SYNOPSIS OF SOUTH AMERICAN BATS OF THE FAMILY EMBALLONURIDAE

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Bats of the family Emballonuridae occur in tropical and subtropical regions of the New World (northern Mexico south to southern Brazil) where the family is represented by two subfamilies, eight genera, and 18 species. Representatives occur also from Africa eastward through the Arabian Peninsula and the Indian subcontinent to southeastern Asia and the Australian region. All eight American genera and 16 of the 18 Neo-tropical species are known certainly from South America. All are insectivorous.

Characteristics of emballonurids include: second manual digit consisting of the metacarpal only and third digit with only two phalanges, the second longer than the first; calcar relatively long; tail slender and about half the length of the uropatagium, which it perforates dorsally; muzzle without special cutaneous outgrowths; well-developed postorbital processes (except Diclidurus); premaxillae incomplete, represented by nasal branches only, which are never fused with each other or with the maxillae. There is a wing sac (Fig. 1) in the antebrachial membrane of some species (may be rudimentary in females). The dental formula of all American taxa is 1/3, 1/1, 2/2, 3/3, total 32; a baculum is present. A key to American genera is given below.

1. Postorbital processes broad, nearly obliterated by markedly broadened supraorbital ridges; rostrum distinctly and deeply dished; color whitish to pale brownish white ........................................ Diclidurus

1'. Postorbital processes slender and well developed; rostrum not dished (except in Cyttarops); color other than whitish ........................................ 2
FIG. 1.—Wing sacs of emballonurid genera occurring in South America (after Sanborn, 1937). *Peronymus* now is regarded as a subgenus of *Peropteryx*.
2. Clavicle expanded medially, width about one-third length; rostrum dished; anterior upper premolar relatively large, essentially filling gap between canine and posterior premolar ............ *Cyttarops*

2'. Clavicle not expanded medially, width about one-sixth length; rostrum not dished; anterior upper premolar small, often a simple spicule, not filling gap between canine and posterior premolar ............ 3

3. Anterior upper premolar laterally flattened or slightly triangular; calcar much longer than tibia; forearm furred with small tufts of whitish hairs ...................... *Rhynchonycteris*

3'. Anterior upper premolar rounded or spiculelike; calcar about same length as tibia; forearm essentially naked ............. 4

4. Anterior upper premolar rounded, tricuspidate; wing sac absent or, if present, long (extending from anterior border of antebrachial membrane almost to elbow) and opening distally ............ 5

4'. Anterior upper premolar spiculelike; wing sac present, small except in *Saccopteryx* in which it opens dorsally ............. 6

5. Wing sac absent; sagittal crest indistinct ........... *Centronycteris*

5'. Wing sac present (described in 4 above); sagittal crest pronounced, extending onto postorbital processes ............. 7

6. Distal part of rostrum with distinct dorsal inflations, separated by evident median depression; known only from northwestern Ecuador ..................... *Balantiopteryx*

6'. Distal pan of rostrum smooth; distribution not including western Ecuador (except *Saccopteryx bilineata*) ............. 7

7. Basisphenoidal pit divided by median septum; dorsum with two more-or-less distinct whitish or buffy longitudinal lines ..... *Saccopteryx*

7'. Basisphenoidal pit not divided by median septum; dorsum not lined .. ............. *Peropteryx*

In the following accounts, genera and subgenera are arranged in conventional phylogenetic sequence following Eisenberg (1989). Species of each genus (or subgenus) are arranged alphabetically. All measurements are in millimeters. Localities of record are listed clockwise, beginning in Venezuela; those in italic type are not plotted on the accompanying distribution map.

**Subfamily** **EMBALLONURINAE** Gervais, 1855

The distribution of this subfamily is the same as outlined above for the Emballonuridae. Of 10 Recent genera, six occur in tropical parts of the New World and four in the Old World. Sanborn (1937) reviewed American members of this group.
Characteristics of emballonurines include long, curved postorbital processes; clavicle with greatest width about one-sixth the length; tibia either subterete or with outer side flattened; rostrum more or less flattened except for inflations in _Balantiopteryx_. Wing sacs are present in four of the six American genera: _Balantiopteryx_, _Cormura_, _Peropteryx_, and _Saccopteryx_.

[Unfortunately, this manuscript was in proof stage prior to our awareness of the paper by B. D. Patterson entitled "Mammals in the Royal Natural History Museum, Stockholm, collected in Brazil and Bolivia by A. M. Olalla during 1934-1938," which was published in Fieldiana Zoology, new series, 66:1-42, 1992. This publication contains records and some natural history observations of the following six emballonurine species: _Rhynchonycteris naso_, _Saccopteryx bilineata_, _S. leptura_, _Cormura brevirostris_, _Peropteryx macrotis_, and _P. leucoptera_.]

**Genus *Rhynchonycteris* Peters, 1867**

_Proboscidea_ Spix, 1823:61; type species _Proboscidea saxatilis_ Spix, 1823, by original designation (= _Vespertilio naso_ Wied); not _Proboscidea_ Brugiere, 1791 (anematode).

_Rhynchonycteris_ Peters, 1867:477; type species _Vespertilio naso_ Wied, 1820, by monotypy.

_Rhynchiscus_ Miller, 1907fc:65; type species _Vespertilio naso_ Wied, 1820, by original designation. A renaming of _Rhynchonycteris_ based on the erroneous assumption that it was preoccupied by _Rhinchonycteris_ Tschudi, 1844 (see discussion by Husson, 1962:35-36).

_Rhynchonycteris_ is a monotypic genus that occurs from southern Mexico southward throughout most of the tropical regions of South America. The genus is characterized as follows: muzzle elongate; tufts of whitish pelage on forearm; interfemoral membrane furred to exsersion of tail; no wing sac; first upper premolar relatively large and slightly triangular in occlusal view; virtually no angle between rostrum and braincase; relatively small size (forearm usually ranging from 35 to 41). The dorsum is grizzled brownish to grayish, with two faint whitish stripes on lower back and rump; venter paler.

**_Rhynchonycteris naso_ (Wied, 1820)**

_Vespertilio naso_ Wied, 1820:25; **type locality** vicinity of Morro d’Arara, Rio Mucuri, Bahia, *Brazil* (see Avila-Pires, 1965:9).

