diphylla the reverse is true. In Desmodus, a well developed fold of skin connects the ear to the upper part of the head and the outer margin of the ear terminates in a larger and much more rounded wart above the eye than in Diaemus (Jentink, 1893). The tragus of Diaemus is hairy on the anterior surface and the outer margin is not toothed as in Desmodus (Jentink, 1893). Compared to Desmodus, the thumb of Diaemus (and Diphylla) is relatively short (approximately one eighth the length of the third digit). In Desmodus, the thumb is approximately one fifth of the length of the third digit. In Diaemus, there is a single pad under the metacarpals. In Diphylla, the metacarpal pads are absent and in Desmodus, there are two pads under each metacarpal. The calcar is absent in Diaemus, greatly reduced in Desmodus, and small (approximately 3 mm) and digitiform in Diphylla (Koopman, 1988). Diaemus is the only vampire genus with white tipped wings. The coronoid process of the mandible is high in Diaemus (Fig. 2) and rises above the condyle. In Diphylla, the coronoid process is very low but rises above the condyle, whereas in Desmodus the coronoid process is high and on a level with the condyle. The dental formula of Diaemus is i 1/2, c 1/1, p 1/2, m 2/1, total 22, but the posterior upper molar is vestigial and often lost in old individuals. The dental formulae of Diphylla and Desmodus are i 2/2, c 1/1, p 1/2, m 2/2, total 26 and i 1/2, c 1/1, p 1/2, m 1/1, total 20, respectively. In Diphylla, the lower incisors are larger and form a more or less continuous cutting edge. The lower incisors of Diaemus tend to be rather irregular and variable in both kind and degree of lobation. The lower incisors of Desmodus are strongly bilobate and in Diphylla, the median incisor has four beadlike lobes, and the lateral incisor has seven. The anterior upper molar has a prominent medial cusp in Diaemus, which is absent in Desmodus and Diphylla (de la Torre, 1956; Goodwin and Greenhall, 1961; Husson, 1962; Koopman, 1988; Fig. 2).

**GENERAL CHARACTERS.** Diaemus youngi is a mediumsized, robust, close-furred bat. The ears are moderately long and separate. The lower lip is grooved vertically, the muzzle is short, and the circumnarial ridge suggests a noseleaf without a secondary noseleaf. The eyes are large and shiny. The forearm is sparsely haired. The calcar is absent and there is no evident tail. The interfemoral membrane is narrow and sparsely haired. Pelage color is usually glossy clay, light brown, or dark cinnamon brown. Borders and edges of the wings are white, and the membrane between the second and third fingers is largely white.

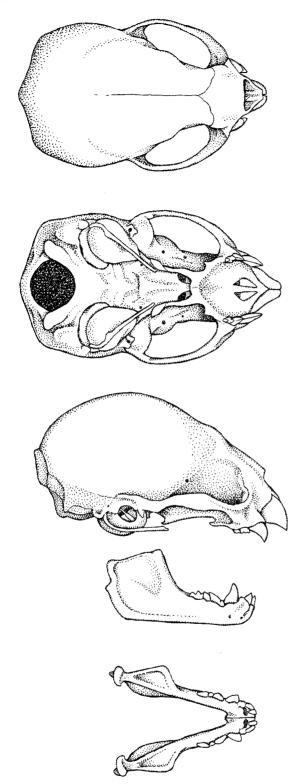
Mean external measurements (mm) of 11 males and four females from Venezuela followed by  $\pm$  SD, are (values for males listed first): length of head and body,  $83.36 \pm 5.35$ ,  $84 \pm 2.94$ ; length of foot, 17.91  $\pm$  1.3, 19.5  $\pm$  1.29; length of ear, 18.18  $\pm$ 1.33, 18.75  $\pm$  0.5; and length of forearm, 51.65  $\pm$  1.39, 53.48  $\pm$ 1.24 (Eisenberg, 1989). Cranial measurements of five males and five females from Venezuela and Trinidad are (values for males listed first): greatest length of skull, 24.6 ± 0.8, 24.8 ± 0.8; zygomatic breath,  $13.8 \pm 0.5$ ,  $13.9 \pm 0.2$ ; postorbital constriction,  $6.1 \pm 0.17$ ,  $6.2 \pm 0.2$ ; breath of braincase,  $13.0 \pm 0.3$ ,  $13.0 \pm$ 0.3; and length of maxillary toothrow,  $3.3 \pm 0.12$ ,  $3.5 \pm 0.2$  (Goodwin and Greenhall, 1961; Swanepoel and Genoways, 1979). Body masses (g) for 10 males and five females from Trinidad are 31.7-41.3 and 37.5-48.1, respectively, and include two gravid individuals (46.2 and 48.1-Goodwin and Greenhall, 1961). Additional measurements appear in Bhatnagar (1988), Goodwin and Greenhall (1961), Hall (1981), Handley (1976), Hussen (1962), Koopman (1988), Lay (1963), Ray et al. (1988), Redford and Eisenberg (1992), Swanepoel and Genoways (1979), and Villa-R. (1967). Photographs of live animals appear in Greenhall (1988), Nowak (1991), and Uieda (1993, 1994).

**DISTRIBUTION.** Diaemus youngi is rare or uncommon throughout most of its geographic range. In North America, the white-winged vampire bat has been recorded from southern Tamaulipas in northeastern Mexico, south through eastern Mexico to



Fig. 1. Diaemus youngi from Tamualipas, Mexico. Photograph by Bruce Hayward.

MAMMALIAN SPECIES 533



2

Fig. 2. Lateral, ventral, and dorsal views of cranium and occlusal and ventral views of mandible of *Diaemus youngi*. Greatest length of cranium is 24.9 mm.

