MAMMALIAN SPECIES No. 343, pp. 1–5, 3 figs.

Chrotopterus auritus.

By Rodrigo A. Medellín

Published 26 October 1989 by The American Society of Mammalogists

Chrotopterus Peters, 1865

Chrotopterus Peters, 1865:505. Type species, *Vampyrus auritus* Peters, 1856*a*:415, by original designation.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Phyllostominae. The genus *Chrotopterus* is monotypic.

Chrotopterus auritus (Peters, 1856*a*)

Woolly False Vampire Bat

Vampyrus auritus Peters, 1856*a*:415. Type locality "Mexico."
Chrotopterus auritus Peters, 1865:505. First use of current name combination.

CONTEXT AND CONTENT. Context as for the genus. Although several authors have agreed with Handley (1966) questioning the existence of subspecies in *C. auritus*, others (for example Peracchi and Albuquerque, 1976) have recognized three subspecies, as follows:

C. a. auritus (Peters, 1856*a*:415), see above.
C. a. australis Thomas, 1905:308. Type locality "Concepcion, Paraguay; alt. 300 m."
C. a. guianae Thomas, 1905:308. Type locality "La Vuelta, Lower Orinoco, Venezuelan Guiana."

DIAGNOSIS. *Chrotopterus auritus* (Fig. 1) is one of the largest microchiropterans; length of forearm ranges from 78.7 to 83.1 mm and body mass from 75 to 96 g (McNab, 1969; Medellín, 1988; Villa-R., 1966). Only three New World phyllostomid bats are of comparable size: *Phyllostomus hastatus*, *Phylloderma stenops*, and *Vampyrum spectrum*. The dorsal hair in *C. auritus* is about 12 mm long, more than twice as long as that of the other three species. The pelage is dense and woolly, blackish gray or brown, and darker than that of either *P. stenops* or *V. spectrum*. *C. auritus* also has longer ears (>40 mm) than *P. hastatus*, *P. stenops*, or *V. spectrum*. As in *P. stenops*, the wing tips are whitish, the extent varying with subspecies (Thomas, 1905). Another character that distinguishes these bats is the presence of two lower incisors, shared only with phyllostomines of the genera *Mimon* and *Tonatia*, both of which are considerably smaller than *C. auritus*. Dental formula is i 2/1, c 1/1, p 2/3, m 3/3.

GENERAL CHARACTERS. The woolly fur is shorter and paler on the venter than on the dorsum. The skull (Fig. 2) is robust, with a wide rostrum. The canines and inner-upper incisors are well developed. The first upper premolar is minute, and displaced on the labial side. The upper molars are strong, and have conspicuous W-shaped lophs, with prominent hypocones and protocones. The thick, solid mandible bears the lower canines distinctly beyond the upper incisors, creating a prognathous condition. Only the first and third lower premolars are well developed. Coronoid processes are low and angular processes are bent outwards. The braincase is inflated, somewhat elongated, with prominent sagittal and lambdoidal crests. Zygomatic arches are wide and strong. Auditory bullae are small. The ribcase is wide and spacious. The manubrium of the sternum shows conspicuous ventral projection, which provides additional attachment surface for the pectoralis muscle. Scapulae are large, elongated, and pointed (Peters, 1856*b*).

The thumb is long, with large, strongly curved claws. Its basal half is hairy (to a lesser extent in *C. a. guianae*; Thomas, 1905), and enclosed in the well-developed propatagium. The plagiopatagium is extensive, and the wings are wide. The first phalanx of the middle finger is >50% of the length of the metacarpal and subequal to the second phalanx (Peters, 1856*b*, 1865). The forearm is heavily furred both dorsally and ventrally for nearly two-thirds of its length. The ventral surface of the plagiopatagium is also furred to at least 1 cm from the elbow, except in *C. a. guianae*, in which the membranes are practically naked (Thomas, 1905). The short tail (<15 mm) is totally enclosed in the wide uropatagium. The large ears are rounded and not connected by a band. The tragus is small, elongated, and pointed. Sometimes whitish patches are apparent at the bases of the ears. The noseleaf is large, broad, and rather blunt, with a thick rib, and a well-developed lower element (Peters, 1865). Warts at the bases of the scarce vibrissae are noticeable. The eyes are medium-sized, black, and beady. The lower lip has two large pads, similar to those in *Micronycteris*, forming the margins of a V-shaped groove (Peters, 1856*b*).

