

*Trachops cirrhosus*. By Michael J. Cramer, Michael R. Willig, and Clyde Jones

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***Trachops* Gray, 1847**

*Istiophorus* Gray, 1825:242. Type *Vampyrus cirrhosus* Spix or possibly *V. soricinus* Spix. Not *Istiophorus* Lacépède, 1802, a fish.

*Histiophorus* Agassiz, 1846:183. An emendation of *Istiophorus* Gray.

*Trachops* Gray, 1847:14. Type *Trachops fuliginosus* Gray (= *Vampyrus cirrhosus* Spix).

*Trachops* Peters, 1865:512. An emendation of *Trachops*?

**CONTEXT AND CONTENT.** Order Chiroptera, suborder Microchiroptera, family Phyllostomidae, subfamily Phyllostominae. The genus *Trachops* is monotypic (Koopman 1993).

***Trachops cirrhosus* (Spix, 1823)**

**Fringe-lipped Bat**

*Vampyrus cirrhosus* Spix, 1823:64. No type locality stated in Spix's description, but on page 53 Spix said the bats were collected in Brazil. Type locality restricted to the state of Pará, Brazil, by Husson (1962:115). Previous restrictions to Pernambuco, Brazil, based on the type locality of *Trachops fuliginosus* Gray, 1847, are invalid.

*Ph[ylostoma]. cirrhosum* Fischer, 1829:126. Name combination.

*Vampyrus cirrhosum* Gray, 1847:14. Emendation of *Vampyrus cirrhosus* Spix.

*Trachops fuliginosus* Gray, 1847:14. Type locality "Pernambuco," Brazil (= *Vampyrus cirrhosus* Spix).

*Tylostoma mexicana* Saussure, 1860:484. Type locality "les régions chaudes du Mexique." Questionable whether this bat is actually assignable to the genus *Trachops* (Goldman 1925). Listed as synonym by Peters (1865) and Dobson (1878). *Tylostoma* later recognized as a junior objective synonym of *Tonatia* (Gardner and Ferrell 1990).

*Trachyops cirrhosus* Dobson, 1878:481. First use of name combination and incorrect subsequent spelling of *Trachops* Gray, 1847.

*Trachops coffini* Goldman, 1925:23. Type locality "Guyo, Peten, Guatemala." Type locality restricted to "El Gallo, 8 mi. W Yaxha, on the Remate-El Cayo trail, Petén, Guatemala" by de la Torre (1956:189).

**CONTEXT AND CONTENT.** Context as above. Three subspecies of *T. cirrhosus* currently are recognized (Jones and Carter 1976).

*T. c. cirrhosus* Spix, 1823:64. Type locality as for *T. fuliginosus* Gray above.

*T. c. coffini* Felten, 1956a:189. Type locality as for *T. coffini* Goldman above.

*T. c. ehrhardti* Felten, 1956b:369. Type locality "Joinville, Sta. Catarina, Brazil."

**DIAGNOSIS.** *Trachops* externally is similar to *Phyllostomus*, except ear is longer than head, and numerous cylindrical wartlike protuberances occur on lips and chin (Miller 1907). A dichotomous key for skull characteristics of Phyllostominae can be found in Miller (1907). *Trachops* has 2 pairs of lower incisors, whereas *Tonatia*, *Mimon*, and *Chrotopterus* have 1. *Trachops* has 3 pairs of lower premolars, whereas *Phyllostomus* has 2. Skull of *Trachops* can be distinguished from that of *Vampyrus* by having a rostrum shorter than braincase and molars narrower than palate. *Trachops* has a p2 that is much smaller than p3, whereas p2 in *Micronycteris* is nearly the same size as p3. Skull of *Trachops* can be distinguished from that of *Lonchorhina* and *Phylloderma* by

position of p2 (displaced inward from toothrow in *Trachops*). Length of rostrum is ca. equal to breadth of braincase in *Trachops*, whereas length of rostrum is much smaller than breadth of braincase in *Macrophyllum* (Miller 1907).

**GENERAL CHARACTERS.** *Trachops cirrhosus* (Fig. 1) has long, woolly pelage, with fur extending along forearm for half its length; upper parts are cinnamon to dark brown, whereas under parts are dull brownish, tinged with grayish brown (Goodwin and Greenhall 1961). Ears are large and erect (Goodwin and Greenhall 1961); tragus is pointed (Ruschi 1953). Chin and lips are studded with conical or cylindrical wartlike protuberances, and noseleaf has a serrated edge. Tail is short and protrudes through dorsum of interfemoral membrane (Goodwin and Greenhall 1961).