Central America and Panama (Hall, 1981; Reddell, 1981; Fig. 3). In South America, its range extends across the Amazon basin and the Guianas south to northern Argentina and southwestern Brazil (Barquez, 1984; Delpietro et al., 1973; Linares, 1987; Osgood, 1912; Sanborn, 1949). It does not occur west of the Andes south of Colombia (Koopman, 1988). In the West Indies, it is found on the islands of Margarita and Trinidad (Goodwin and Greenhall,

1961). There is no fossil record for *Diaemus youngi* (Ray et al., 1988).

FORM AND FUNCTION. In *Diaemus youngi*, both sexes possess cup-shaped oral scent glands (Fig. 4) located bilaterally inside the mouth. These glands are not obvious until the bat is disturbed, at which time the glands are directed forward and emit an offensive odor. The following amino acids are present in these glands: aspartate, glutamate, alanine, norvaline, and (doubtfully) lysine. The function of the glands is unknown, but it may be an anti-predator mechanism (Goodwin and Greenhall, 1961; Greenhall, 1988) or involved in territory marking and individual recognition (Schutt, 1995). An individual taken in July from Margarita Island, Venezuela, had quiescent glands while those of other specimens, collected the same month on the nearby mainland, were active (Smith and Genoways, 1974).

Teeth in *Diaemus youngi* are similar to *Desmodus* but with lower incisors curving inward. The median incisors and canines are pointed and have long cutting edges utilized for shaving hair and feathers, and for piercing skin for feeding. The cheek teeth are non-occlusive and without grinding surfaces (Miller, 1907). The teeth of *Desmodus* are kept sharp by thegosis, a process in which individual cutting edges of a tooth cross with the cutting edges of other teeth. This tooth sharpening mechanism appears similar in *Diaemus youngi* (Greenhall, 1972). It was initially reported that, unlike most mammalian teeth, those of vampire bats lack enamel (Greenhall, 1988). Another report, however, indicated that all three genera of vampires possess teeth with fully developed enamel (Bhatnagar and Wimsatt, 1989).

Because of their unique blood feeding habits, vampire bats face the problem of inactivating the hemostatic mechanism of their host. Limited information on white-winged vampire bats indicates that their saliva (like *Desmodus*) possesses a plasminogen activator (an enzymatic substance which causes rapid lysis of blood clots), a platelet aggregation inhibitor, and several anticoagulants (Cartwright and Hawkey, 1968; Hawkey, 1988). Whereas desmokinase (the plasminogen activator from *Desmodus* saliva) shows considerable specificity for mammalian blood, the substance extracted from *Diaemus youngi* saliva also could activate avian plasminogen (Hawkey, 1988). The stomach of *Diaemus youngi* is elongated but is less tubular and more conical in shape than the intestiniform stomach of *Desmodus* (Forman et al., 1979).

In the post-cranial skeleton, the sternum has a manubrium, six sternebrae and a xiphoid process. The first costal cartilage is large and wide and the second attaches at the sternal angle. The costal cartilages are parallel to each other and about as long as the wings of the manubrium. The humerus is robust with a prominent pectoral ridge. The ulna is fused distally with the radius. The pelvic spine is long and diverging at the cranial tip. The inferior ischial rami are thick (Bhatnagar, 1988). The femur is robust and thicker relative to its length than in most species of bats. It was proposed that sturdy hindlimb bones reflect the increased compressive forces under which vampire bat hindlimb bones are loaded during quadrupedal locomotion (Howell and Pylka, 1977). The lateral and medial surfaces of the tibia are grooved and the anterior surface is rounded (but less so than in Desmodus). The tibia is T-shaped in cross section. The fibula is complete, thin cranially, and laterally compressed (Bhatnagar, 1988; Koopman, 1988). The sturdy hind limb bones of Diaemus youngi and Desmodus appear to be adaptations for complex quadrupedal locomotion. The shorter thumb, however, resembles that of Diphylla, and may be one of several factors which prevent Diaemus youngi from exhibiting the agile ambulatory acrobatics of Desmodus (Schutt et al., 1993).

The thumb and hindlimb digits of white-winged vampire bats do not have the digital locking mechanism seen in most bats (Schutt, 1992, 1993). As in *Desmodus* and *Diphylla*, there are two digital flexor tendon retinacula, the inner surfaces of which are devoid of plicae. Additionally, digital flexor tendon surfaces are smooth and lack scales or foliations. Absence of the passive digital lock in vampire bat ancestors may have been one of a number of factors that 'preadapted' these bats to the highly specialized quadrupedal locomotion required for blood feeding (Schutt, 1993).

Vampire bats have very high indices of encephalization (approximately 240), which are comparable to the family Pteropodidae. Six specimens of *Diaemus youngi* from Venezuela, with body masses ranging from 31.6–38.0 g, had brain masses which ranged from 910–1,020 mg. In comparison, 12 specimens of *Desmodus* from

MAMMALIAN SPECIES 533 3

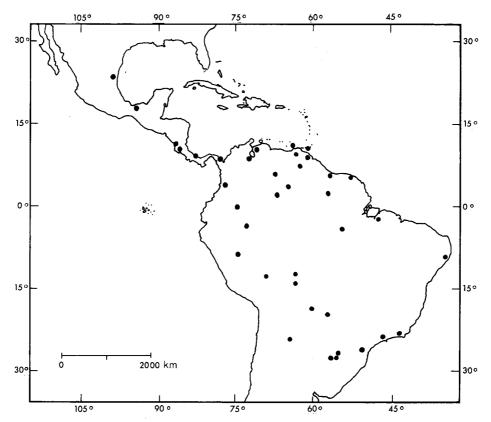


Fig. 3. Geographic distribution of Diaemus youngi. See text for collecting localities and marginal records.

