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Pteronotus davyi.

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Pteronotus davyi Gray, 1838

Lesser Naked-backed Bat

Pteronotus davyi Gray, 1838:500. Type locality "Trinidad."

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Mormoopidae, Genus and Subgenus *Pteronotus*. A key to the three subgenera and six species of *Pteronotus* (*davyi*, *gymnonotus* [=*suapurensis*], *parnellii*, *personatus*, *macleayii*, and *quadridens* [=*fuliginosus*]) is included in Herd (1983). Three subspecies of *P. davyi* are recognized (Smith, 1972):

P. d. davyi Gray, 1838, see above.
P. d. fulvus (Thomas, 1892). Type locality "Las Peñas, Jalisco, Mexico" (*calvus* Goodwin is a synonym).
P. d. incae Smith, 1972. Type locality "4 mi. west of Suyo, 1000 ft., Piura Province, Peru."

DIAGNOSIS. *Pteronotus davyi* (Fig. 1) is among the smallest of mormoopids. It is distinguished from the only other mormoopid of similar size (*P. personatus*) by having the wing membranes originating from the dorsal midline of the body, giving the bat a naked-backed appearance. It shares this condition (within the Microchiroptera) only with *P. gymnonotus*, from which it is readily distinguished by the sparsely distributed, long hairs on the wing membranes (Smith, 1972). *P. gymnonotus* has shorter, denser, velvety hairs on the chiropatagium and usually is larger in body size; length of forearm for *P. davyi* is <50 mm, whereas the length of forearm of *P. gymnonotus* usually is >50 mm (Herd, 1983; Smith, 1972).

GENERAL CHARACTERS. The sexes of *P. davyi* show little dimorphism in size, except in the most northern populations (Sonora), where males are significantly larger than females in length of forearm and several cranial measures (Smith, 1972). Individuals of all populations in Mexico are small, but a progressive increase in size is noticeable through Central America, with the largest individuals occurring in South America (*P. davyi incae*). The uropatagium is large, connected by long calcars to the tibiae, and extends posteriorly farther than the feet. The tail is approximately 22 mm long (18 to 25 mm) and extends two-thirds the length of the uropatagium, with the last 10 to 15 mm projecting dorsally from the uropatagial membrane. At rest, *P. davyi* flips the uropatagium forward, which may give the bat a free-tailed appearance (Fig. 1; Hill and Smith, 1984). Ranges for other measurements (in mm) are: total length, 71 to 85; length of foot, 9 to 12; length of forearm, 40.6 to 49.6 (one female *P. davyi fulvus* had a length of forearm of 51; Goodwin, 1969); length of ear from notch, 16 to 19; condylobasal length, 13.7 to 15.7; zygomatic breadth, 8.3 to 9.5; rostral breadth, 6.2 to 7.5; length of maxillary toothrow, 6.0 to 7.0; and depth of cranium, 6.7 to 8.3 (Smith, 1972). Metacarpal and phalangeal measurements for the type specimen are (in mm): thumb, 6.5; third metacarpal, 41.9; first phalanx of third finger, 8.9, second phalanx, 15.4, third phalanx, 12.7; fourth metacarpal, 35.6; first phalanx of fourth finger, 8.9, second phalanx, 10.2; fifth metacarpal, 33.0; first phalanx of fifth finger, 10.2, second phalanx, 8.9 (Dobson, 1878). Mass ranges from 6.5 to 8.2 g for males from Mexico, to 9.3 g for pregnant females (Alvarez, 1968; Bateman and Vaughan, 1974; Jiménez-Guzmán, 1968), to 10 g for *P. d. davyi* from Trinidad (Goodwin and Greenhall, 1961).