Skull (Fig. 2) is large and elongate, with a well-developed sagittal crest and a large rounded braincase elevated above an elongated rostrum (Goodwin and Greenhall 1961; Ruschi 1953). Selected morphometric characters (in mm; mean  $\pm$  SD) for *T. c. cirrhosus* (Brazil,  $n = 35$  unless otherwise specified—Willig 1983) are: total length,  $99.60 \pm 7.84$ ; length of tail,  $15.68 \pm 2.17$ ; length of hindfoot,  $16.26 \pm 0.81$ ; length of ear,  $33.00 \pm 1.97$ ; mass (g),  $39.03 \pm 6.33$ ; length of forearm,  $61.09 \pm 1.52$ ; length of tibia,  $28.06 \pm 1.59$ ; greatest length of skull ( $n = 34$ ),  $28.02 \pm 0.71$ ; condylobasal length ( $n = 34$ ),  $24.90 \pm 0.55$ ; zygomatic breadth ( $n = 34$ ),  $14.39 \pm 0.52$ ; mastoidal breadth ( $n = 34$ ),  $5.28 \pm 0.18$ ; postorbital constriction ( $n = 34$ ),  $13.70 \pm 0.35$ ; breadth of braincase ( $n = 34$ ),  $11.69 \pm 0.25$ ; depth of braincase ( $n = 34$ ),  $14.66 \pm 0.40$ ; greatest length of mandible ( $n = 34$ ),  $18.75 \pm 0.43$ ; length of mandibular toothrow ( $n = 34$ ),  $11.21 \pm 0.25$ ; length of maxillary toothrow ( $n = 33$ ),  $10.31 \pm 0.24$ ; length of upper molariform toothrow ( $n = 34$ ),  $8.30 \pm 0.21$ ; breadth across upper canines ( $n = 33$ ),  $6.12 \pm 0.14$ ; and breadth across upper molars ( $n = 34$ ),  $10.33 \pm 0.33$ . Selected external (Mexico,  $n = 3$ —Alvarez-Castañeda and Alvarez 1991) and cranial (El Salvador,  $n = 22$ —Burt and Stirton 1961) morphometric characters (in mm; range) for *T. c. coffini* are: total length, 87.0–94.0; length of tail, 10.0–15.0; length of hindfoot, 13.0–17.0; length of ear, 20.0–30.0; length of forearm, 58.9–59.1; length of tibia, 25.3 (Guatemala,  $n = 1$ —Goldman 1925); greatest length of skull, 27.8–29.2; condylobasal length, 24.1–24.5 (Mexico and Nicaragua,  $n = 4$ —Swanepoel and Genoways 1979); zygomatic breadth, 13.3–14.2; width of postorbital constriction, 4.8–5.0 (Mexico and Nicaragua,  $n = 4$ —Swanepoel and Genoways 1979); width of least interorbital constriction, 4.8–5.3; breadth of braincase,



FIG. 1. Photograph of *Trachops cirrhosus* from Finca La Selva, Heredia Province, Costa Rica. Photograph courtesy of J. Scott Altenbach.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral 4 view of mandible of an adult male *Trachops cirrhosus* (TTU [Texas Tech University] 9779) from Blanchisseuse, Trinidad. Greatest length of skull is 30.05 mm. Photograph courtesy of Frank Yanney.

11.1–11.9; greatest length of mandible, 18.3–19.2; length of mandibular tooththrow, 9.9–10.1 (Mexico,  $n = 3$ —Alvarez-Castañeda and Alvarez 1991); length of maxillary tooththrow, 9.7–10.3; breadth across upper canines, 5.7–5.8 (Mexico,  $n = 3$ —Alvarez-Castañeda and Alvarez 1991); and breadth across upper molars, 9.3–10.0. Selected external and cranial morphometric characters (in mm; mean  $\pm$  SD for *T. c. ehrhardti* (Brazil,  $n = 3$  unless otherwise specified—Carter and Dolan 1978) are: length of ear ( $n = 1$ ), 31; length of forearm,  $58.5 \pm 2.0$ ; length of tibia,  $23.2 \pm 0.5$ ; greatest length of skull,  $28.0 \pm 0.5$ ; condylobasal length,  $24.8 \pm 0.4$ ; zygomatic breadth,  $13.8 \pm 0.4$ ; mastoidal breadth,  $13.1 \pm 0.3$ ; width of postorbital constriction,  $5.0 \pm 0.1$ ; breadth of braincase,  $11.4 \pm 0.1$ ; depth of braincase,  $13.4 \pm 0.1$ ; greatest length of mandible ( $n = 2$ ),  $17.6 \pm 0.5$ ; length of mandibular tooththrow,  $10.8 \pm 0.2$ ; length of maxillary tooththrow,  $10.1 \pm 0.2$ ; breadth across upper canines,  $5.7 \pm 0.2$ ; and breadth across upper molars,  $9.7 \pm 0.1$ .