_Proboscidea saxatilis_ Spix, 1823:62; **type locality** Rio SSo Francisco, Brazil.
Proboscidea rivalis Spix, 1823:62; type locality Rio Amazonas, Brazil.
Emballonura lineata Temminck, 1841:297; type locality Suriname.
Proboscidea villosa Gervais, 1855:68; type locality state of Goyaz, Brazil.
Rhynchonycteris naso, Peters, 1867:478; first use of current name combination.

Marginal localities of record (South America only, see Fig. 2).—

Rhynchonycteris naso currently is considered to be a monotypic species (Sanborn, 1937); however, G. M. Alien (1914) did propose the subspecific name R. n. priscus based on specimens from the Mexican state of Quintana Roo.

Natural history.—This species frequents slow-moving water courses and lakes in lowland regions (up to about 900 meters), usually roosting in groups of no more than a dozen bats (but up to 45 have been reported) in well-lighted areas on shaded cliff facings or tree trunks, beneath overhanging logs, rocks, or exposed roots, under bridges, and occasionally beneath large leaves. The underside of large trunks overhanging rivers and streams seems to be preferred. There usually is a well-defined space between roosting individuals, which frequently are arranged in vertical order; when disturbed the bats take flight, in the same linear "formation" in a rapid, weaving pattern, to another roost. Most feeding apparently takes place over water.

Gravid females have been taken in most months of the year at one place or another in the American tropics, and reproduction may be asynchronous and essentially aseasonal in Rhynchonycteris; females may produce two successive young annually (Bradbury and Vehrencamp, 1977).

Genus Saccopteryx Illiger, 1811

Saccopteryx Illiger, 1811:121; type species Vespertilio leptura Schreber, 1774, by monotypy.
FIG. 2.—South American distribution of *Rhynchonycteris naso* (left) and *Saccopteryx bilineata* (right).

*Urocryptus* Temminck, 1838:31; type species *Urocryptus bilineatus* Temminck, 1838, by monotypy,

Small- to medium-sized bats (forearm ranging from 35 to 52); females larger than males in most species. The dorsal pelage is dark gray or brown to black, with two white longitudinal lines (see key below). The wing sac is of moderate size to extremely large, located near the elbow and opening dorsally, and especially large and seasonally active in males. Wings are attached to the tarsals (to metatarsals in *S. gymnura*). Cranial characters include: only a slight angle between rostrum and braincase; premaxillae large; postorbital processes long and broad; sagittal crest well developed; basisphenoidal pit large and divided by a median septum; anterior upper premolar a tiny spicule. The genus occurs throughout Middle America (Mexico to Panama) south to Paraguay and southern Brazil, and is represented by four species, all of which occur in South America.

A key to species follows. Measurements and other key characters are based on Sanborn (1937) and Husson (1962). Davis (1976) discussed and illustrated characteristics that distinguish *Saccopteryx leptura* from *S. canescens*.
1. Wing attached to metatarsus; known only from Santarem, Para, Brazil. \textit{Saccopteryx gymnura}

1'. Wing attached to tarsus or at ankle \textldots; 2

2. Dorsal pelage and membranes black; wingiac extremely large and prominent (especially in males); length of forearm more than 43; length of maxillary toothrow usually more than 7 (6.4-7.4); greatest width across molars (M3-M3) more than 7 (7.2-7.6). \textit{Saccopteryx bilineata}

2'. Dorsal pelage uniformly brown or grayish brown; wing sac not greatly developed (more so in males); length of forearm less than 43 (see below); length of maxillary toothrow less than 6 (see below); greatest width across molars (M3-M3) less than 7 (see below) \ldots; 3

3. Dorsal pelage uniformly brown; longitudinal dorsal lines (stripes) usually distinct; length of forearm 37.4-42.3 (males 37.4-40.0, females 39.1-42.3); length of maxillary toothrow more than 5 (5.1-5.5); greatest width across molars (M3-M3) usually more than 6 (5.9-6.3) \textit{Saccopteryx leptura}

3'. Dorsal pelage gray or brown with grizzled appearance; longitudinal lines (stripes) indistinct or barely visible; length of forearm 35.8-40.8 (males 35.8-37.5, females 36.5-40.8); length of maxillary toothrow 5 or less (4.6-5.0); greatest width across molars (M3-M3) less than 6 (5.1-5.6) \textit{Saccopteryx canescens}

\textbf{Saccopteryx bilineata (Temminck, 1838)}


\textbf{Marginal localities of record} (South America only, see Fig. 2).—VENEZUELA (Handley, 1976): Zulia, near Cerro Azul, 33-39 km. NW La Paz, 75-80 m.; Falcon, Boca de Yaracuy, 28 km. WNW Puerto Cabella, 2 m.; Miranda Birongo, 60 m.; Sucre, Manacal, 26 km. ESE Caripano, 200-575 m. TRINIDAD: St. George, Caura (type locality of \textit{S. perspicillifer}). GUYANA: Essequibo, Kalacoon (Sanborn, 1937). SURINAME: no precise locality (type locality). FRENCH GUIANA: St. Elie (Brosset and Charles-Dominique, 1990: 515). BRAZIL: Amazonas, Utin, near Santerem (Sanborn, 1937); Piauhy, Deserto (Sanborn, 1937); Ceara, Floresta Nacional Araripe-Apodi, 9 km. S Crato (Mares et al., 1981); \textit{Minas Gerais, Rio Piracicaba} (Vieira, 1942); Rio de Janeiro, Rio de Janeiro (Sanborn, 1937). BOLIVI A: Santa Cruz, Rio Palometillas (Sanborn, 1937); Santa Cruz, Rio Ichilo, 52 km. S mouth Rio Chapare (Anderson et al., 1982). PERU: Cuzco, Huajyumbe near Marcapata (Sanborn, 195 la); Pasco, Oxapampa, San Juan, 900 ft. (Tuttle, 1970); Ucayali, Yarinacocha, 5 mi. NW Pucalpa (Sanborn, 1949); Tumbes, Matapalo (Koopman, 1978). ECUADOR: Guayas, Paca	an'tambo (Brosset, 1965); Napo, Limoncocha, 300 m. (Baker, 1974);
Esmeraldas, Cachabf (=Urbina) (Sanbom, 1937). COLOMBIA: Narino, IslaGorgona, sea level (Niceforo, 1947); Antioquia, Santa Teresa, near Mutata (Morales-Alcardn et al., 1968); Magdalena, Bonda (J. A. Alien, 1900).