The rostrum is noticeably upturned (Fig. 2), broad in comparison to length of maxillary toothrow, and on essentially the same plane as the elongated braincase. The proximal part of the nasals are depressed, forming a distinct "basin." The premaxillaries are solidly fused with each other, the maxillary, and palatine bones. The upper incisors are reduced and a diastema is present between I2 and C. Lower incisors are trilobed and reduced (Smith, 1972) and P2 is strongly reduced (Phillips and Jones, 1968; 2 of 197 individuals examined lacked one P2). The dental formula is i 2/2, c 1/1, p 2/3, m 3/3, total 34.

DISTRIBUTION. Lesser naked-backed bats are most common in moist to dry, deciduous tropical forest at low elevations throughout the Neotropics (Fig. 3; Smith, 1972) but have a wide altitudinal tolerance. In Peru, *P. davyi* occurs at elevations up to 2,000 m (Koopman, 1978, 1982) and has been taken at 1,650 m near Jamay, Jalisco, Mexico (Smith, 1972; Villa-R. et al., 1967).

The northernmost subspecies, *P. davyi fulvus*, is found in Mexico (but is absent in the northern interior) from Sonora, Ta-

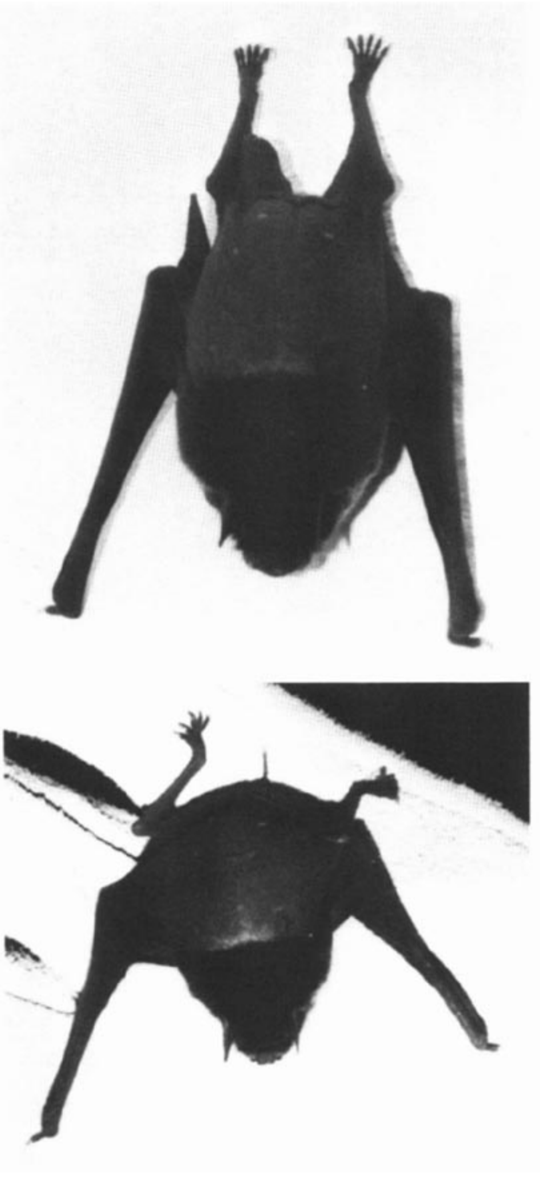

FIG. 1. *Pteronotus davyi fulvus* in roosting posture from El Salto Falls, San Luis Potosí, Mexico (above). Same specimen showing free-tailed appearance when uropatagium folded under (below).

FIG. 2. Dorsal, ventral, and lateral views of the skull, and lateral view of the mandible of *Pteronotus davyi* (University of Kansas 64748, male, Laquin Cave, 311.5 m, Guatemala). Greatest length of skull is 14.8 mm.