Populations of fringed-lipped bats from northeast Brazil exhibit almost no sexual dimorphism (Willig 1983). For 29 cranial and external characters only breadth across upper canines showed secondary sexual variation at a significant level (males,  $6.18 \pm 0.12$ ,  $n = 16$ ; females,  $6.07 \pm 0.14$ ,  $n = 19$ —Willig 1983). However, multivariate analyses indicated no sexual dimorphism between sexes (Willig et al. 1986).

**DISTRIBUTION.** *Trachops cirrhosus* occurs from southern Mexico (Oaxaca), to the Guianas, as well as in parts of Brazil, Bolivia, Ecuador, and Trinidad (Fig. 3—Koopman 1993). *T. c. cir-*



FIG. 3. Geographic distribution of *Trachops cirrhosus*. Sub-species ranges are indicated by numbers: 1, *T. c. cirrhosus*; 2, *T. c. coffini*; 3, *T. c. ehrhardti*. Type localities for each subspecies are indicated by black circles.

*rhosus* occurs in Costa Rica and southward through most of the South American range of the species; *T. c. coffini* occurs from Mexico to Nicaragua; and *T. c. ehrhardti* occurs in southern Brazil and Bolivia (Jones and Carter 1976).

*Trachops cirrhosus* generally occurs at lower elevations (<500 m). In Venezuela, it occurred below 500 m (Eisenberg 1989) and was found from sea level to 330 m in Belize (McCarthy 1987). In Chiapas, Mexico, *T. cirrhosus* was found at sites with an average elevation of 300 m (Medellín 1994). No fossils are known for the fringe-lipped bat.

**FORM AND FUNCTION.** Dental formula of *T. cirrhosus* is  $i\ 2/2$ ,  $c\ 1/1$ ,  $p\ 2/3$ ,  $m\ 3/3$ , total 34 (Goodwin and Greenhall 1961). The I2 is small (Ruschi 1953), and I1 and I2 form a continuous row between canines (Goodwin and Greenhall 1961). I1 and I2 are large and slightly notched (Dobson 1878). The p2 is small and located internal to the tooththrow (Dobson 1878). Molars have tubercular depressions on cusps (Ruschi 1953), which are W-shaped (Dobson 1878).

Brain of *T. cirrhosus* is modified highly compared with other phyllostomines. Cerebral hemispheres are relatively long, and sulci anterior to relatively shallow pseudocentral sulci are deep. As in other phyllostomids, *T. cirrhosus* has well-developed olfactory bulbs and a broad medulla oblongata. Inferior colliculi are exposed dorsally and contiguous middorsally. Cerebellum is simple in appearance. Vermiform body of cerebellum has secondary foliation at its lateral edge and protrudes anteriorly to cover posterior portions of inferior colliculi (McDaniel 1976).

Ear is highly modified for low-frequency hearing. Outer ear consists of a large pinna, which enhances detection of sounds at lower frequencies and intensities. The large pinna also allows accurate lateralization, to help localize a particular sound (Obrist et al. 1993). Middle ear contains an intermediate sized eardrum ( $3.8\ \text{mm}^2$ ), which aids perception of both high- and low-frequency sounds. Cochlea is relatively large (3.25 turns) and contains structural elements that suggest sensitivity to a wide range of frequencies. Basilar membrane is remarkably long (14.5 mm) and may extend the overall frequency range of hearing compared to other phyllostomids. A high density of cochlear receptors (121.5 inner hair cells/mm) exists on apical half of the organ of Corti, which may be an adaptation for sensitivity to low-frequency sounds. In addition, *T. cirrhosus* has a large number (40,500) of cochlear neurons in the spiral ganglion (Brunns et al. 1989).