Sanborn (1937) concluded that *S. bilineata* exhibited considerable size variation across its range, but he did not recognize geographic races. Bats from Mexico and Central America have been referred to *S. b. centralis* Thomas, 1904 (see Alvarez, 1986). We follow Husson (1962) and Carter et al. (1981) in considering *perspicillifer* from Trinidad as indistinguishable from the nominate subspecies, *S. b. bilineata*, which occurs throughout South America.

**Natural history.**—Detailed information on population dynamics, social structure, and reproduction are available for *S. bilineata* from Costa Rica and Trinidad (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976, 1977). Bats roost in colonies (up to 40 or 50 individuals) in hollow trees, in cavities within the buttresses of large forest trees, and occasionally in caves. Roost sites are maintained for extended periods of time, but colonies move seasonally according to insect availability. Colonies consist of well-defined social units that include a single male with a harem of up to eight females. Aggressive behavior for territorial defense and mate competition is exhibited by males.

Reproduction is highly synchronized; females bear a single young from late May to mid-June in Trinidad, coinciding with the advent of the rainy season. Young females disperse at 10 to 12 weeks of age, whereas juvenile males may remain in or near the parental colony.

*Saccopteryx canescens* **Thomas, 1901**

*Saccopteryx canescens* Thomas, 1901a:366; type locality Obidos, Para, Brazil.
*Saccopteryx pumila* Thomas, 1914:410; type locality Altagracia, lower Rio Orinoco, Venezuela.

**Marginal localities of record (see Fig. 3).**—VENEZUELA (Handley, 1976): Falcón, Boca de Yaracuy, 28 km. WNW Puerto Cabello, 2 m.; Miranda, Biringa, 60 m.; Sucre, Ensenda Cauranta, 9 km. NE Guiria, 2 m. SURINAME: Saramacca, Paramaribo (Husson, 1962). FRENCH GUIANA: Isle le Pere, Cayenne (Sanborn, 1937). BRAZIL: Para, Boca de Igarape Piaba, Ilhade Marajo (Sanbom, 1937). PERU: Huanuco, Puerto Victoria, Rio Pachitea (Sanborn, 1937). COLOMBIA: Tolima, Purificacion, 30 m. (Niceforo, 1947); Bolivar, Norosi, 120 m. (HershkoVitz, 1949); Magdalena, Mamatoco, 15 m. (Sanborn, 1937); Guajira, Dibulla (Sanborn, 1937).

No Subspecies are recognized in *S. canescens*. Thomas (1914) named *S. pumila* (see above) on the basis of the size of the molars and nature
FIG. 3.—Distribution of *Saccopteryx canescens* (left) and one known locality of record for *Saccopteryx gymnura* (right).

of the basisphenoidal pit, and Cabrera (1958) treated it as a distinct species. We follow Sanbom (1937), Husson (1962), and Koopman (1982), however, in placing *S. pumila* in synonymy with *S. canescens*.

*Natural history.*—Little is known regarding the natural history of *S. canescens*. Compared with other species in the genus, which prefer densely vegetated forests, it has been captured in more open areas (Handley, 1976). Roosting colonies averaging about a dozen individuals in size may share hollows in trees or caves with other species of bats according to Eisenberg (1989).

*Saccopteryx gymnura* Thomas, 1901

*Saccopteryx gymnura* Thomas, 1901a:467; type locality Santarem, Para, Brazil.

*Marginal localities of record* (see Fig. 3).—BRAZIL: Para, Santarem (type locality)—see also Vieira (1942).

Remarks.—Known only from the type specimen and paratypes, this species may occur throughout the Amazonian River drainage system. The holotype is in poor condition, but the attachment of the wing mem-
branes to the metatarsals distinguishes it from other species of *Saccopteryx* (Sanbom, 1937; Carter and Dolan, 1978).

### Saccopteryx leptura (Schreber, 1774)

*Saccopteryx leptura* Schreber, 1774:pl. Ivii (name), 1775:173 (description); type locality Suriname.

*Saccopteryx leptura*, Peters, 1867:471; first use of current name combination.

#### Marginal localities of record (South America only, see Fig. 4).—VENEZUELA (Handley, 1976): Falcdn, Boca de Yaracuy, 28 km. WNW Puerto Cabella, 2 m.; Miranda, Birongo, 60 m.; Nueva Esparta, Isia de Margarita, El Valle (Pirlot and Le6n, 1965); Sucre, Manacal, 26 km. ESE Canipano; Bolivar, El Manaco, 59 km. SE El Dorado, 150 m. TRINIDAD: St. George, Blanchisseuse (Carter et al., 1981). GUYANA: Essequibo, 24 mi. along Potaro Rd. from Bartica (Hill, 1964). SURINAME: no precise locality (type locality); see also map in Eisenberg (1989). FRENCH GUIANA: St. Elie (Brosset and Charles-Dominique, 1990:515). BRAZIL: Ceara, Sitio Luanda, 4 km. S Crato (Mares et al., 1981); Espirito Santo, Colatina, Vieira, 1942). BOLIVIA (Anderson et al., 1982): Beni, Río Mamoré; Beni, Río Iténez, bank opposite Costa Marquez, Brazil. PERU: Cuzco, Bella Vista, Río Apurimac (Sanbom, 1937—locality restricted by Tuttle, 1970, but see Ceballos-Bendeuz, 1968); Junín, Chanchamayo, neart Tarma, ca. 3000 ft. (Thomas, 1893); Ucayali, Yarinacocha, 5 mi. NW Pucalpa (Sanbom, 1949). ECUADOR: Napo, Avila, 450-500 m. (Albuja, 1983); Napo, Santa Cecilia, 340 m. (Webster and Jones, 1984). COLOMBIA: Tolima, Espinal (Niceforo, 1947); None de Santander, Río Zuila (Niceforo, 1947); Magdalena, Santa Marta (Bangs, 1900); Guajira, Villanueva, 274 m. (Hershkovitz, 1949).