maulipas, and Nuevo Leon southward into Honduras (Hall, 1981; McCarthy, 1987; Matson and Baker, 1986; Polaco and Muñiz-Martínez, 1987; Sánchez-Herrera et al., 1986; Smith, 1972). *P. d. davyi* occurs from Nicaragua into northwestern Costa Rica (Hall, 1981; Wilson, 1983), and from Colombia (Aellen, 1970; Marinkelle, 1982) through coastal Venezuela (Handley, 1976; Smith, 1972) to eastern Brazil (Vieira, 1955). *P. d. davyi* is also recorded from Trinidad and the Lesser Antilles as far north as Guadeloupe (Jones and Phillips, 1970). *P. davyi* has not been recorded from Guyana, Suriname, or French Guiana. An isolated population (*P. d. incae*) exists in Cajamarca and Piura provinces, Peru (Graham, 1987; Koopman, 1978; Smith, 1972). Of the mormoopid fossils discovered, none are assignable to *P. davyi* (Koopman, 1958; Silva-Tabaoda, 1974).

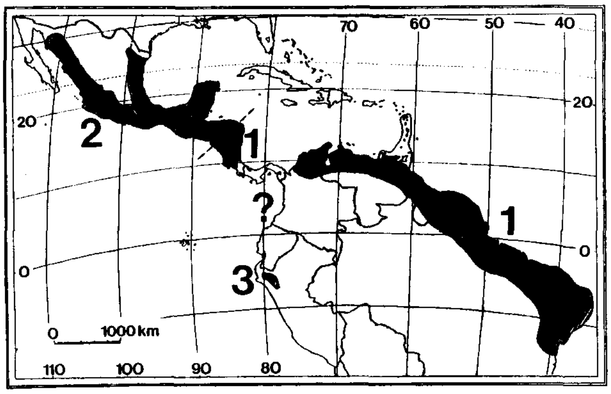

FIG. 3. Distribution of *Pteronotus davyi*: 1, *P. d. davyi*; 2, *P. d. fulvus*; and 3, *P. d. incae* (modified from Hall, 1981; Jones and Phillips, 1970; Koopman, 1982; Smith, 1972). "?" indicates an area with no confirmed captures of *P. davyi*.

FORM AND FUNCTION. Lesser naked-backed bats share prominent lip and chin features with other mormoopids. The lips are large and form a funnel when open, possibly for focusing orally emitted echolocating signals and for catching prey on the wing (Hill and Smith, 1984); short, bristle-like hairs surround the mouth and may aid in catching insects (Smith, 1972). The lower lip has an expanded "chin" plate, a large tubercle bordered by many concentric rows of smaller bumps (Sites et al., 1981). This plate has striated muscle fibers underlying a thick dermis, in which there is a moderate amount of sebaceous tissue. Submaxillary and sublingual glands are mucousoid (Dalquest and Werner, 1954). The nostrils are incorporated into the upper lip (Nowak and Paradiso, 1983). The ears are funnel-shaped and distinctly lanceolate. The tragus is spatulate, haired inwardly, and has a prominent secondary fold (Smith, 1972). The hairs (of the head and shoulders) are unmodified, with completely circular, closely appressed scales (Howell and Hodgkin, 1976; Smith, 1972).

The pelage of *P. davyi* is dense. Two pelage color phases are caused by an annual molt, usually from May to July, though both the dark and light phases have been found together in November (Matson and Patten, 1975); Allen (1894) believed the color phases were independent of season. The progression of molt in *P. parnellii* is similar to that of *P. davyi* (Smith, 1972). Freshly molted individuals are snuff brown to clove brown, fading to tawny dorsally and cinnamon ventrally through the year (Villa-R., 1967); some may appear bright-ochraceous orange (Smith, 1972). Individual hairs are darker basally (Jones, 1966; Smith, 1972); the dark bases are more noticeable ventrally, on the back under the chiropatagium, and before molt. Hairs on the back (under the wing) are 8 to 9 mm in length compared to hairs 4 to 5 mm in length elsewhere on the body (Jones, 1966).