Venezuela and Mexico had body masses ranging between 21.1–35.6 g, and brain masses of 660–930 mg (Pirlot and Stephen, 1970). One explanation for higher indices of encephalization in *Diaemus* and *Desmodus* (compared to *Leptonycteris*, *Artibeus jamaicensis* and *Carollia*) may be the specialized feeding habits of vampire bats. These bats utilize complicated behavior (including highly variable quadrupedal locomotion and stealth) when approaching prey.

The cerebral hemispheres in *Diaemus youngi* are less elongate but are well convoluted and deeply sulcated compared to *Desmodus*. Pseudo-temporal lobes are angular as in *Desmodus* and the inferior coliculi are not dorsally exposed. The cerebellum has a low medial crest and secondary foliations along the lateral edges of the vermiform body. The internal morphology of *Diaemus youngi* is similar to *Desmodus*. The interhemispheric sulcus descends to a well-formed cingulate sulcus, and descends farther and flares laterally just above the corpus callosum to form a callosal sulcus. The cingulate lobes of the cerebrum protrude ventrally into the inter-



Fig. 4. Oral scent glands of *Diaemus youngi* from Campinas, State of São Paulo, Brazil. Photograph by Wilson Uieda.

hemispheric sulcus. The lateral olfactory tracts are located on the ventral surface of the brain (McDaniel, 1976). The lateral thalamic nuclei project dorsally to the level of the habenular nuclei whereas the lateral geniculate bodies are large and deep. The thalamus is wide and shallow. The amygdaloid nuclei are large and the anterior ends are not as distant from each other in *Diaemus youngi* as in *Desmodus*. The pons is deep and narrow, with flat floor and the sides rise steeply to the level of the cerebellar peduncles (McDaniel, 1976).

Vampire bat eyes are relatively large when compared to those of other microchiropterans of similar body mass and approach eye size found in frugivorous species. Peculiar retinal folds were observed in both eyes of a single *Diaemus youngi*. These folds may represent an infolded retina rather than retinal detachment, resembling superficially the undulating appearance in the megachiropteran retina (Bhatnagar, 1988), although this observation is based on one specimen.

Diaemus youngi probably relies strongly on olfaction and chemoreception given that it possesses highly developed vomeronasal organs. In white-winged vampire bats, the entire receptor-free epithelium bears cilia, whereas there are mixed nonciliated and ciliated cells in Desmodus and only a few ciliated cells in Diphylla. This suggests that the vomeronasal organ is more efficient for chemoreception in Diaemus youngi compared to the other two vampires (Bhatnagar, 1988).

Audition seems to be the most important sensory modality in vampire bats, but there is little knowledge of their hearing ability (Schmidt, 1988b). Compared to other microchiropterans, the auditory ossicles are small in *Diaemus youngi*, but the middle ear muscles are large. Paauw's cartilage is present and the stapedial artery is persistent (Hinchcliffe and Pye, 1969). The cochlea is conical and mean cochlear height is 2.43 mm (Pye, 1967). There is a thickening of the basilar membrane, especially at the base (Bhatnagar, 1988; Pye, 1967). *Diaemus youngi* produced frequency modulated pulses of short duration (0.8 to 1.6 msec) and the strongest component was 66 kilocycles per second, falling off at 40 kilocycles per second (Pye, 1967). In a recent study, captive whitewinged vampire bats were recorded during aggression/dominance interactions, grooming, and feeding (Faure et al., 1995). They emit-

4 MAMMALIAN SPECIES 533

ted calls that were linear or hyperbolic downward sweeps containing 2–4 harmonics, usually with maximal energy located in the fundamental (although a number of unusual call "types" were recorded). In addition to containing audible frequencies, social signals were rich in ultrasound (bandwidth range=37.4–71.6 kHz). Social calls were extremely variable in duration (range=2.7–42.7 msec) and frequency (peak frequency range=16–33.9 kHz; lowest frequency=7.4–21.1 kHz; highest frequency=50.6–90.6 kHz).

Diaemus youngi possesses both overhair and underhair. Scale forms are short, repand to sinuate and coronal, with minor marginal irregularities. Melanin granules are dispersed generally through all portions of the filament and there are prominent basal bulbs. Scales are medium and entire coronal and medullae never are present (Benedict, 1957).

A study on temperature regulation in Neotropical bats determined that vampire bats are not as effective as nectar, fruit, and meat-eating bats at thermoregulation (McNab, 1969). Within the vampire bats, *Diaemus youngi* and *Diphylla* maintain lower body temperatures than does *Desmodus*. The reason for this difference is not known.

Sperm morphology in *Diaemus youngi* is similar to that of *Desmodus*, but very different from that of *Diphylla* (Forman and Genoways, 1979). Testes in *Diaemus youngi* average 3.4 by 2.0 mm and the epididymis is large and leaf-like (Bhatnagar, 1988). Mean measurements ( $\mu$ m) with  $\pm SD$  characterizing spermatozoa are: length of head,  $5.61 \pm 0.2$ ; acrosome length,  $3.20 \pm 0.17$ ; nuclear length,  $4.50 \pm 0.14$ ; midpiece length,  $12.51 \pm 0.3$ ; and width of head,  $3.11 \pm 0.3$  (Forman and Genoways, 1979).

ECOLOGY. Diaemus youngi is monotocous and polyestrous; otherwise its breeding habits are unknown (Carter, 1970; Schmidt, 1988). On 22 October, in southern Trinidad, white-winged vampire bats found in a hollow immortelle tree (Erythrina micropteryx), consisted of four breeding males, one immature male, one lactating female, and one non-gravid female. Two lactating females, each with a single juvenile male, were taken on 23 August in northern Trinidad; one of the young was estimated about two weeks of age, the other about two months (Goodwin and Greenhall, 1961).