#### Natural history.—Population structure, social behavior, and reproduction have been extensively studied by Bradbury and Emmons (1974) and Bradbury and Vehrencamp (1976, 1977). The biology of *S. leptura* is remarkably different than that of *S. bilineata*. The species prefers more open roost sites, having been observed in shallow depressions on tree trunks. *S. leptura* roosts singly or in small groups (up to nine individuals) and apparently is monogamous. Groups change location of roost sites frequently and the composition of groups can change over time. Males do not actively defend individual territories or exhibit special behavior for attracting mates. Nonetheless, *S. leptura* does maintain group foraging territories that are actively defended. Females may produce two successive young per year (Bradbury and Vehrencamp, 1977).

### Genus Cormura Peters, 1867

*Cormura* Peters, 1867:475; type species *Emballonura brevirostris* Wagner, 1843, by monotypy.
FIG. 4.—South American distribution of *Saccopteryx leptura* (left) and *Cormura brevirostris* (right).


Size medium for emballonurines, feet short; length of head and body 50 to 60, forearm 43 to 50. The dorsal pelage is blackish brown to reddish brown, whereas the underparts are paler. The wing sac is in the center of the antebrachial membrane, long, extending from the anterior border almost to the elbow, and opening distally. The wings are attached to the metatarsals. Cranial characters include: rostrum short and broad; no angle between rostrum and braincase, orbits and zygoma broad; postorbital processes short; sagittal crest well developed and extending onto postorbital processes; basisphenoidal region without marked pitting or median septum; anterior upper premolar rounded, with distinct anterior posterior cusps.

*Myropteryx* Miller, 1906, has been considered as distinct from *Cormura* (Miller, 1907a; Sanbom, 1937), but we place *Myropteryx pullus* in synonymy with *C. brevirostris* following Thomas (1913), Cabrera (1958), Husson (1962), and Carter and Dolan (1978), and the genus thus is monotypic. It occurs from South America northward to southern Mexico.
Cormura brevirostris (Wagner, 1843)

Emballonura brevirostris Wagner, 1843:367; type locality Bananerira, Rio Mamore, Rondônia, Brazil (see Caner and Dolan, 1978:19).

Cormura brevirostris, Peters, 1867:475; first use of current name combination.

Myropteryx pullus Miller, 1906:59; type locality Suriname.

Marginal localities of record (South America only, see Fig. 4).—VENEZUELA (Handley, 1976): Sucre, Manacal, 26 km. ESE Carupano; Bolivar, 40 km. NE Icabaru, 964 m. GUYANA: Essequibo, 24 mi. on Potaro Rd. from Bartica (Hill, 1964). SURINAME (Husson, 1962): Marowijne, Coppenname River above Kaaimanston; Marowijne, Galibi, mouth of Marowijne River. FRENCH GUIANA: St. Elie (Brosset and Charles-Dominique, 1990:516). BRAZIL: Para, Belem (Handley, 1967); Rondônia, Bananeira, Rio Mamore (type locality).


As noted above C. brevirostris is monotypic. Husson (1962) carefully considered the taxonomic status of Myropteryx pullus Miller and placed it as a junior synonym of C. brevirostris. There is no compelling evidence to recognize geographic races in the species.

Natural history.—Little is known regarding the biology of this rare emballonurid. Specimens have been taken from hollow trees in Suriname (Sanbom, 1941) and Peru (Tuttle, 1970), and in hollow trees and logs in Venezuela (Handley, 1976). Most individuals known from Venezuela have been taken at elevations below 500 meters.

Fleming et al. (1972) examined the stomachs of nine bats from Costa Rica; all contained remains of insects. In Panama, pregnant females have been collected in April and May, whereas nonpregnant females have been taken in June, July, September, and October (Fleming et al., 1972).

Genus Peropteryx Peters, 1867

Peropteryx Peters, 1867:472; type species Vespertilio caninus Wied, 1821 (=Emballonura macrotis Wagner), by original designation.


These are small- to medium-sized bats (head and body 45 to 55, forearm 38 to 54); females are larger than males in most body dimensions (see key below). The dorsal pelage ranges in color from dark buffy brown to dark blackish brown, underparts paler. The wing sac is
small and located near the anterior border of the antebrachial membrane, opening distally. The wing is attached to the tibia. The skull has an expanded rostrum, a distinct angle between the rostrum and forehead, relatively short postorbital processes, a basisphenoidal pit that is not divided by a median septum, and a spiculelike anterior upper premolar.

The genus contains three species representing two subgenera, *Peropteryx* and *Peronymus*. Some workers have recognized the latter as a distinct genus (Miller, 1907a; Sanborn, 1937; Husson, 1962; Linares, 1986; Brosset and Charles-Dominique, 1990), but we follow recent treatments that have placed *P. leucopterus*, the lone representative of *Peronymus*, as a species within the genus *Peropteryx* (Cabrera, 1958; Honacki et al., 1982; Koopman, 1982, 1984). Two species, *P. kappleri* and *P. macrotis*, occur northward to southern Mexico, whereas *P. leucopterus* is known only from South America.

In the following key to South American species, measurements and other key characters are based on Sanborn (1937) and Husson (1962). Measurements for specimens recently reported from Suriname (Genoways et al., 1981), Ecuador (Albuja, 1983), Brazil (Willig, 1983), and Venezuela (Eisenberg, 1989) are in accord with those used here.

1. Wing white beyond forearm; ears connected by a low band across forehead; pterygoid pits large ........... *Peropteryx leucopterus*

1'. Wings black, ears separate, not connected across forehead; pterygoid pits small .................................. 2

2. Smaller, length of forearm 38.3-48.2 (males 38.3-44.3, females 43.5-48.2); greatest length of skull 15 or less (12.0-15.0); length of maxillary toothrow less than 6.5 (4.6-6.2); greatest width across molars (M3-M3) less than 7 (5.5-6.8) ....... *Peropteryx macrotis*

2'. Larger, length of forearm 45.0-53.6 (males 45.0-51.0, females 47.9-53.6); greatest length of skull 16 or more (16.0-17.1); length of maxillary toothrow more than 6.5 (6.8-7.8); greatest width across molars (M3-M3) 7 or more (7.0-8.3) ........... *Peropteryx kappleri*

*Peropteryx kappleri* Peters, 1867

*Peropteryx Kappleri* Peters, 1867:473; type locality Suriname.