The basioccipital region between the auditory bullae, which are nearly masked by large tympanic rings, is extremely broad, with two shallow pits for insertion of the muscularis longus capitus (Smith, 1972). The distal-articular surface of the humerus is offset to one side and is divided into three surfaces (the trochlea and two separate ridges of the capitulum) separated by grooves; the innermost of these, the trochlea, articulates with the ulna and part of the radius. The spinous process also is well developed for muscle attachment. The radius, which is strongly curved, has an enlarged articular facet for the trochlea of the humerus. The articular surface of the ulna is moderately developed and the olecranon process is small, but larger than in many other bats. The shaft of the humerus is in line with the articulation of the elbow joint, which restricts lateral movement of the forearm, and muscles have moved their insertion points away from the center of rotation of the elbow joint. Functionally, this leads to certain extensors being stretched upon flexion of the elbow and some flexors being stretched with extension. The muscles have reduced elasticity due to interstitial fascial sheets and extended tendons spanning much of their respective muscles, and respond to being stretched by snapping back "automatically." The flexor muscles of the forearm insert on all digits so that they either fold or expand the entire chiropatagium; the flexor carpi ulnaris and the flexor digitorum profundus, which proximally are inserted on the spinous process of the humerus, tend to flex the phalanges and fold the chiropatagium whenever the forearm is flexed proximally. The increased efficiency of this "automatic" flight mechanism has allowed for the reduction in size of many muscles, lightening the wings and providing for long, enduring flight (Vaughan and Bateman, 1970). The wing aspect ratio of *P. davyi* is high relative to most bats, which allows for fast, enduring flight. The wings of *P. davyi* can be used for thermoregulation. Blood vessels that feed the wings are equipped with valves for controlling blood flow, and necessarily the shunting of heat, into the wings (E. Stashko, personal communication).

The laryngeal region of *P. davyi* is extended into a large resonating chamber composed of five to eight expanded tracheal rings that narrow into the tubular larynx. The lateral walls of the larynx, upon which the unusually large posterior cricothyroid muscle inserts, are uncalcified and elastic, and action of the posterior cricothyroid muscle serves to increase the total volume of the larynx. The morphology of the laryngeal region is similar to a Helmholtz resonator, which can be tuned to resonate (and amplify) particular frequencies. In *P. davyi*, the second harmonic (60 to 80 kHz) receives most of the vocal energy, apparently due to the specialized structure of the laryngeal region (Griffiths, 1978).

Brain size in relation to body size for *P. davyi* is relatively large for an insectivorous bat (endocranial volume, 0.188 cm^3). However, the cerebral hemispheres are small and the cerebelli unusually large, a condition common to other insectivorous bats (Findley, 1969).

In *P. davyi*, the glans of the penis is fan-shaped with numerous lengthwise folds and grooves (most likely associated with specialized vaginal morphology) and the clitoris has an acute pendant tip. No baculum is present (Smith, 1972).

ONTOGENY AND REPRODUCTION. *Pteronotus davyi* exhibits seasonal monoestry (Wilson, 1973), with copulation probably occurring in January or February. Ovulation is dominated by the right ovary, with only an occasional ovum being produced by the left. Consequently, implantation is most frequent in the right uterine horn (Hill and Smith, 1984). The litter size is one. Birth is coincident with the onset of the rainy season, which increases number and availability of insect resources (Bateman and Vaughan, 1974). Lactation may continue through July. Maturation of young is rapid, enhanced by the seasonal abundance of insects (Smith, 1972).

Embryonic development has been studied most extensively in the northern *P. d. fulvus*. The reproductive cycle is initiated earlier in southern parts of the range. Full-term embryos averaging 25 mm in length were collected from four females in Nicaragua on 9 May (Jones et al., 1971). A female collected 7 March at Jocotán, Guatemala, carried an embryo 11 mm in length (Jones, 1966). Seven embryos measuring 6 to 15 mm were collected from 11 to 24 April in Yucatán (Birney et al., 1974) and 15 females examined from Michoacán and Guerrero, Mexico, in early May carried embryos from 16 to 22 mm in length (Alvarez, 1968; Cockrum, 1955). Sixteen embryos recovered in Jalisco from 25 May to 7 June averaged 21.1 mm in length (Watkins et al., 1972) and a female collected in Sinaloa on 22 June contained a 21-mm embryo (Jones et al., 1972).