Diaemus youngi exhibits flexibility with regard to foraging sites and roost preference. It appears to prefer moist, open areas but also forages in dry deciduous forests as well as in multistratal evergreen forest (Eisenberg, 1989). Diaemus youngi is both a cave and tree dwelling species in Trinidad, roosting in colonies of up to 30 individuals (Goodwin and Greenhall, 1961). In well lighted caves, Diaemus youngi was found sharing roosts with Saccopteryx bilineata and Desmodus rotundus. In the lowlands of southeastern Mexico, white-winged vampire bats have been collected in Cocona Cavern near Teapa, Tabasco, along with great numbers of Desmodus (Villa-R., 1967). Diaemus youngi populations roosting in caves in Mexico have been characterized as fragile (Arita, 1993). In Panama, Diaemus youngi is a rare, forest-dwelling bat (Handley, 1966). On Margarita Island, Venezuela, it was numerous, especially in the forest around Cerro Copey, and commonly attacked cattle. Seven bats were collected in a hollow tree, at the base of which were pools of typical, tarry vampire excrement (Musso, 1962). In Venezuela, Diaemus youngi and Desmodus had separate habitats: Diaemus youngi lived around human dwellings and Desmodus preferred forests (Pirlot, 1964). Specimens also were collected by mist netting in scattered localities (<500 m elevation) in the following habitats: yards, pastures, orchards, and forests (evergreen, thorn forests, dry forest, very dry and moist) (Handley, 1976). In a karst region of southeastern Brazil, white-winged vampire bats were found in caves in association with eight other species of bats including Peropteryx macrotis, Chrotopterus auritus, Anoura caudifer, Carollia perspicilata, Sturnira lilium, Artibeus lituratus, Vampyrops lineatus, and Desmodus (Trajano, 1984). In the Utinga forest, near Belem, Brazil, 0.003 white-winged vampire bats were caught per net hour in nets set at ground level (Handley, 1967). They were also present in remnant Atlantic rain forest near Pernambuco, Brazil (Mares et al., 1981) and in French Guiana (Brosset and Charles-Dominique, 1990). In Peru, Diaemus youngi is confined to the lowlands (Eisenberg, 1989). In eastern Peru, it shared large cave roosts with C. perspicilata, C. auritus, Desmodus rotundus, Glossophaga soricina, Lonchophylla handleyi, Micronycteris minuta, Phyllostomus hastatus, Pteronotus parnellii, P. personatus and V. infuscus (Graham, 1988). Near the Panguana Biological Station in Amazonian Peru, both Diaemus youngi and

Diphylla ecaudata were collected near huts and surrounding gardens at the forest edge (Hutterer et al., 1995).

Ectoparasites found on Diaemus youngi include two families of mites, (Macronyssidae and Thrombiculidae) and bat flies (family Streblidae). Species of mites of the family Macronyssidae include Nycteronyssus desmodus (which is species specific), Radfordiella desmodi, and R. oudemansi. Thrombiculids included Euschoengastia colombiae, and Perissopalla exhumatus. Bat flies included Strebla diaemi, Trichobius dugesii, T. parasiticus, and an undescribed species of Trichobius (Anciaux de Favroux, 1971; Goodwin and Greenhall, 1961; Mendez, 1988; Saunders and Yunker, 1973). The thrombiculids Euschoengastia colombiae and Perissopalla exhumatus are not primarily associated with Diaemus youngi, whereas the streblid fly Strebla diaemi, a species known from Panama and Venezuela, is species specific (Mendez, 1988).

Diaemus youngi is also host to a diverse endoparasite fauna, although knowledge of such parasites is fragmentary (Mendez, 1988). The presence of an undescribed filarial nematode (family Filariidae) in the olfactory mucosa of white-winged vampire bats from Trinidad suggested that either ticks, mosquitoes, or other blood sucking arthropods may act as the intermediate host and vector of this nematode (Lichtenfels et al., 1981). The protozoan parasites Trypanosoma cruzi marikellei (order Kinetoplastida: family Trypanosomidae) which infests Diaemus youngi in Colombia, appears to be non-pathogenic to man and laboratory animals. It is regarded as subspecifically distinct from the human pathogen T. cruzi cruzi, the cause of Chagas' disease (Constantine, 1988). Rabies virus and rabies related viruses are classified in the genus Lyssavirus. The virus has been reported from all three genera of vampires, but the only reports of rabies transmission by Diaemus youngi have been from Trinidad (Constantine, 1988; Goodwin and Greenhall, 1961).

**BEHAVIOR.** White-winged vampire bats are swift and deliberate fliers. Under appropriate lighting conditions their white wing tips can be seen clearly (Goodwin and Greenhall, 1961; Musso, 1962).

Although avian blood is the preferred diet of *Diaemus youngi*, it will take mammalian blood (Gardner, 1977; Goodwin and Greenhall, 1961; Nowak, 1991; Schutt, 1995). In Trinidad, it preyed upon poultry, pigeons, goats and occasionally cattle. When poultry, pigeons, and goats were attacked, cattle and equines in the area were excluded from predation. During field observations of white-winged vampire bats in Brazil, there was a negative correlation between frequency of observed feeding behavior and environmental factors such as wind (over 27 km/h), rain, and the presence of intense moonlight (Uieda, 1992).

In Trinidad, although cattle were attacked in the wild, captive Diaemus youngi refused to feed upon non-citrated bovine blood (Goodwin and Greenhall, 1961; Greenhall, 1988). Of 23 newly caught adult white-winged vampire bats examined, 13 fed upon mammalian blood (cattle, pig, and some unidentifiable samples). Of the remaining 10 bats, eight fed upon avian blood in combination with mammalian blood and two fed exclusively on avian blood (Greenhall, 1970, 1988). In other studies, captive specimens of Diaemus youngi have been maintained successfully on a diet of defibrinated bovine blood supplemented weekly with fresh chicken blood (Muradali et al., 1993; Schutt, 1995).