Ranges of external and cranial measurements (in mm) are: total length, 110 to 125; length of tail, 7 to 17; length of ear, 40 to 48; length of forearm, 78.7 to 86.5; greatest length of skull, 35.3 to 38.5; condylobasal length, 30.4 to 32.9; zygomatic breadth, 17.9 to 20.4; postorbital constriction, 5.9 to 6.5; braincase breadth, 12.9 to 14.5; mastoidal breadth, 15.2 to 18.8; width at M3-M3, 11.0 to 12.6; length of maxillary toothrow, 12.6 to 13.9 (Myers and Wetzel, 1983; Starrett and Casebeer, 1968; Swanepoel and Genoways, 1977; Taddei, 1975; Villa-R., 1966; Villa-R. and Villa-C., 1971). Mass varies from 66.8 (Peracchi and Albuquerque, 1976) to 96.1 g (McNab, 1969).

DISTRIBUTION. *Chrotopterus auritus* occurs (Fig. 3) in tropical rainforest (Handley, 1966), tropical deciduous forest (Wilson, 1983), and cloud forest (Medellín, 1988), from 0 to 2,000 m (Handley, 1976; Medellín, 1988). In México, there are records from the states of Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz, and Yucatán (Ramírez-P. et al., 1986). It extends south through Central America (Hall, 1981) to South America from Venezuela to Paraguay, southern Brazil, northern Argentina, Perú, and Bolivia (Acosta y Lara, 1951; Anderson, 1985; Handley, 1976; Myers and Wetzel, 1983; Terborgh et al., 1984).

FOSSIL RECORD. A skull and a pair of mandibles of *C. auritus* were found on the floor of Lara Cave (Actún Lara) in Yucatán, and another mandible was found in the upper 30 cm of earth in Actún Spukil Cave in Yucatán, both dating from the sub-Recent (Hatt et al., 1953). The oldest remains of *C. auritus* are from the Pleistocene (about 28,400 years B. P.), and there is material from the transition Pleistocene-Holocene and Holocene from Loltún Cave, Yucatán, México (Arroyo-C. and Alvarez, in press). Late Pleistocene fossil material of *C. auritus* was found in caves at Lagoa Santa, Minas Gerais, Brazil (Paula Couto, 1953), and an almost

FIG. 1. *Chrotopterus auritus* from Chajul, Lacantún River, Chiapas, México.