Greatest length of testes is coincident with the mating season. Two males collected 7 February in Yucatán had testes averaging 7.25 mm in length (Jones et al., 1973) and LaVal (1972) reported a range of 2 to 6 mm for testes from four males collected in Puebla in January. Jones (1966) also reported an average of 3.1 mm in length for testes recovered from 13 males collected in mid-January in Guatemala. Males collected later in the year, outside of the breeding season, generally have smaller testes. Measurements for testes from 14 males collected 11 April to 2 May in Yucatán averaged 2.6 mm in length (Jones et al., 1973) and testes of four males from Michoacán in July averaged 1.5 mm (Alvarez, 1968; Polaco and Muñiz-Martínez, 1987). In Jalisco, testes from four males captured 29 May averaged 2.5 mm in length, and another male collected 2 July had testes 1 mm in length (Watkins et al., 1972).

ECOLOGY. Lesser naked-backed bats occur in moist to seasonally dry habitats (Bateman and Vaughan, 1974; Birney et al., 1974; Matson and Patten, 1975; Smith, 1972; Wilson, 1983). *P. davyi incae* occurs in mesic habitats on both sides of the Andes in Peru (Koopman, 1978). Within these habitats, *P. davyi* selects the darker recesses of hot, humid caves and mines (Bateman and Vaughan, 1974; Birney et al., 1974; Goodwin and Greenhall, 1961; Villa-R., 1967). Manmade structures, such as chicken pens, are sometimes utilized as roosts (Goodwin and Greenhall, 1961). Daytime roosts are shared with numerous other species of bats, but most notably other mormoopids, *Natalus*, *Artibeus jamaicensis*, *Macrotus*, *Tadarida brasiliensis*, and *Desmodus rotundus*. Lesser naked-backed bats often are the dominant species in a roost (Bateman and Vaughan, 1974; Birney et al., 1974), but they rarely roost alone (Villa-R., 1967). Population numbers in a roost may be considerable; an estimated 62% of 400,000 to 800,000 bats in one mine near Panuco, Sinaloa, were *P. davyi* (Bateman and Vaughan, 1974). The other three species roosting in the mine were *Mormoops megalophylla*, *Pteronotus parnellii*, and *P. personatus*; all insectivorous mormoopids. These four species maintained specific flyways to and from foraging areas, some more than 3.5 km away from the roost, suggesting that they were actively involved in partitioning the available resources. Specific flyways disappeared with the onset of the rainy season (Bateman and Vaughan, 1974). In the extreme north of the range, there may be some resource partitioning between males and females, and this may be why there is measurable sexual dimorphism in the most northerly populations (Smith, 1972). *P. davyi*, excluded from the temperate areas due to physiological limitations (Novick, 1963), dominates the insectivorous guild in some neotropical areas (Vaughan and Bateman, 1970).

Lesser naked-backed bats maintain relatively constant population levels in some areas. In Sinaloa, where these bats are at the edge of their range, one colony maintained high numbers over 3 successive years (Bateman and Vaughan, 1974) and a colony in Sonora, dominated by *Tadarida brasiliensis*, had >100 *P. davyi* from February through November (Cockrum and Bradshaw, 1963).

Long-range movements of lesser naked-backed bats have not been recorded, but *P. davyi* is the only mormoopid to have invaded the Lesser Antilles (Jones and Phillips, 1970). Of 117 bat species on adjacent continental South America, only 12 have succeeded in colonizing the Antilles (Koopman, 1982). The enduring flight capabilities of *P. davyi* probably aided in overseas migration onto these islands. Pleistocene fluctuations in climate may have allowed the establishment of populations in Peru that later differentiated into *P. d. incae* (Smith, 1972).