Marginal localities of record (South America only, see Fig. 5).—VENEZUELA (Handley, 1976): Falc6n, Riecito, 30 km. SW Mirimire, 300 m.; Monagas, San Agustfn, 3 km. SW Caripe, 854 m. SURINAME: no precise locality (type locality—see Husson, 1962). BRAZIL: Bahia, Salvador (Vieira, 1955); Rio de Janeiro, Terezopolis (Vieira, 1942); Sao Paulo; Sao Sebastiao (Sanbom, 1937; Vieira, 1942). PERU: Cuzco, Quispicanchis, Hacienda Cadena (type locality of *P. k. intermedius*—Sanbom, 1951ft); Pasco, OXapampa, San Juan, 900 ft. (Tuttle,
Two subspecies are recognized, *Peropteryx kappleri kappleri* Peters, 1867 (type locality listed above), and *Peropteryx kappleri intermedius* Sanborn, 1951:&476 (type locality Hacienda Cadena, Quispicanchus, Cuzco, Peru). The latter is known only from its type and locality, whereas *P. k. kappleri* occupies the remainder of the geographic range in South America.

**Natural history.**—Specimens have been taken at elevations from sea level to 1500 meters in shallow caves, rock crevices, hollow trees, and fallen logs. The species prefers evergreen forested areas, but tolerates drier habitats, and will forage over open clearings and fields. Mating is based on a monogamous pair system, and the male defends the female against other males. Births have been recorded from March to December (Arata and Vaughan, 1970; Bradbury and Vehrencamp, 1976; Rasweiler, 1982). A detailed histological study of a population in Colombia demonstrated a highly synchronous breeding season (Rasweiler, 1982). A peak of births occurred there during the March-May rainy season in the Cauca Valley; bats conceived in May and June were born from October to December.

**Peropteryx macrotis** (Wagner, 1843)

*Vespertilio caninus* Wied, in Schinz, 1821:179; type locality restricted to Timicui, Rio Belmonte, Bahia, Brazil, by Avila-Pires, 1965:8; preoccupied by *V. caninus* Blumenbach, 1797.


**Peropteryx macrotis**, Peters, 1867:472; first use of current name combination.

**Marginal localities of record** (South America only, see Fig. 5).—

**VENEZUELA** (Handley, 1976): Falc6n, Riecito, 3 km. S Mirimire, 300 m.; Miranda, Bironga; Nueva Esparta, Isia de Margarita, El Valle (Smith and Genoways, 1974). **TRINIDAD**: Port-of-Spain (type locality of *P. m. trinitatus*). **TOBAGO**: Robinson Crusoe's Cave (Goodwin and Greenhall, 1961). **SURINAME**: Saramacca, Voltzberg, 10 m. (Genoways et al., 1981). **FRENCH GUIANA**: St. Elie (Brosset and Charles-Dominique, 1990:516). **BRAZIL**: Piauhy, Arara (Sanborn, 1937); Rio Grande de Norte, Natal (Sanborn, 1937); Bahia, Facenda Lajeido, km. 147 on Route BA 130 (Mares et al., 1981); Rio de Janeiro, Angra dos Reis (Peracchi and Albuquerque, 1971); Sao Paulo, Iguape (Vieira, 1942.) **PARAGUAY**: Alto Paraguay, Fuerte Olimpo (Meyers et al., 1983); Concepcion, 1 km. NE San Lazaro (Meyers et al., 1983). **BOLIVIA**: Beni, Versalles (Anderson et al., 1982). **PERU**: Puno, La Pampa (Sanborn, 195 vhl); Pasco, Oxpampa, San Juan, 900 ft. (Tuttle, 1970); Ucayali, Lagarto, Rio Ucayali (Thomas, 1920a); San Martin, no precise

Three subspecies are recognized. The nominate race is found on the island of Tobago, the South American mainland, and in Central America, whereas Peropteryx macrotis trinitatus (Miller, 1899:178), type locality, Port-of-Spain, Trinidad, is known from Trinidad, adjacent Venezuela, and coastal French Guiana. It was regarded by Handley (1976) and Brosset and Charles-Dominique (1990) as a distinct species, and its status is deserving of continued study. A third subspecies, P. m. phaea, occurs on the Antillean island of Grenada.

Natural history.—This bat is widely distributed in South America, including the islands north of Venezuela. It inhabits small caves, rocky crevices, and tree hollows where it has been found roosting in small groups (Tamsitt and Valdivieso, 1963; Genoways et al., 1981; Mares et al., 1981; and Brosset and Charles-Dominique, 1990), most often in evergreen forest. The social organization of these groups has not been described. Willig (1985) noted pregnant females in September and
October and lactating females in January in the Caatingas of northeastern Brazil.

**Peropteryx leucopterus** Peters, 1867

*Peropteryx leucoptera* Peters, 1867:474; type locality Suriname.

*Peropteryx leucopterus* Peters, 1868:145; first use of current name combination.

*Peronymus cyclops* Thomas, 1924:531; type locality Tushemo [=Tushma], near Masisea, R(o Ucayali, Ucayali, Peru.

**Marginal localities of record (see Fig. 6).—**VENEZUELA: Amazonas, Buena Vista, Rio Casiquiare (Sanborn, 1937). SURINAME: Para, Zanderij (Genoways et al., 1981). FRENCH GUIANA: St. Elie (Brosset and Charles-Dominique, 1990:516). BRAZIL: Para, Ihia de Marajó, Cahcoeira (=Arariuna) (Vieira, 1942); Para, Camet^ (Thomas, 1920A); Pernambuco, Rio Formoso, Saltinho (Guerra, 1980). PERU: Ucayali, Tushma, near Masisea (type locality of *P.cyclops*). COLOMBIA: Meta, Campamento Chamusa (=Campamento Izawa), 250 m. (Lemke et al., 1982).

Two subspecies currently are recognized. *P. I. cyclops* is known only from the type locality in Peru (Sanborn, 1937), whereas *P. I. leucopterus* occurs elsewhere in the known range of the species.

**Natural history.**—This species is a lowland bat that has been collected along streambanks, from within hollow trees, and in mist nets (Sanborn, 1937; Genoways et al., 1981; Lemke et al., 1982). Little is known regarding reproductive patterns but Sanborn (1937) reported pregnancies in March, April, May, and June from Brazil. In Suriname, Genoways et al. (1981) mist-netted the following species with their one specimen: *Cormura brevirostris*, *Saccopteryx leptura*, *Phyllostomus discolor*, *P. elongatus*, *Tonatia silvicola*, *Trachops cirrhosus*, *Artibeus* sp., and *Eptesicus brasiliensis*.