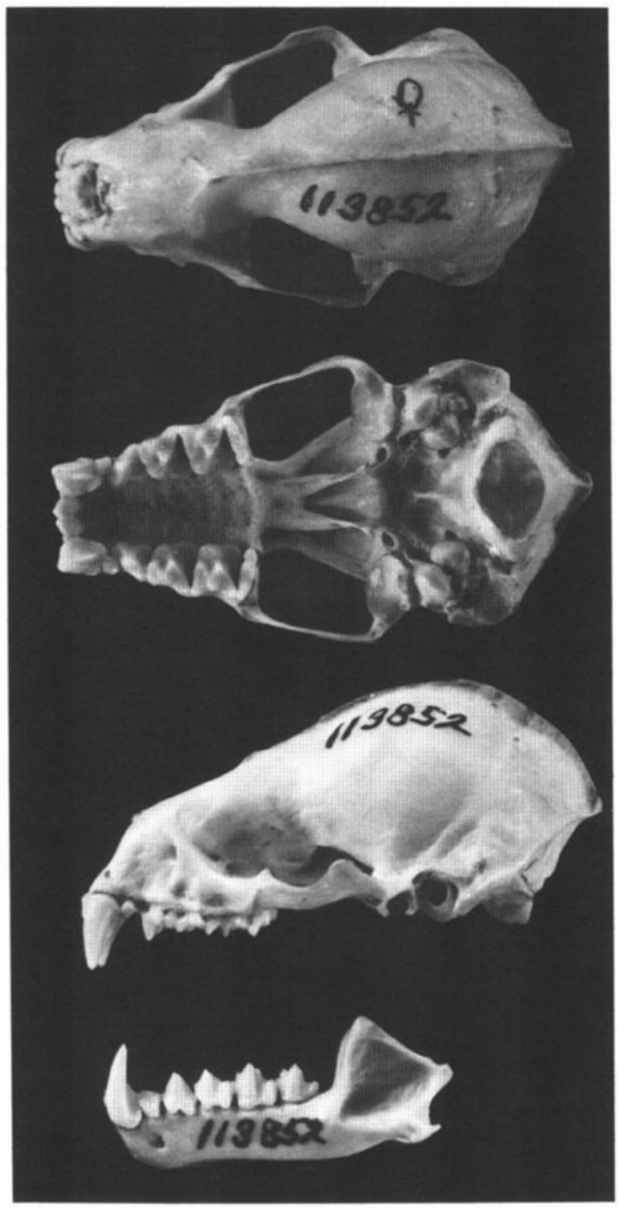

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Chrotopterus auritus* (United States National Museum of Natural History 113852) from Brazil. Greatest length of skull is 37.5 mm. Photographs courtesy of D. E. Wilson.

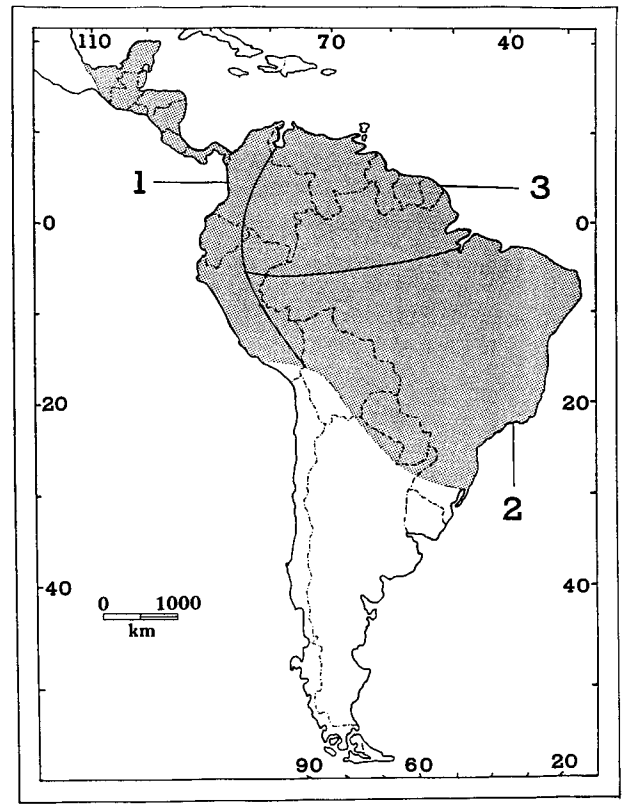

FIG. 3. Distribution of *Chrotopterus auritus*: 1, *C. a. auritus*; 2, *C. a. australis*; 3, *C. a. guianae*.

complete skull was found in a cave at Iporanga, Sao Paulo, Brazil, dating from the Platan or Lujanian in the Postpampean (late Pleistocene; Ameghino, 1907).

FORM AND FUNCTION. A canonical analysis based on morphological characters showed that *Vampyrum spectrum* and *C. auritus* clearly diverged from the rest of the phyllostomids, mainly due to two components: length of head and body is greater for these species than for any other; and they have comparatively shorter wings. *C. auritus* also ranked high in wing loading values (18.81 newtons/m^2), second only to members of the genus *Phyllostomus* within the subfamily (Smith and Starrett, 1979). There is a glandular structure on the ventral surface of the neck in males (Nowak and Paradiso, 1983).