Experiments were conducted in Trinidad on captive white-winged vampire bats to determine which native birds were available prior to introduction of domestic fowl (see Buchanan, in Greenhall, 1988). Live birds included representatives of Columbidae, Psittacidae, Picidae, Dendrocalaptidae, Pipridae, Tyrannidae, Mimidae, Turdidae, Icteridae, Thraupidae, and Fringillidae. Range of masses of these birds was from 15 to 200 g. Diaemus youngi successfully attacked and fed upon individuals of all families. In each case, feeding continued until the bird's death. A 7-g trochilid was not attacked, resembling the behavior of Desmodus toward Mus sp. and Microtus sp., and other mammals smaller than themselves (Greenhall, 1988). Feeding behavior of captive Diaemus youngi was observed on domestic pigeons, collared doves, and half-grown chickens. Perch diameter of less than 2 cm and prey masses were proposed as factors limiting attacks on smaller birds (Uieda et al., 1992).

In Tamaulipas, Mexico, a white-winged vampire bat was captured while feeding on a chicken (Villa-R., 1967) and its feeding behavior on free-ranging poultry has been observed in Brazil (Sa-

MAMMALIAN SPECIES 533 5

zima and Uieda, 1980; Uieda, 1992, 1993, 1994) and Trinidad (Greenhall, 1988). After landing on a branch, *Diaemus youngi* typically moved to the underside, holding on with thumbs and toes. When preying upon chickens or guinea fowl, bites usually were made on the tarsi, toes and cloaca (turkeys were bitten on the bare skin of the lower breast). Occasionally, feeding was interrupted when the bat groomed itself or when the prey became momentarily disturbed. During these latter instances, *Diaemus youngi* usually retreated to the undersurface of the branch and aligned itself with it. This behavior may be defensive, with the branch shielding the bat against pecking by the bird. In other instances when the bird became disturbed, the white-winged vampire bat crawled onto its prey and hid under its wing and belly. There have been no reports of attacks on ground-sleeping birds (Greenhall, 1988).

Two displays by a feeding bat toward another flying individual were observed. In both instances, the feeding bat stretched its neck, bared its teeth and uttered high-pitched cries. Apparently these demonstrations were effective, since no bat was observed landing near a defended prey (Greenhall, 1988).

In captivity, Diaemus youngi was extremely vocal and made a variety of hisses, screams and chirps (Goodwin and Greenhall, 1961; Muradali et al., 1993; Schutt, 1995). Mated pairs cleaned and groomed one another. One pair appeared quite disturbed when separated (Goodwin and Greenhall, 1961). In Brazil, two adult females were kept in captivity and fed live chickens (Uieda and de Araújo, 1987). One of the bats gave birth after 217 days of captivity. Captive specimens of Diaemus youngi were observed feeding on adult chickens (Gallus gallus) perched on branches (Muradali et al., 1993; Schutt, 1995).

Before bites were made, the potential bite area was always licked for periods lasting from 10 seconds to two minutes. It is not known if white-winged vampire bat saliva contains anesthetic or enzymatic components to aid in bite preparation or if licking softens the keratinized reticulate scales that cover the surface of the digit. Additionally, most bites were made on the posteriorally directed hallux (digit I). Feeding from this digit may keep the bat concealed under its prey to a greater degree than would occur if an anteriorly directed digit (digits I–IV) was fed upon (Schutt, 1995).

A force platform and high speed photography were used to measure differences in quadrupedal locomotor performance (e.g. flight initiation) between captive specimens of *Diaemus youngi* and *Desmodus* (Schutt et al., 1993). These differences are thought to be related to principle prey selection. Whereas the terrestrially feeding *Desmodus* employed flight initiating jumps from a horizontal surface, *Diaemus youngi*, which feeds arboreally, did not jump from the ground to initiate flight.

GENETICS. The karyotype of Diaemus youngi has a diploid number of 32 and a fundamental number of 60. Except for one pair of medium subtelocentric chromosomes, all autosomes are either metacentric or submetacentric. The X-chromosome is a large submetacentric and the Y-chromosome, a minute acrocentric (Baker et al., 1988; Forman et al., 1968). The smallest pair of autosomes has a nucleolar organizer region on the longest arm near the centromere. C-band positive regions occur at the centromeres of some telomeres. Analysis of C- and G-band variation suggest that among vampire bats the karyotype of Diaemus youngi is least modified from the proposed primitive karyotype for the family Phyllostomidae and that Desmodus and Diphylla form a clade relative to Diaemus (Bass, 1978). However, this relationship is not supported by data from studies using molecular techniques. Data from starch gel electrophoresis and albumin immunology indicate a closer relationship between Diaemus youngi and Desmodus relative to Diphylla (Baker et al., 1988; Honeycutt 1981). These latter studies support morphological evidence which indicated that Diaemus youngi and Desmodus form a clade relative to Diphylla (Cadena, 1977; Koopman, 1988; Miller, 1907; Schutt, 1995; Slaughter, 1970).

**REMARKS.** Diaemus youngi was included within Desmodus by Handley (1976), Koopman (1978), and Honacki et al. (1982), but Koopman (1988) later concluded that the two vampires are generically distinct (Koopman, 1993). A partial bibliography of literature on the three species of vampire bats, with 626 references was compiled by Linhart (1970).

We wish to thank Karl F. Koopman for his critical review of the manuscript and Guy G. Musser for assistance in obtaining the services of Pat Wynn, illustrator, for preparation of the map and figures of the skull. Additionally, we thank Rob Voss, Nancy Simmons, Darrin Lunde, and John W. Hermanson for their input and suggestions. We are most appreciative to Kimberly Brockmann for her helpful comments and assistance in preparing this manuscript.