Echolocation calls of *T. cirrhosus* reflect adaptations for orientation and location of prey in dense, cluttered environments (Belwood 1988). The fringe-lipped bat produces broad-bandwidth calls of low intensity and short duration to orient and locate prey in heavy clutter, although analysis of echolocation calls is complicated because bats continue to call even when using prey-generated cues to locate food (Neuweiler and Fenton 1988). This observation, along with the wide range of frequencies heard by *T. cirrhosus*, indicates that it uses echolocation as well as prey-generated cues to locate potential food items. Echolocation calls are of short duration (0.58 ms), and comprise 2 to 4 harmonically related, frequency-modulated pulses, with a frequency sweep of ca. 25–13 kHz (Barclay et al. 1981). Pulses of low intensity (<70 dB) are produced in flight every 25 ms, but rates can increase in final stages of prey attack to ca. 12.5 ms (Barclay et al. 1981).

The manner in which *T. cirrhosus* forages may be reflected in its noseleaf morphology. Noseleaf of *T. cirrhosus* has a well-developed horseshoe but a comparatively small spear because auditory cues, rather than echolocation, usually are used to locate prey (Arita 1990). However, the importance of noseleaf morphology on foraging is contested (Bogdanowicz et al. 1997).

Cellular morphology of accessory submandibular glands is unusual. Secretion by follicular cells involves cytoplasmic bodies, and mitochondria within these cells frequently have intracrystalline structures. Follicles and ducts are innervated heavily by hypolemmal nerve terminals. Structure of accessory submandibular glands may be an adaptation to consumption of anurans, many of which produce epithelial toxins. Follicles within salivary glands store large amounts of preformed saliva, which may be released to counter frog toxins (Tandler et al. 1997).

*Trachops cirrhosus* has a low wing-aspect ratio (leading edge of wing is short compared to total wing area) and high wing loading (body mass is high compared to total wing area) compared with other bats (Smith and Starrett 1979). Thus, *T. cirrhosus* must fly faster than do other bats to maintain lift. Also, *T. cirrhosus* has a higher tip index (third digit is longer than forearm) than do other bats; this reduces drag, and enhances speed and maneuverability in flight (Smith and Starrett 1979).

**ONTOGENY AND REPRODUCTION.** *Trachops cirrhosus* breeds during the dry season (January–June) in the tropics (Willig 1985; Wilson 1979). Pregnant females have been collected in Oaxaca, Mexico, during March (Villa-R. 1967); in Chiapas, Mexico, during March, April, and December (Alvarez-Castañeda and Alvarez 1991; Carter et al. 1966; Villa-R. 1967); in Guatemala during March and April (Jones 1966); in El Salvador during February (Burt and Stirton 1961); in Nicaragua during May (Carter et al. 1966); in Panama during August (Fleming et al. 1972); in Trinidad during March (Goodwin and Greenhall 1961); in Peru during July (Tuttle 1970); in Venezuela during February and June (Ibañez 1981); and in Brazil during January and February (Willig 1985). In Mexico, the reproductive pattern of *T. cirrhosus* is bimodal polyestry, with pregnant females captured in March, May, and December (Sánchez-Hernández and Romero-Almaraz 1995). Lactating females have been collected in Brazil during March, April, and May (Willig 1985); in Honduras during August (Valdez and LaVal 1971); in Venezuela during May (Ibañez 1981); and in Costa Rica during March and August (Armstrong 1969; Carter et al. 1966). Additionally, evidence of postpartum estrus exists for Venezuelan bats in February (Ibañez 1981). Females generally have 1 offspring per litter (Alvarez-Castañeda and Alvarez 1991; Burt and Stirton 1961; Carter et al. 1966; Fleming et al. 1972; Jones 1966; Tuttle 1970). In Guatemala, embryos were carried in the left uterine horn (Jones 1966). Crown–rump measurements of embryos range from 13 to 34 mm (Carter et al. 1966; Fleming et al. 1972; Jones 1966; Tuttle 1970). Although little detailed information is available concerning embryonic development, parturition, or parental care, some evidence indicates that young associate with a parent for a considerable period (Eisenberg 1989).