The basic structure of the stomach of *C. auritus* and other phyllostomines is simple and is the least specialized among phyllostomids. The pyloric tube between the esophagus and duodenum of *C. auritus* is similar to that of *Micronycteris*, being only relatively longer (Forman et al., 1979). The gastric muscles of the caecum of *C. auritus* are considerably thicker than those in any stenodermatine examined (Forman, 1973). The Brunner's glands in the intestine of *C. auritus*, probably protecting the pyloric mucosa from large quantities of digestive acids, are relatively numerous, but less conspicuous than those in *Phyllostomus* (Forman et al., 1979). In *C. auritus*, Peyer's patches (gut-associated lymphoid tissue related to the immune system) are neither abundant nor large, probably as a result of its feeding habits. The largest Peyer's patches are found in frugivorous species (Forman, 1974).

Body temperatures of *C. auritus* subjected to environmental temperature changes do not vary greatly (McNab, 1969), indicating a considerable ability for temperature regulation. Probably due to its carnivorous habits, *C. auritus* has a high basal metabolic rate (McNab, 1982).

A sonogram of the echolocating call of *C. auritus* shows a remarkable similarity with the calls of other foliage gleaning bats, as they all share a short duration (<2 msec), low amplitude, and high frequency with multiple harmonics. These features are useful in a high-resolution, clutter-rejection strategy (Belwood, 1989).

ONTOGENY AND REPRODUCTION. As in other phyllostomids, litter size is one. Pregnant females have been found in México in April and in Argentina in July. A lactating female was reported from México in July (Wilson, 1979). Subadults have been reported from Costa Rica in July (Starrett and Casebeer, 1968) and from Guatemala in August (Rick, 1968). Males with scrotal testes have been found in Nicaragua in July (Jones et al., 1971) and in Argentina in July (Villa-R. and Villa-C., 1971). A female, captured and maintained live in isolation, gave birth 99 days after its capture; no date is given, but evidence from seven individuals revealed female reproductive activity only in the second half of the year (Taddei, 1976). These data are consistent with a monestrous cycle, varying geographically.

ECOLOGY. Most *C. auritus* have been collected in mature tropical rainforest and cloud forest, frequently in mist nets set on trails, streams, and clearings (Handley, 1976; Jones et al., 1971), but also among secondary, thick scrub (Olrog, 1973). *C. auritus* frequently is found in areas with a high bat-species richness. In the cloud forest of Chiapas, México, *C. auritus* was found with *Pteronotus parnellii, Mormoops megalophylla, Glossophaga commis-*

sarisi, Anoura geoffroyi, Hylonycteris underwoodi, Sturnira ludovici, Artibeus hartii, A. aztecus, A. toltecus, Desmodus rotundus, Myotis keaysi, Eptesicus fuscus, E. andinus, and *Lasiurus borealis* (Medellín, 1988). Three nights of radio-tracking showed that the foraging area of a young female in Costa Rica was within 4 ha of swamp forest adjacent to a roost in a hollow tree (A. Brooke, in litt.).

Roosts of *C. auritus* have been located in caves, mines (Davis et al., 1964; Handley, 1976; Villa-R. and Villa-C., 1971), abandoned buildings, Mayan ruins (Peracchi and Albuquerque, 1976; Rick, 1968), hollow termite nests (Sanborn, 1932), and hollow trees, including at least *Ceiba* sp., *Dipteryx panamensis,* and *Quercus crispifolia* (A. Brooke, in litt.; Carter et al., 1966; McNab, 1969; Medellín, 1988; Starrett and Casebeer, 1968). No correlation between type of roost and environment is evident, as the bats may occupy either caves or trees at low or high altitudes. Although generally these roosts are occupied only by *C. auritus* (Medellín, 1988; Rick, 1968; Sanborn, 1932; Sazima, 1978), two roosts in Brazil (Peracchi and Albuquerque, 1976), a small cave in Argentina (Villa-R. and Villa-C., 1971), and a tree roost in Costa Rica (Starrett and Casebeer, 1968) also were inhabited by a colony of *Desmodus rotundus.* In Veracruz, *C. auritus* was found in a cave that contained several *Balantiopteryx io* and *Artibeus jamaicensis* (Hall and Dalquest, 1963). *Glossophaga soricina* also was present in a cave in Brazil (Acosta y Lara, 1951). The huge cave of Zapaluta (=Trinitaria) in Chiapas, where *C. auritus* was found, also contains colonies of *P. parnellii, A. jamaicensis,* and *Tadarida brasiliensis* (Davis et al., 1964). In Venezuela, *C. auritus* inhabited a cave in which *Peropteryx macrotis, Pteronotus davyi, Phyllostomus hastatus,* and *D. rotundus* also were present (Ochoa, 1985).