We wish to dedicate this review of *Diaemus youngi* to Aurelio Malaga Alba of the Pan American Health Organization and Colin C. Sanborn of the Field Museum of Natural History.

#### LITERATURE CITED

AELLEN, V. 1970. Catalogue raisonné des chiroptères de la Colombie. Revue Suisse de Zoologie, Tome 77, 1:1-37.

AGUIRRE, L. F. 1994. Estructura y ecología de las communidades de murciélagos de la Sabana de Espíritu (Beni, Bolivia). Tesis de Licenciatura, Universidad Mayor de San Andres, La Paz, Bolivia, 167 pp.

ANCIAUX DE FAVEAUX, M. 1971. Catalogue des Acariens parasites et commensaux des Chiropteres. Institute Royal Science Natural, Belgique (Brussels), Working Document Number 7, pp. 201–327.

ANDERSON, S. 1993. Los mamíferos Bolivianos: Notas de distribución y claves de identificatión. Publicación Especial del Instituto de Ecología (Colección Boliviana de Fauna), La Paz, Bolivia, 147 pp.

ARITA, H. T. 1993. Conservation biology of the cave bats of Mexico. Journal of Mammalogy, 74:693–702.

BAKER, R. J., R. L. HONEYCUTT, AND R. A. BASS. 1988. Genetics. Pp. 31–40, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.

BAKER, R. J., AND J. K. JONES. 1975. Additional records of bats from Nicaragua, with a revised checklist of Chiroptera. Occasional Papers of the Museum, Texas Tech University, 32:1– 13.

BARQUEZ, R. M. 1984. Significativa extensión del rango de distribución de *Diaemus youngi* (Jentink 1893) (Mammalia, Chiroptera, Phyllostominae). Historia Natural, 4:67–68.

BASS, R. 1978. Systematics of the Desmodontinae and Phyllonycterinae (Chiroptera: Phyllostomatidae) based on G-band chromosomal homologies. M.S. thesis, Texas Tech University, Lubbock, 53 pp.

BENEDICT, F. A. 1957. Hair structure as a generic character in bats. University of California Publications in Zoology, 59:285– 548.

BHATNAGAR, K. P. 1988. Anatomy. Pp. 41-70, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.

BHATNAGAR, K. P., AND W. A. WIMSATT. 1988. Vampire bats do have fully developed enamel. The Anatomical Record, 223: 144

BROSSET, A., AND P. CHARLES-DOMINIQUE. 1990. The bats from French Guiana: a taxonomic, faunistic and ecological approach. Mammalia, 54:509-559.

CADENA, A. 1977. A systematic study of vampire bats, Desmodontinae (Phyllostomatidae, Chiroptera). Ph.D. dissert., University of Kansas, Lawrence, 189 pp.

CARTER, D. C. 1970. Chiropteran reproduction. Pp. 233–246, in About bats (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist University Press, Dallas, Texas, 399 pp.

CARTWRIGHT, T., AND C. HAWKEY. 1968. Activation of the blood fibrolytic mechanism in birds by saliva of the vampire bat *Diaemus youngi*. Journal of Physiology, 201:45–52.

CONSTANTINE, D. C. 1988. Transmission of pathogenic organisms by vampire bats. Pp. 167–189, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.

DE LA TORRE, L. 1956. The dental formula of the bats of the genus *Diaemus*. Proceedings of the Biological Socociety of Washington, 69:191-192.

DELPIETRO, R., R. D. LORD, L. LAZARO, AND R. GARCIA. 1973. Extensión de la distribución del vampiro de alas blancas (*Diaemus youngi*). Physis, 32:224.

EISENBERG, J. F. 1989. Mammals of the Neotropics: the northern Neotropics. Vol. 1. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, 449 pp.

FAURE, P. A., K. A. BROCKMANN, W. A. SCHUTT, JR., F. MURADALI, AND J. W. HERMANSON. 1995. Behavior and vocalizations of