Breeding males have been reported from Trinidad during December (Goodwin and Greenhall 1961) and Ecuador during February (Albuja 1982). In Ecuador 3 males had descended testes measuring (length by width in mm) 7 by 5, 7 by 6, and 8 by 6 (Albuja 1982).

**ECOLOGY AND BEHAVIOR.** *Trachops cirrhosus* occurs in tropical dry and moist forests (Fleming et al. 1972; Handley

1976; Jones 1966; Valdez and LaVal 1971; Willig and Mares 1989) and sometimes near ponds or streams (Fleming et al. 1972; Handley 1976; Krull and Kalko 1994; Starrett and Casebeer 1968; Tuttle 1970). In the semiarid Caatinga, *T. cirrhosus* was captured in areas containing rock outcroppings or small granitic mountains (Willig 1983).

*Trachops cirrhosus* roosts mainly in trees and hollow logs (Armstrong 1969; Goodwin and Greenhall 1961; Handley 1976; Krull and Kalko 1994; Kunz 1982; Patterson 1992), but has roosted in caves (Jones 1966), culverts (Handley 1976; Starrett and Casebeer 1968), buildings (Tuttle 1976), and an abandoned railroad tunnel (Starrett and Casebeer 1968). This species shares roosts with many other species of bats, including *Desmodus rotundus*, *Diphylla ecaudata*, *Tonatia brasiliense*, *Miconycteris megalotis*, *Glossophaga soricina*, *Anoura geoffroyi*, *A. caudifer*, *Carollia perspicillata*, *Saccopteryx leptura*, *S. bilineata*, *Macrophyllum macrophyllum*, *Lonchorhina aurita*, *Lonchophylla mordax*, *Mimon bennettii*, *Myotis nigricans*, *Tadarida espiritosantensis*, and *Pteropteryx kappleri* (Goodwin and Greenhall 1961; Marques 1985; Perotti 1953). *T. cirrhosus* roosts in groups of up to 50 individuals (Hall and Dalquest 1963), and both sexes may roost together (Nowak 1999).

*Trachops cirrhosus*, is considered an opportunistic foliage-gleaning omnivore (Humphrey et al. 1983) that consumes whatever it can capture and overpower (Pine and Anderson 1979). It mainly feeds on insects (Fleming et al. 1972), especially coleopterans (*Diploptaxis* and *Phyllophaga*—Belwood 1988; Humphrey et al. 1983; Pine and Anderson 1979; Whitaker and Findley 1980), and, to a lesser extent, orthopterans (Belwood 1988; Gardner 1979). However, *T. cirrhosus* will consume lizards (Pine and Anderson 1979), such as geckos and anoles (Goodwin and Greenhall 1961; Valdez and LaVal 1971; Whitaker and Findley 1980). On Barro Colorado Island, Panama, *T. cirrhosus* preys on the frog *Physalaemus pustulosus* (Barclay et al. 1981; Tuttle and Ryan 1981). In addition, *T. cirrhosus* may prey on the bat *Artibeus jamaicensis* (Morrison 1975), although this is unlikely based on its foraging behavior and similarity in size. The fringed-lipped bat also consumes fruit and seeds (Humphrey et al. 1983; Whitaker and Findley 1980).

Based on analyses of rarity indices, *T. cirrhosus* is a common member of most Neotropical bat communities (Arita 1993). *T. cirrhosus* is a common (100–999 individuals) member of the bat community at Barro Colorado Island in Panama (Kalko et al. 1996) and in the Brazilian Caatinga (Willig 1983; Willig and Moulton 1989). During a 7-year period on Barro Colorado Island, Panama, *T. cirrhosus* exhibited small year-to-year fluctuations in population size (Kalko et al. 1996).

Ectoparasites of *T. cirrhosus* (Webb and Loomis 1977) include species of Trombiculidae (Mexico), Labidocarpidae (Suriname), Streblidae (Panama and Guatemala), Argasidae, and Spinturnicidae (Venezuela and Panama). In Panama (Wenzel and Tipton 1966), arthropods known to parasitize *T. cirrhosus* include spinturnicid mites (*Periglischrus tiptoni* and *P. vargasi*—Furman 1966), ixodid ticks (*Ornithodoros brodyi* and *O. hasei*—Fairchild et al. 1966), and streblid batflies (*Speiseria ambigua*, *Strebla altmani*, *S. carrolliae*, *S. (?) mirabilis*, *Trichobius dugesii*, *T. dugesioides*, and *T. joblingi*—Wenzel et al. 1966). However, the population of *Strebla mirabilis* on *T. cirrhosus* may represent a separate, cryptic species (Wenzel et al. 1966). Endoparasites (Ubelaker et al. 1977) include the nematode *Tricholeiperia leiperi* and the protozoan *Trypanosoma (vespertilionis-type)*.