**Remarks.**—Thomas (1924) named *P. cyclops* on the basis of a single individual and no additional specimens have been obtained. It seems probable that additional material from Peru will demonstrate that *P. leucopterus* is monotypic (Sanborn, 1937).

**Genus Centronycteris** Gray, 1838

*Centronycteris* Gray, 1838:499; type species *Vespertilio calcaratus* Wied, 1821 (=V<*maximiliani* Fischer, 1829), by original designation.

The dorsal pelage of *Centronycteris* is long and soft, raw umber to tawny in color; the underparts are paler, and the interfemoral membrane and fur between the eyes are reddish. No wing sac has been reported;
FIG. 6.—Distribution of *Peropteryx leucopterus* (left) and South American distribution of *Centronycteris maximiliani* (right).

Wings are attached to the metatarsals. There is no angle between the rostrum and braincase; the lower border of the orbits is not expanded as in most emballonurids so the toothrows are visible from above; postorbital processes relatively short; sagittal crest indistinct; basisphenoidal pit well developed and divided by a median septum. The anterior upper premolar is tricuspidate, with distinct anterior and posterior cusps.

The genus is monotypic (Sanborn, 1937; Husson, 1962). It is known from widely scattered records from southern Mexico southward to Peru and eastern Brazil.

**Centronycteris maximiliani** (Fischer, 1829)


*Vespertilio. maximiliani* Fischer, 1829:112-113; renaming of *V. calcaratus* Wied, 1821, preoccupied by *V. calcaratus* Rafinesque, 1818.

*Saccopteryx wiedi* Palmer 1898:110; renaming of *K calcaratus* Wied, 1821, but antedated by *V. maximiliani* Fischer, 1829.

*Centronycteris maximiliani*. Miller, 1907a:91; first use of current name combination.
Centronycteris centralis Thomas, 1912:638; type locality Bogava, Chiriqui, Panama.

Marginal localities of record (South America only, see Fig. 6).—VENEZUELA: Amazonas, locality mapped by Eisenberg (1989). SURINAME: Saramacca, Tibiti River (Husson, 1978); Marowijne, Oelemarie (Williams et al., 1983). BRAZIL: Para, Utinga, near Belem (Thomas, 1913); Espírito Santo, Rio Jucu, near Rio Espírito Santo (type locality); Amazonas, Sitio Isidore, near Tefé (Sanbom, 1937). PERU: no precise locality (Tuttle, 1970). ECUADOR: Mera, Rio Alpuyuca (Sanborn, 1937); Esmeraldas, Rio Toachi, (Albuja, 1983). COLOMBIA: Cordoba, Rio Ure (Lemke et al., 1982).

Two subspecies currently are recognized, but virtually nothing is known of geographic variation in this bat. The subspecies are: Centronycteris maximiliani maximiliani (Fischer, 1829), known only from the type locality listed above; Centronycteris maximiliani centralis Thomas, 1912, type locality listed above, which occurs throughout the known range of the species except in the vicinity of the type locality of C. m. maximiliani (Thomas, 1912; Sanborn, 1937; Husson, 1962).

Natural history.—This bat is uncommon and information regarding natural history is limited to reports involving individual specimens. One from Ecuador was found in a hole in a tree (Sanbom, 1937). Apparently a lowland species, C. maximiliani inhabits tropical and subtropical rainforests (Baker and Jones, 1975; Greenbaum and Jones, 1978; Albuja, 1983; Williams et al., 1983). Williams et al. (1983) reported the following bats as captured with Centronycteris in Suriname: Pteronotus parnelli, Phyllostomus elongatus, Tonatia silvicola, Lonchothylla thomasi, Carollia perspicillata, Rhinophylla pumilio, and two species of Artibeus.

Remarks.—Thomas (1912) described C. centralis as distinct from C. maximiliani on the basis of slight overall differences in size and in possessing shorter basisphenoidal pits. Examination of material led Sanborn (1937) to conclude that the two taxa were only subspecifically distinct. Husson (1962) reviewed the characters and taxonomic history of the species.

Genus Balantiopteryx Peters, 1867

Balantiopteryx Peters, 1867:476; type species Balantiopteryx plicata Peters, 1867, by monotypy.

Small- to medium-sized bats (forearm ranging from 34 to 46 depending on species, 37.5-40.4 in known specimens from South America);
dorsal pelage ranging from dark grayish to dark brownish in color, venter slightly paler. The wing sac is located near the center of the antebrachial membrane, the opening directed proximally. The distal part of the rostrum is inflated on either side of a median depression in all species, and the rostrum also is inflated proximally in *B. infusca*; the basisphenoidal pit may or may not be divided by a median septum. The genus occurs in Middle America (Mexico south to Costa Rica, represented by two species) and in northwestern Ecuador, represented by a third species, *B. infusca*. However, one of the Middle American taxa, *B. plicata*, was listed by Cuervo Diaz et al. (1986:474) as occurring in "Costa de Colombia (Guajira, Villanueva)." We have not included *plicata* here, awaiting additional information as to its status in South America; it is not known from elsewhere on the continent or from Panama.

**Balantiopteryx infusca** (Thomas, 1897)

*Saccopteryx infusca* Thomas, 1897:546; type locality Rio Cachabi, 500 ft., Esmeraldas, Ecuador.

*Bfalanliopteryx]. infusca* Thomas, 1904:252; first use of current name combination.

**Marginal localities of record** (see Fig. 7).—Recorded only from the type locality, also known as Urbina, in northwestern Ecuador; probably occurs at least also in adjacent Colombia.

**Natural history.**—Virtually nothing is known of the natural history of this monotypic species; its northern congeners roost in caves, abandoned mines, crevices in rocks, and the like. The holotype and other known specimens of *B. infusca* were taken "from the cave in bank of R. Cachabi" (Carter and Dolan, 1978:22) on 5 January 1897.