Relative humidity and temperature inside the roost ranged from 77 to 93% and from 14 to 22°C, respectively, at four sites in Brazil (McNab, 1969). Five *C. auritus* were caught in Argentina in a mine at relative humidity of 80% and 20°C (Villa-R. and Villa-C., 1971).

The species is mostly carnivorous and insectivorous (Gardner, 1977*a*), taking small vertebrates and large insects (McCarthy, 1987; Medellín, 1988; Peracchi and Albuquerque, 1976). There is one record where *C. auritus* is considered to be hematophagous and frugivorous as well (Ruschi, 1953). *C. auritus* refused to eat fruit offered in captivity, but readily killed and ate small vertebrates (Peracchi and Albuquerque, 1976).

Vertebrate prey taken in the wild include: gekkonid lizards (*Thecadactylus rapicaudus*), doves (*Columbina* (=*Columbigallina*) *talpacoti*), antshrikes (*Thamnophilus*), tyrants (*Knipolegus cabanisi*), tanagers (*Chlorospingus ophthalmicus*), solitaires (*Myadestes obscurus*), warblers (*Dendroica townsendi*), mouse oppossums (*Marmosa*), shrews (*Sorex*), and mice (*Heteromys goldmani, Reithrodontomys mexicanus, Peromyscus oaxacensis, P. guatemalensis, Nyctomys sumichrasti,* and *Ototylomys phyllotis*; Acosta y Lara, 1951; McCarthy, 1987; Medellín, 1988; Ólrog, 1973; Peracchi and Albuquerque, 1976; Tuttle, 1967). Bats are not routinely taken in the wild as prey items; only one record from the wild reports *C. auritus* taking *G. soricina* (Acosta y Lara, 1951), and several other authors fed smaller bats to this species in captivity (Constantine, 1966; Peracchi and Albuquerque, 1976; Villa-R. and Villa-C., 1971). Insect prey includes Cerambycidae, Scarabeidae, and Sphingidae (Medellín, 1988).

Food resource partitioning may occur with the largely sympatric *Vampyrum spectrum.* Significant selection of non-passerine birds has been reported (Vehrencamp et al., 1977) for *V. spectrum* in Costa Rica, while the three species of birds taken by *C. auritus* in Chiapas, México, were passerines (Medellín, 1988). Mass of the prey items of *V. spectrum* in Costa Rica ranges from 20 to 150 g (Vehrencamp et al., 1977), overlapping entirely with the mass range of *C. auritus.* Prey items of *C. auritus* range from 10 to 35 g, with a maximum of 70 g (Medellín, 1988). Although *V. spectrum* is known to prey on mammals (Navarro and Wilson, 1982), all of the prey items reported for *V. spectrum* by Vehrencamp et al. (1977) were birds, except for the humerus of one small bat. Mammalian prey of *C. auritus* in Chiapas accounted for 79% of the vertebrates and 68% of the prey items (Medellín, 1988). This suggests that *V. spectrum* takes relatively large avian prey and some bats (McCarthy, 1987), while *C. auritus* most frequently preys upon rodents and small birds, seldom taking any bats.