Few species prey on *T. cirrhosus*, although the gray four-eyed opossum, *Metachirops opossum*, will take fringe-lipped bats, and the false vampire bat, *Vampyrum spectrum*, may prey on *T. cirrhosus* (Barclay et al. 1981). Other gleaning omnivores of similar size that are sympatric with *T. cirrhosus* are potential competitors. These include *Mimon crenulatum*, *Tonatia bidens*, and *Tonatia silvicola* (Humphrey et al. 1983). *T. cirrhosus* and *Tonatia silvicola* may partition the acoustic environment (Tuttle et al. 1985). In northeastern Brazil, *Phyllostomus discolor* has similar feeding habits to those of *T. cirrhosus*; however, the former consumes more fruit, whereas *T. cirrhosus* consumes more animal material, making competition between these species negligible (Willig 1986).

The fringe-lipped bat uses echolocation as well as prey-generated acoustic cues to locate food (Barclay et al. 1981). It responds to relatively low frequencies (<5 kHz) characteristic of frog calls (Barclay et al. 1981; Ryan et al. 1983). Moreover, *Trachops* can discriminate among calls of different anurans (Ryan and Tuttle

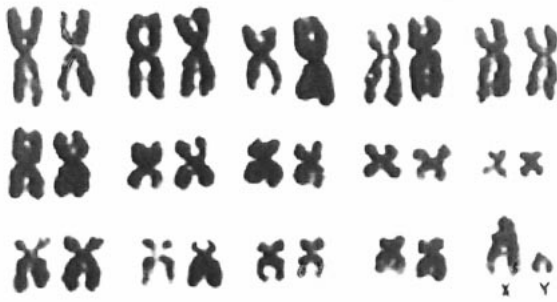


FIG. 4. Idiogram of male *Trachops cirrhosus*, courtesy of Robert J. Baker.

1983). Bats approached speakers playing prerecorded calls of a nonpoisonous frog (*Hyla boulengeri*) more often than calls of a poisonous toad (*Bufo typhonius*). Additionally, bats responded more often to calls of a small, easily handled frog species (*Physalaemus pustulosus*), than to a species (*Leptodactylus pentadactylus*) too large for it to capture (Tuttle and Ryan 1981). Predation by *T. cirrhosus* probably influenced the evolution of frog vocalization in the tropics (Tuttle and Ryan 1981). For example, male *P. pustulosus* stop calling when foraging *T. cirrhosus* are detected (Tuttle et al. 1982). Both wing morphology and evidence that it utilizes prey-generated cues to locate prey indicate that *T. cirrhosus* forages while in flight and generally consumes nonairborne prey (Fenton 1990). In contrast, information from radio-tracking suggests that this bat may employ a sit-and-wait foraging strategy (Kalko et al. 1996; Krull and Kalko 1994).

**GENETICS.** Karyotype of *T. cirrhosus* (Fig. 4) is similar to that of *Macrotus* and *Phyllostomus*. It has a diploid number of 30 and a fundamental number of 56. All autosomes are biarmed, the X chromosome is a large submetacentric, and the Y chromosome is a small acrocentric (Baker 1967).

**REMARKS.** The name *Trachops cirrhosus* is derived from the Greek *trach* meaning "harsh" and *ops* meaning "eye." The specific epithet, *cirrhosus*, is derived from the Greek word *kirros* meaning "yellow brown." *T. cirrhosus* is also known as the frog-eating bat (Tuttle 1982), but use of this particular name is discouraged, because the fringe-lipped bat eats frogs only in a limited portion of its range (Barro Colorado Island, Panama).

Although classically included in the subfamily Phyllostominae, immunologic, morphologic, chromosomal, and restriction-site evidence suggest that the genus *Trachops* belongs to a monophyletic group including *Vampyrum* and *Chrotopterus* (Baker et al. 1989; Honeycutt and Sarich 1987; Van Den Bussche 1992). This clade is recognized as the subfamily Vampyrinae by Baker et al. (1989).

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