- the white-winged vampire bat during blood feeding. Bat Research News, 36:63-64.
- FORMAN, G. L., AND H. H. GENOWAYS. 1979. Sperm morphology. Pp. 177-204, in Biology of bats of the New World family Phyllostomatidae. Part 3 (R. J. Baker, J. K. Jones and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 16:1-441.
- FORMAN, G. L., R. J. BAKER, AND J. D. GERBER. 1968. Comments on the systematic status of vampire bats (Family Desmodontidae). Systematic Zoology, 17:417–425.
- FORMAN, G. L., C. J. PHILLIPS, AND C. S. ROUK. 1979. Alimentary tract. Pp. 205–228, in Biology of bats of the New World family Phyllostomatidae. Part III (R. J. Baker, J. K. Jones, and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 16:1–441.
- GARDNER, A. L. 1977. Feeding habits. Pp. 293-350, in Biology of bats of the New World family of Phyllostomatidae. Part II (R. J. Baker, J. K. Jones, and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 13:1-364.
- GARDNER, A. L., R. K. LA VAL, AND D. E. WILSON. 1970. The distributional status of some Costa Rican bats. Journal of Mammalogy, 51:712-729.
- GOODWIN, G. G., AND A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. Bulletin of the American Museum of Natural History, 122:187-302.
- GRAHAM, G. L. 1988. Interspecific associations among Peruvian bats at diurnal roosts and roost sites. Journal of Mammalogy, 69:711-720.
- Greenhall, A. M. 1970. The use of precipitan test to determine host preferences of vampire bats, *Desmodus rotundus* and *Diaemus youngi*. Bijdragen Dierkunde, 40:36–39.
- ——. 1972. The biting and feeding habits of the vampire bat, Desmodus rotundus. Journal of the Zoological Society of London, 68:451–461.
- ——. 1988. Feeding behavior. Pp. 111–131, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.
- HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1-600 + 90.
- HANDLEY, C. O., JR. 1966. Checklist of the mammals of Panama. Pp. 753-795, in Ectoparasites of Panama (R. J. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois, 861 pp.
- . 1967. Bats of the canopy of an Amazonian forest. Atas do Simpósio Sôbre a biota Amazônica. Zoologia, 5:211-215.
- 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University, Science Bulletin, Biological Series, 20:1–91.
- HAWKEY, C. M. 1988. Salivary antihemostatic factors. Pp. 133–141, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.
- HINCHCLIFFE, R., AND A. PYE. 1969. Variations in the middle ear of the Mammalia. Journal of the Zoological Society of London, 157:277-288.
- Honackt, J. H., K. E. Kinman, and J. W. Koeppl. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Lawrence, Kansas, 694 pp.
- HONEYCUTT, R. L. 1981. Molecular evolution in New World leafnosed bats of the family Phyllostomidae with comments on the superfamily Noctilionoidea. Ph.D. dissert., Texas Tech University, Lubbock, 105 pp.
- HOWELL, D. J., AND J. PYLKA. 1977. Why bats hang upside down: a biomechanical hypothesis. Journal of Theoretical Biology, 69:625-631.
- HUSSON, A. M. 1962. The bats of Suriname. Zoologische ver hande lingen Riskmuseum Van Natuurlijke Historil, Leiden, 282 pp.
- HUTTERER, R., M. VERHAAGH, J. DILLER, AND R. PODLOUCKY. 1995. An inventory of mammals observed at Panguana Biological Station, Amazonian Peru. Ecotropica, 1:3–20.
- JENTINK, L. A. 1893. On a collection of bats from the West Indies. Notes of the Leyden Museum, 15:278-283.
- KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. American Museum Novitates, 2651:1–33.
- ----. 1988. Systematics and distribution. Pp. 7-17, in Natural

history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.

- . 1993. Order Chiroptera. Pp. 137–241, in Mammal species of the World. Second ed. (D. E. Wilson and D. M. Reeder, eds.). The Smithsonian Institution Press, Washington, D.C., 1,206 pp.
- LAY, D. M. 1963. Seis mamíferos nuevos para la fauna de México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, 33:373–377.
- LICHTENFELS, J. R., K. P. BHATNAGAR, F. H. WHITTAKER, AND H. D. FRAHM. 1981. Filaroid nematodes in olfactory mucosa, olfactory bulb and brain ventricular system of bats. Transactions of the American Microscience Society, 100:216.
- LINARES, O. J. P. 1987. Murciélagos de Venezuela. Cuadernos Lagoven, Caracas, Venezuela, 121 pp.
- LINHART, S. B. 1970. A partial bibliography of the vampire bats (*Desmodus*, *Diphylla*, *Diaemus*). Bureau of Sport Fisheries and Wildlife, Wildlife Research Center, Denver, Colorado, 53 pp.
- Mares, M. A., M. R. Willig, K. E. Streilein, and T. E. Lacher, Jr. 1981. The mammals of northeastern Brazil: a preliminary assessment. Annals of Carnegie Museum, 50:81-137.
- McDaniel, J. R. 1976. Brain anatomy. Pp. 147-200, in Biology of bats of the New World family Phyllostomatidae. Part I (R. J. Baker, J. K. Jones, and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 10:1-218.
- McNab, B. K. 1969. The economics of temperature regulation in Neotropical bats. Comparative Biochemical Physiology, 31: 227-268.
- MENDEZ, E. 1988. Parasites of vampire bats. Pp. 191-296, in
   Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.
- MILLER, G. S., JR. 1906. Twelve new genera of bats. Proceedings of the Biological Society of Washington, 9:84-86.
- . 1907. The families and genera of bats. Bulletin of the United States National Museum, 57:1–282.
- MURADALI, F., N. MONDOL, AND W. A. SCHUTT, JR. 1993. Observations on feeding behavior in the white-winged vampire bat, *Diaemus youngi*. Bat Research News, 34:121A.
- MUSSO, A. Q. 1962. Lista de los mamíferos conocidos en la Isla de Margarita. Memorias Sociedad Ciencia Natural La Salla (Caracas), Venezuela, 27:163–180.
- NOWAK, R. M. 1991. Walker's Mammals of the World. Fifth ed. Johns Hopkins University Press, Baltimore, Maryland, 1:1-642.
- OSCOOD, W. H. 1912. Mammals from western Venezuela and eastern Colombia. Field Museum of Natural History, Zoological Series, 155:32-66.
- Peracchi, A. L., and S. E. de Albuquerque. 1971. Lista provisória dos quirópteros dos Estados do Rio de Janeiro e Guanabara, Brasil (Mammalia, Chiroptera). Review of Brazilian Biology, 31:405–413.
- PIRLOT, P. 1964. Nota sobre la ecología de ciertos quirópteros de la región del Rio Palmar (Estado Zulia). Revista Universidad Zulia. Kasmera (Venezuela), 1:289–307.
- . 1965. Chiropteres de L'est du Venezuela. II. Delta de L'Orénoque. Mammalia, 29:375–389.
- PIRLOT, P., AND H. STEPHEN. 1970. Encephalization in chiroptera. Canadian Journal of Zoology, 48:433-444.
- PYE, A. 1967. The structure of the cochlea in Chiroptera. III. Microchiroptera. Journal of Morphology, 121:241-246.
- RAY, C. E., O. J. LINARES, AND G. S. MORGAN. 1988. Paleontology. Pp. 19–30, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.
- REDDEL, J. R. 1981. A review of the cavernicole fauna of Mexico, Guatemala and Belize. Texas Memorial Museum, University of Texas Bulletin, 27:1–327.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics: Volume 2. The southern cone: Chile, Argentina, Uruguay, Paraguay. The University of Chicago Press, Chicago, Illinois, 430 pp.
- SANBORN, C. C. 1949. Mammals from the Rio Ucayali, Peru. Journal of Mammalogy, 30:277-288.
- SAUNDERS, R. C., AND C. E. YUNKER. 1973. Venezuelan Macronyssidae II. *Nycteronyssus desmodus*, n. gen., n. sp., of a vampire bat. Journal of Medical Entomology, 10:381–384.