Predation on *P. davyi* has been reported only once; bones from two specimens were found in barn owl (*Tyto alba*) pellets in Guerrero, Mexico (Ramírez-Pulido and Sánchez-Hernández, 1972). Ticks (Argasidae, *Ornithodoros viguerasi*; Goodwin and Greenhall, 1961) and larval chiggers (Trombiculidae, *Wagenaaria similis*; Loomis, 1969) have been recorded from lesser naked-backed bats, as have a streblid bat fly (*Trichobius* sp.; Wenzel et al., 1966) and a spinturnicid bat mite (*Cameronieta thomasi*; Kingston et al., 1971). Another streblid bat fly, *Nycterophilia fairchildi*, was recorded from an unconfirmed Panamanian specimen of *P. d. davyi* (Wenzel et al., 1966).

In Nicaragua, the endoparasitic nematode *Websternema parnelli* was present at densities of 1 to 47 in three *P. davyi*. Another nematode, *Linustrongylus pteronoti*, was found in two specimens; up to eight individuals, always of the same sex, were found in each bat (Vaucher and Durrette-Desset, 1986). No nematodes were recovered from 10 *P. davyi* from Sonora (Cain and Studier, 1970). Similarly, no trypanosomes were recovered from 12 *P. davyi* from Colombia. High temperature of roost sites (up to 50°C) may inhibit parasitaemia (Marinkelle, 1982).

Rabies has been recorded from *P. davyi* in Trinidad (Goodwin and Greenhall, 1961) and in Jalisco, Mexico (Villa-R. et al., 1967). These bats aggressively bite when handled and could pose a health hazard if infected with rabies. In Jalisco, these bats were sharing the roost with vampire bats, *Desmodus rotundus*; the vampire bats were the likely vector for the rabies infection. Many dead and dying *P. davyi* may be found in caves where they share a roost with *D. rotundus*, so rabies may be an important mortality factor for lesser naked-backed rats (Villa-R., 1967). Nearly 42% of the *P. davyi* examined from Jalisco had some histological evidence of rabies; 25% had positive tests from the salivary glands, indicating that these individuals were infectious. Most of the bats, however, were asymptomatic (Villa-R. et al., 1967).

The diet of lesser naked-backed bats includes many species of Lepidoptera (Howell and Burch, 1974), some dipterans, and occasionally earwigs (Forficulidae, *Sphingolabis* sp.; Villa-R., 1967). *P. davyi* drinks on the wing (Hill and Smith, 1984). Lesser naked-backed bats do not adapt well to drinking from a dish in the lab, but quickly learn to pursue and catch flying insects in an enclosed room. *P. davyi* may capture 25 fruitflies/min (Novick, 1963). The species probably is not in much direct danger from man's development, due to the undesirability of the unusually hot, humid caves favored by *P. davyi* (Birney et al., 1974), though destruction of foraging areas could endanger some populations.

BEHAVIOR. Foraging flights begin before dark, with considerable "light testing" previous to departure. Foraging takes place close to the ground and may continue throughout the night; *P. davyi* seems most active in the first half of the night, but may have a second foraging flight, returning to the roost at sunup (Bateman and Vaughan, 1974). Lesser naked-backed bats are agile climbers (Vaughan, 1986) and will climb to the top of the roost entrance and launch themselves at top speed away from the entrance. This may be a defense against capture by predators waiting outside the entrance. The recorded flight speed for *P. davyi* is 12.9 km/h (Kennedy et al., 1977). These bats evidently remain flying while away from the daytime roosts, as no nighttime roosts are known (Bateman and Vaughan, 1974).

Large colony size may help the bats with thermoregulation during cooler times of the year at the most northerly roosting sites (Bateman and Vaughan, 1974). During cold periods when few insects are active, *P. davyi* is only active for about 0.5 h at sunset, flying to obtain water and then returning to roost.