**Remarks.**—This species is among the least known of South American bats. In the original description, it was described as similar to *B. plicata* "but rather smaller and less thickly built, much darker in color, with decidedly narrower ears, less hairy interfemoral [membrane] and no white line along the posterior edge of the wing-membrane" (Thomas, 1897:546). More recently, Hill (1987:559) characterized the cranium as follows: "As in *plicata* the braincase of *infusca* is rather elongate posteriorly and less rounded than in *io*, and there is a moderate frontal depression, less evident in *plicata* but differing quite sharply from the very slightly depressed frontal region of *io*. The rostral swellings in *infusca* differ markedly from those of its congeners. In all the rostrum is inflated anteriorly by paired dorsal swellings, more or less separated by
FIG. 7.—One known locality of record for Balantiopteryx infused (left) and South American distribution of Cytтарops alecto (right).

... a longitudinal median trough. ... The anterior rostral swellings of infusca are similar to those oplicata but in contrast to this species and to io the rostrum is more dilated posteriorly, the posterior compartments inflated and raised on each side of the median trough that extends without interruption from the narial rim posteriorly to the frontal depression." Hill also listed cranial measurements for four specimens.

Subfamily DICLIDURINAE Gray, 1866

This subfamily is confined to the New World tropics and contains two genera: Cytтарops, which is monotypic, and Diclidurus, in which four species currently are recognized. Diclidurines are characterized by a distinctly dished rostrum, prominent supraorbital ridges that extend onto the rostrum, a strong angle between rostrum and braincase, an expanded clavicle in which the greatest width is about one-third the length, a deeply grooved tibia, and no wing sac. The color varies from dark gray (Cytтарops) to pale brownish or white (Diclidurus).
Genus Cyttarops Thomas, 1913

*Cyttarops* Thomas, 1913:134; type species *Cyttarops alecto* Thomas, 1913, by original designation.

The single species of this genus, *C. alecto*, is of medium size among emballonurids (forearm 45 to 47) and has long, silky pelage that is smoky gray, sometimes almost black. Unlike *Diclidurus*, the postorbital processes are long and distinct and the uropatagium bears no specialized glands. There is no evident gap between the two upper premolars as in most other emballonurids. The known distribution extends from Nicaragua to northern South America.

*Cyttarops alecto* Thomas, 1913

*Cyttarops alecto* Thomas, 1913:135; type locality Mocajatuba, Para, Brazil (see Remarks).

Marginal localities of records (South America only, see Fig. 7).—GUYANA: Essequibo, Mazaruni River (Thomas, 1913:135). BRAZIL: Para, Mocajatuba (type locality).

Natural history.—Little information is available on the natural history of this rare monotypic species; most of what is known has been reported from Costa Rica. There (Starrett, 1972), the bats have been found in small groups (up to four individuals) as they roosted by day beneath fronds of coco palms; roosts were located in fairly open areas near buildings actively occupied by humans. Both sexes were taken in roosting groups in Costa Rica and all specimens examined were free of ectoparasites. Like all emballonurids, *C. alecto* is insectivorous. All records of this species are from coastal lowlands at elevations no higher than 300 meters.

Remarks.—Starrett (1972) attempted to locate the type locality of *C. alecto* in northeastern Brasil, and found several places in the vicinity of Belem with spellings similar to that used in the original description. "The most reasonable of these is Mocajatuba, located . . . some 40 km. east of Belem along the south bank of the Rio Guama . . .." Starrett restricted the type locality to that place.

Genus Diclidurus Wied, 1820

*Diclidurus* Wied, 1820:1629; type species *Diclidurus albus* Wied, 1820, by original designation.

*Depanycteris* Thomas, 1920fc:271; type species *Depanycteris Isabella* Thomas, 1920, by original designation. Possibly valid as a subgenus.
The genus *Diclidurus*, represented by four species (Koopman, 1982), is known to occur from Mexico southeastward to eastern Brazil. All four species occur in South America, three recorded only from the northern part of that continent. Members of this genus commonly are referred to as "ghost bats" because of their whitish coloration.

These are medium-sized to large emballonurids (forearm ranging from about 50 to 74) with relatively long, soft, whitish to pale brownish (*D, Isabellas*) pelage. The first upper premolar is small and not in contact with the second. The supraorbital ridges are more prominent and the rostrum more distinctly dished than in *Cyttarops*. The postorbital processes are indistinct and fused to the supraorbital ridges. There is a large and distinct glandular area on the uropatagium (especially prominent in males during the breeding season) at, and posterior to, the place the tail perforates the membrane, a characteristic unique to this genus. A key to the four species is given below.

<table>
<thead>
<tr>
<th>1. Color pale brownish; posterior border of palate deeply emarginate, emargination evenly rounded anteriorly and reaching to anterior end of M3</th>
<th><em>D. isabellus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1'. Color generally whitish to pale grayish white; posterior border of palate not deeply emarginate, emargination terminating far short of M3 and with anterior projection (which in <em>D. scutatus</em> is confluent with large palatine foramina)</td>
<td><em>D. albus</em></td>
</tr>
<tr>
<td>2. Length of forearm more than 70; greatest length of skull more than 20</td>
<td><em>D. ingens</em></td>
</tr>
<tr>
<td>2'. Length of forearm less than 70; greatest length of skull less than 20</td>
<td><em>D. scutatus</em></td>
</tr>
<tr>
<td>3. Forearm less than 60; length of maxillary toothrow less than 7; large palatine foramina that are confluent with posterior palatal emargination</td>
<td><em>D. albus</em></td>
</tr>
<tr>
<td>3'. Forearm more than 60; length of maxillary toothrow more than 7; no palatine foramina</td>
<td><em>D. albus</em></td>
</tr>
</tbody>
</table>

**Diclidurus albus** Wied, 1820

*Diclidurus albus* Wied, 1820:1630; type locality Canavieiras, Rio Pardo, Bahia, Brazil (see Avila-Pires, 1965:5).

*Diclidurus Freyreisii* Wied, 1821:76; type locality Canavieiras, Rio Pardo, Bahia, Brazil (based on same specimen as *D. albus*—see Carter and Dolan, 1978:23).

*Diclidurus virgo* Thomas, 1903:377; type locality Escazú, 3600 ft., San José, Costa Rica.
Marginal localities of record (South America only, see Fig. 8).—


Infraspecific variation in *D. albus* has not been studied in detail. Our arrangement, including distributional status, therefore, must be regarded as tentative. Most recent authorities seem to agree that *D. virgo*, which averages slightly larger than *albus* is no more than a subspecies of the latter.