MAMMALIAN SPECIES 533

SAZIMA, I. 1978. Aspectos do comportamento alimentar do morcegos hematofogos, *Desmodus rotundus*. Boletin Zoological Universidade, São Paulo, Brasil, 3:97.

- SAZIMA, I., AND W. UIEDA. 1980. Feeding behavior of the whitewinged vampire bat, *Diaemus youngi* on poultry. Journal of Mammalogy, 61:102.
- SCHMIDT, C. 1988. Reproduction. Pp. 99-109, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.
- Schmidt, U. 1988. Orientation and sensory functions in *Desmodus rotundus*. Pp. 143–166, in Natural history of vampire bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida, 246 pp.
- SCHUTT, W. A., Jr. 1992. Preliminary anatomical studies on the chiropteran hindlimb: does the digital flexor retinaculum help bats get the hang of it? Bat Research News, 33:74–75A.
- . 1993. Digital morphology in the Chiroptera: the passive digital lock. Acta Anatomica, 148:219–227.
- . 1995. The chiropteran hindlimb: functional, behavioral, and evolutionary correlates of morphology. Ph.D. dissert., Cornell University, Ithaca, New York, 155 pp.
- Schutt, W. A., Jr., J. W. Hermanson, J. E. A. Bertram, D. Cul-Linane, Y. H. Chang, F. Muradali, and J. S. Altenbach. 1993. Aspects of locomotor morphology, performance and behavior in two vampire bats, *Desmodus rotundus* and *Diaemus* youngi. Bat Research News, 34:127-128A.
- SLAUGHTER, B. H. 1970. Evolutionary trends in chiropteran dentition. Pp. 51-83, in About bats (B. H. Slaughter and W. D. Walton, eds.). Southern Methodist University Press, Dallas, Texas, 339 pp.
- SMITH, J. D., AND H. H. GENOWAYS. 1974. Bats of Margarita Island, Venezuela, with zoogeographic comments. Bulletin of the Southern California Academy of Sciences, 73:64.
- SWANEPOEL, P., AND H. H. GENOWAYS. 1979. Morphometrics. Pp. 13–106, in Biology of bats of the New World family Phyllostomatidae. Part III (R. J. Baker, J. K. Jones, and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 16:1–441.
- THOMAS, O. 1928. The Godman-Thomas Expedition to Peru VIII.
  On mammals obtained by Mr. Hendee at Pebas and Iquitos,
  Upper Amazons. Annals and Magazine of Natural History, 2:
  285-294.
- TRAJANO, E. 1984. Ecologia de populações de morcegos caver-

nicolas em uma regiao carstica do Sudeste do Brasil. Revista Brasiliera de Zoologia, 2:255-320.

7

- UIEDA, W. 1982. Aspectos do comportamento alimentar dos tres especies do morcegos hematófagos (Chiroptera, Phyllostomidae). M. B. thesis, Instituto Biologico Universidade Estadual de Campinas, Brasil, 168 pp.
- ———. 1986. Aspectos da morfologia lingual das três espécies de morcegos hematófagos (Chiroptera, Phyllostomidae). Review of Brasilian Biology, 46:581–587.
- dos morcegos hematófagos (Phyllostomidae) no sudeste do Brasil. Review of Brasilian Biology, 52:563–573.
- ——. 1993. Comportamento alimentar do morcego hematófago Diaemus youngi, em aves domésticas. Review of Brazilian Biology, 53:529–538.
- -----.. 1994. Comportamento alimentar do morcegos hematófagos ao atacar aves, caprinos e suínos, em condições de cativeiro. Ph.D. dissert., Instituto Biologico Universidade Estadual de Campinas, Brasil, 178 pp.
- UIEDA, W., AND V. F. DE ARAÚJO. 1987. Manutenção dos morcegos hematófagos Diaemus youngii e Diphylla ecaudata (Chiroptera, Phyllostomidae), em cativeiro. Seminário de Ciências da Fiube, Faculdades Integradas de Uberaba, 1:30–42.
- UIEDA, W., BUCK, S., AND I. SAZIMA. 1992. Feeding behavior of the vampire bats *Diaemus youngi* and *Diphylla ecaudata* on smaller birds in captivity. Journal of the Brazilian Association for the Advancement of Science, 44:410-412.
- VILLA-R., B. 1964. Diaemus youngi (Jentink) el vampiro overo, en el sur de Tamualipas, México. Annales del Instituto de Biología, Universidad Nacional Autónoma de México, 35:127– 128.
- . 1967. Los Murcielagos de México, Instituto Biología, Universidad Autónoma de México, México City, México, 491 pp.
- Editors of this account were DUKE S. ROGERS, ELAINE ANDERSON AND KARL F. KOOPMAN. Managing editor was ALICIA V. LINZEY.
- A. M. Greenhall, Department of Mammalogy, The American Museum of Natural History, New York, New York 10024; W. A. Schutt, Jr., Department of Mammalogy, The American Museum of Natural History, New York, New York 10024 and The Division of Natural Sciences, Bloomfield College, Bloomfield, New Jersey 07003.