Predators of *C. auritus* have not been recorded, nor has any instance of natural mortality. Probably these bats depend on the existence of primary forests to find roosts and food.

Chrotopterus auritus is known to host several species of ectoparasites (Webb and Loomis, 1977), including a nycteribiid fly (*Basilia hughscotti*; known only from *C. auritus*), a red mite (*Hooperella vesperuginis*), a tick (*Ornithodoros brodyi*), and two streblid flies (*Strebla wiedemanni* and *Trichobius dugesioides*). A new species of trematode, the only endoparasite reported (Strigeonidea: Diplostomidae: *Neodiplostomum vaucheri*), was described from the intestine of a *C. auritus* from Perú (Dubois, 1983).

BEHAVIOR. Colonies vary in size from one to seven (Medellín, 1988; Starrett and Casebeer, 1968). Most frequently groups of three to five occur (Constantine, 1966; Rick, 1968; Sazima, 1978).

This species uses audible and other similar clues to locate its prey (Medellín, 1988), in a manner similar to that of *Macroderma gigas, Megaderma lyra* (Fiedler, 1979; Guppy and Coles, 1983), and other large animalivorous bats. Prey of captive *C. auritus* routinely is consumed from the head down. The killing bites are delivered after the prey item has been wrapped in the wing membranes and locked with the thumbs. The bat directs its bites to the nape or throat when the prey item is a bat or mouse, and birds are killed by biting the top of the head (Medellín, 1988). Prey items are consumed when the bat has recovered its regular, head-down position. In general, rostra and beaks are rejected, as are other hard, bony areas, limbs, or long feathers. Viscera frequently are discarded as well. The prey item subsequently is held by the mouth or is placed on the internal surface of one wing, folded to serve as a platform (McCarthy, 1987; Medellín, 1988).

GENETICS. The karyotype of *C. auritus* has a fundamental number of 52 chromosomal arms and the diploid number is 28. The X chromosome is submetacentric, and the Y chromosome is acrocentric (Yonenaga et al., 1969). The standard karyotype shows that *C. auritus* is most closely related to bats of the genus *Tonatia* (Gardner, 1977*b*). A phylogenetic tree generated from albumin immunological distances yielded a close association between *C. auritus* and *V. spectrum.* The amount of change since the two lineages split is about one and two albumin immunological distance units, respectively, the shortest intergeneric distance presently known among bats (Honeycutt and Sarich, 1987).

REMARKS. The generic name *Chrotopterus* follows the Greek roots *chrotos* (skin, color), and *pteron* (wing). The specific epithet *auritus* refers to the large ears. These bats have been kept in captivity for over a year, on a diet of raw beef, bats, house sparrows, and laboratory rats and mice (Peracchi and Albuquerque, 1976).

Carter and Dolan (1978) found information suggesting that the type specimen used by Peters in the original description came from Santa Catarina, Brazil. However, the type (Peters, 1856*a*: 415) is clearly referred to as originally from México. According to A. L. Gardner (in litt.), the type of *Vampyrus auritus* was collected by Deppe in 1825 in Oaxaca or Veracruz, México, is deposited in the Zoologisches Museum der Humboldt, University of Berlin, with the number 10058, and consists of a cleaned skull and skeleton with parts of the body still in alcohol. I thank D. E. Wilson, J. J. Belwood, A. L. Gardner, and R. J. Baker for helpful comments on an earlier draft. This paper was partially supported by grant 52701, CONACyT México, and is contribution no. 31 of the Program for Studies in Tropical Conservation, University of Florida, and contribution no. 9117 of the Journal Series, Florida Agricultural Experiment Station.

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Editors of this account were TROY L. BEST and SYDNEY ANDERSON. Managing editor was DON E. WILSON.

R. A. MEDELLÍN, DEPARTMENT OF WILDLIFE AND RANGE SCIENCES, 118 NEWINS-ZIEGLER HALL, AND FLORIDA STATE MUSEUM, UNIVERSITY OF FLORIDA, GAINESVILLE, FLORIDA 32611.