*D. a. albus* Wied, 1820, apparently is distributed throughout the South American range of the species except for the Caribbean drainage in the north. *D. a. virgo* Thomas, 1903, evidently occurs from Mexico southeastward through Middle America to Venezuela and Trinidad (Ojasti and Linares, 1971).

**Natural history.**—Relatively little has been published concerning the biology of *D. albus* (see Ceballos and Medellín, 1988). It has been recorded as roosting singly by day, except in the breeding season, beneath the fronds of coco palms in western Mexico and on Trinidad (Goodwin and Greenhall, 1961; Sanchez and Chavez, 1984). The holotype of *albus* also was taken in such a situation (Avila-Pires, 1965). In Venezuela (Handley, 1976:12), specimens were shot in flight, most often "near stream banks and other moist areas," but also in drier sites over yards or village streets or in evergreen or cloud forest. This species evidently is seasonally migratory. It is known from elevations up to about 1500 meters.

In the breeding season, small groups consisting of a male and several females have been found roosting together; breeding takes place in western Mexico in January and February; females bear a single young in May or June (Sanchez and Chavez, 1984). As with other emballonurids, species of *Diclidurus* are insectivorous. One specimen from Trinidad tested for rabies was found to be positive (Goodwin and Greenhall, 1961).

**Remarks.**—In addition to the report of this bat listed above from an unknown locality in Suriname, Albuja (1983) mentioned a possible specimen from Ecuador. Vieira (1942, 1955) listed the occurrence of *D. albus* in the Brazilian State of Espírito Santo, but we know of no speci-
mens to substantiate that claim. Cabrera (1958) regarded *D. scutatus* as a synonym of *D. albus*.

We have followed convention in attributing the specific name *albus* to Wied. As Carter and Dolan (1978) pointed out, Oken may well have been the author.

**Diclidurus ingens** Hernandez-Camacho, 1955

*Diclidurus ingens* Hernandez-Camacho, 1955:87; type locality Puerto Leguizamo, Caqueta (=Putumayo), Colombia.

*Marginal localities of record* (see Fig. 8).—VENEZUELA: Sucre, Canipano (Ojasti and Linares, 1971); Amazonas, San Juan, Rio Manapiare, 163 km. ESE Puerto Ayacucho, 155 m. (Handley, 1976). COLOMBIA: Putumayo, Puerto Leguizamo, (type locality). VENEZUELA: Amazonas, Puerto Ayacucho, 99 m. (Handley, 1976).

*Natural history.*—Little is known of the biology of this monotypic species. Handley (1976) reported specimens collected in Venezuela as shot in flight over stream banks and in other moist areas, "in yards," and in evergreen forest. The holotype was taken in "silva higrofila" (Hernandez-Camacho, 1955).
Remarks.—*D. ingens* is, among species of *Diclidurus*, most closely related to *D. albus*, being larger and differing in some proportions from the latter but otherwise resembling it.

K. F. Koopman (personal communication) has examined specimens of *D. ingens* from Guyana and Amazonian Brazil in the collections of the Royal Ontario Museum and Carnegie Museum, respectively, which helped form our basis for mapping the distribution of this species. Insofar as we know, fewer than 10 specimens of this bat currently reside in museum collections.

**Diclidurus isabellus (Thomas, 1920)**

*Depanycteris isabella* Thomas, 1920A:271; type locality Manacapuru, Rio Solimões, Amazonas, Brazil.

*Diclidurus isabellus* Handley, 1976:12; first use of current name combination.

**Marginal localities of record (see Fig. 9).**—VENEZUELA (Handley, 1976): Amazonas, San Juan, Rio Manapiare, 163 km. ESE Puerto Ayacucho, 155 m.; Amazonas, Boca Mavaca, 84 km. SSE Esmeralda, 138 m. BRAZIL: Amazonas, Manacapuru (type locality).

**Natural history.**—As for other members of this genus, few natural history data are available. Handley (1976) reported specimens shot in flight over streams or stream banks in evergreen forest. Evidently, species of *Diclidurus* are difficult to capture in mist nets; we are unaware of any specimens taken in this manner.

Remarks.—*Diclidurus isabellus* is a monotypic species that originally was described as the sole member of the genus *Depanycteris*, which was regarded as distinct at the generic level by Cabrera (1958) and others, even though its close relationship to *Diclidurus* has been recognized. Recent authors (Handley, 1976; Koopman, 1982), however, have recognized *Depanycteris* at best at the subgeneric level. Our own analysis argues that *D. isabellus* is no more distinct than *D. scutatus* from other members of the genus and that subgeneric distinction probably is unwarranted.

**Diclidurus scutatus Peters, 1869**

*Diclidurus scutatus* Peters, 1869:400; type locality restricted to Belem, Para, Brazil, by Husson, 1962:59.

**Marginal localities of record (see Fig. 9).**—VENEZUELA (Handley, 1976); Amazonas, Puerto Ayachucó, 99 m.; Amazonas, San Juan, Rio Manapiare, 163 km. ESE Puerto Ayachucó, 155 m.; Bolivar, Icabani. GUYANA: no precise locality.
FIG. 9.—Distribution of *Diclidurus Isabellas* (left) and *Diclidurus scutatus* (right).


**Natural History.**—As in other species of this little-known genus, virtually nothing has been recorded as to the biology of *D. scutatus*. Han
dley (1976:12) reported that specimens shot in flight "near stream banks and other moist areas" and "over yards and streets in towns," in Venezuela. According to Husson (1962:62), a Mr. Bolten observed white bats, probably *D. scutatus*, "suspended from overhanging trees on the Marowjine River near Albina" in Suriname, and saw them flying in sunlight. Thomas (19206:271) listed a specimen from Belem, Brazil, as: "Caught in the old town."

**Remarks.**—*D. scutatus* is unique among diclidurine bats in having large, conjoined, posterior palatine foramina that are confluent via a narrow connection with the posterior emargination of the palate.

As noted in the account of *D. albus*, Cabrera (1958) regarded *D. scutatus* as a synonym of the former. The two bats recorded by Vieira
(1942, 1955) as *albus* from Taracua, Brazil, are so small (forearm 50) that they clearly represent *scutatus* as pointed out by Husson (1962).

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**LITERATURE CITED**


———. 1841. Monographies de mammalogie .... Leiden and Paris, 2:273-292 (published in two volumes, each containing several separately issued parts, between 1824 and 1841);


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