Echolocation signals consist of a 1 millisecond (msec) constant frequency component at about 39 kHz, with most of the energy going to the second harmonic (78 kHz; Griffiths, 1978; Novick, 1977). This is followed by a frequency modulated component (2 msec) that drops to 31 kHz (second harmonic of 62 kHz). Entire pulse duration is 3.1 msec (range, 2.3 to 3.5; Novick, 1963). Echolocating capabilities of *P. davyi* are excellent; this bat can detect and approach 2 to 3-mm food (*Drosophila*) from 0.5 to 0.75 m away (Hill and Smith, 1984). Detection, approach, and capture of prey take 0.5 s; the approach is characterized by increase in number of calls from 10 to 12 pulses/s during search flight to approximately 35 pulses/s, followed by a rapid burst of calls (200 pulses/s) during the terminal stage (Novick, 1977). Pulses are shortened as distance to the target is reduced, in approximately a linear fashion (Schnitzler and Henson, 1980). The bulk of the shortening is in the constant frequency portion; the frequency modulated component is shortened only after the constant frequency portion has been eliminated. Pulses are shortened to about 1 msec in the terminal phase of approach (Novick, 1977).

Pteronotus davyi first exhibits a behavioral response to a target at the point of first overlap of a returning echo with an outgoing pulse (at a distance of about 700 mm from a target). These bats use pulse-echo overlap for distance information, and may also use comparison of pulse and potentially Doppler-shifted echo frequencies to tell direction of flight of potential prey. Once pursuit is initiated, pulse-echo overlap is maintained through shortened pulses at about 1.5 msec during approach and at 1 msec during the terminal phase (Novick, 1977). During all but the terminal stage, *P. davyi* groups pulses to correspond with wingbeat and respiratory cycle, with expiration occurring during wing upstroke (Novick, 1977; Schnitzler and Henson, 1980).

GENETICS. The karotype of *P. davyi* is virtually indistinguishable from that of other *Pteronotus*; the fundamental number is 60 and the diploid complement is 38, which apparently is ancestral for mormoopids. There are six large, four medium, and two small metacentric or submetacentric pairs, as well as six small acrocentric pairs among the autosomes. The small Y chromosome is acrocentric and the X is a medium submetacentric (Baker, 1967). The G-band pattern for the entire genome (236 bands total) is shared by all six species of *Pteronotus*, but not *Mormoops*. Three nucleolar-organizer regions have been identified in the centromeric regions of three of the acrocentrics in *P. davyi* (Sites et al., 1981). Systematically, serum proteins set this bat apart from *P. parnellii*. *P. davyi* (and *P. personatus psilotis*) has two hemoglobins with distinctive electrophoretic migration rates (one in *P. parnellii*); mobility relative to human hemoglobin A for these hemoglobins are 0.35 and 0.66 (Mitchell, 1970).

REMARKS. *Chilonycteris gymnonotus* Natterer, 1843 was for many years considered a junior synonym of *Pteronotus davyi* Gray, 1838. Smith (1977), upon examination of the type specimen of *C. gymnonotus*, found that the specimen actually represented the larger congener, *P. suapurensis*. The name *C. gymnonotus* predates *P. suapurensis* by 61 years, and is now accepted (Honacki et al., 1982) as the correct name of the big naked-backed bat.

The subgenus *Pteronotus* is most closely related and most similar to the subgenus *Chilonycteris*; *Phyllodia* represents an earlier evolutionary divergence in the *Pteronotus* lineage (Smith, 1972). Within the subgenus *Pteronotus*, Smith (1972) considered *P. davyi* to have diverged less in an evolutionary sense than *P. gymnonotus*.

A number of other vernacular names have been applied to *P. davyi*; the little naked-backed bat and Davy's naked-backed bat are most common (Hall, 1981; Smith, 1972). In Spanish literature, this bat is more appropriately called "murciélago de falsas espaldas desnudas," meaning false naked-backed bat (Villa-R., 1967:180). In Trinidad, it has been called the Trinidadian naked-backed bat (Goodwin and Greenhall, 1961).

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