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Noctilio albiventris.

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Noctilio albiventris Desmarest, 1818
Lesser Bulldog Bat

Noctilio albiventris Desmarest, 1818:15. Type locality Rio Sao Francisco, Bahia, Brazil.
Noctilio albiventer Spix, 1823:58, an emendation.
Noctilio affinis D'Orbigny, 1836:lam. 10, Fig. 1. Type locality "Bolivia."
Noctilio zaparo Cabrera, 1907:57. Type locality Ahuano, Rio Napo, Ecuador.
Noctilio minor Osgood, 1910:30. Type locality Encontrados, Zulia, Venezuela.
Dirias irex Thomas, 1920:273. Type locality Rio Iriri, Para, Brazil.

CONTEXT AND CONTENT. Order Chiroptera, Family Noctilionidae. The genus *Noctilio* contains two living species, *Noctilio albiventris* and *N. leporinus*. Four subspecies of *N. albiventris* are recognized (Davis, 1976) as follows:

N. a. albiventris Desmarest, 1818:15, see above (*irex* Thomas a synonym).
N. a. affinis D'Orbigny, 1836:1am. 10, Fig. 1, see above (*zaparo* Cabrera a synonym).
N. a. minor Osgood, 1919:30, see above.
N. a. cabrerai Davis, 1976:704. Type locality Fuerte Olimpo Depto. de Olimpo, Paraguay.

DIAGNOSIS. The following diagnosis was taken primarily from Davis (1973, 1976). *Noctilio albiventris* resembles *N. leporinus* in most external features; however, *N. albiventris* can be distinguished by its smaller size. Adult specimens with foot shorter than 20 mm, combined tibia and foot shorter than 40 mm, forearm shorter than 70 mm, wingspan about 400 mm, weight less than 40 g, and maxillary toothrow 8.5 mm or less are considered to be *N. albiventris*; in contrast *N. leporinus* have length of foot 25 mm or more, combined tibia and foot more than 50 mm, forearm more than 75 mm, wingspan about 500 mm, weight more than 50 g, and maxillary toothrow more than 10 mm. The long hindlimbs, enormous feet, and well-developed claws of *N. leporinus* are adaptations to a piscivorous lifestyle and are not as well developed in *N. albiventris*.

GENERAL CHARACTERS. External characteristics include muzzle and nose without excrescences but with strongly projecting nose pad. Lips are full and swollen; chin has well-developed cross ridges, giving these bats a "bulldog-like" appearance. Internal cheek pouches are present. Ears are separate, narrow, and pointed; tragus is pinnately lobed with finger-like projections. Tail is more than half as long as femur, extending about to middle interfemoral membrane; tip of tail is free on dorsal surface of interfemoral membrane. Feet are large and robust, but not greatly enlarged as in *N. leporinus*. Calcar is well developed and bony. Humerus has trochiter smaller than trochin; articulation with scapula is slight; proximally, epitrochlea and spinous process are well developed and capitulum is off-line with humeral shaft. Seventh cervical vertebra is not fused with first thoracic; pelvis has ischia fused and in contact with laterally compressed, urostyle-like sacrum.

Skull lacks distinct postorbital processes; premaxillaries have nasal and palatal branches fused together and with maxillaries; palate is complete and closed anteriorly. Form of skull (Fig. 1) is characteristic, with high, deep braincase, prominent flaring shelf-like mastoids, and distinctive saggital crest (greatly developed in males). Rostrum is only half as long as braincase, highly arched; nares nearly tubular and open forward with a slight posterior emargination. Palate is distinctly concave when viewed laterally, but flat anteroposteriorly; maxillary toothrows are aligned nearly in parallel. Auditory bullae are relatively small, but cover about half of cochlea. Upper incisors are greatly unequal and crowded at midline between canines; inner pair are twice as high as long, with posterior heel, their shafts curving outward distally, but strongly in contact at about middle; outer pair are small and slightly behind the inner, their single cusps barely extending above the cingulum of the inner pair. Lower incisors are equal in size and crowded at midline between canines; crowns are longer than high and broad as long, but narrow posteriorly; the upper surface is concave, but not deeply bilobed. Upper canines are high and short with a distinct, extremely oblique cingulum and no secondary cusps. The inner surfaces are slightly concave with a median ridge; the outer are uniformly convex. Lower canines have a slight twist in the shaft near middle. Upper premolar is nearly parallel-sided, twice as broad as long, and cusps are well developed. First and second molars are nearly equal with no posterior emargination, so that unlike *N. leporinus*, spaces between the teeth are not noticeable. *Noctilio albiventris* also differs from *N. leporinus* in possessing a large hypocone and a conspicuous commissure between protocone and metacone in first and second upper molars. Occlusal area of third upper molar is half that of the second. The above description is taken from Davis (1976) and Miller (1907).

External and cranial measurements were given by Davis (1976); extensive non-geographic and geographic variation exists within and among the four subspecies. Ranges of external measurements for pooled samples of adult *N. albiventris* were as follows (in mm): head and body length, 65 to 68; length of tail, 13 to 16; length of ear, 22 to 24; wingspan, 285 to 380; length of forearm, up to 70. Davis (1976) noted that males were significantly larger than females ($P < 0.05$) in six of nine variables measured, including length of maxillary toothrow, length of mandibular toothrow, condylobasal length, zygomatic breadth, width across M3-M3, and length of mandible. Sexual dimorphism also was evident in development of the saggital crest in adult males. Davis (1976) presented means and

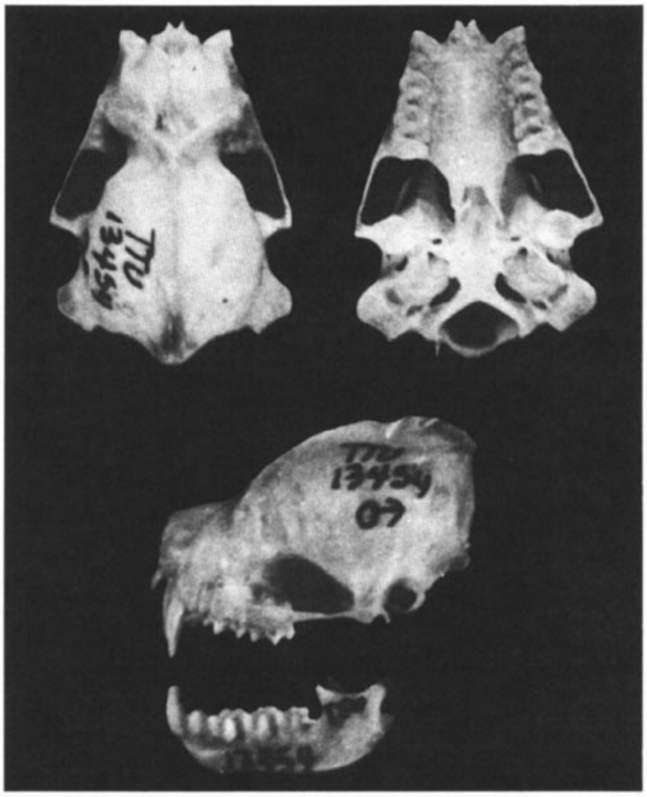

FIGURE 1. Dorsal, ventral, and lateral views of skull, and lateral view of lower jaw (TTU 13454) of a male *Noctilio albiventris* from Cortez, 23 mi N San Pedro Sula, Honduras. Greatest length of skull is 21.6 mm.

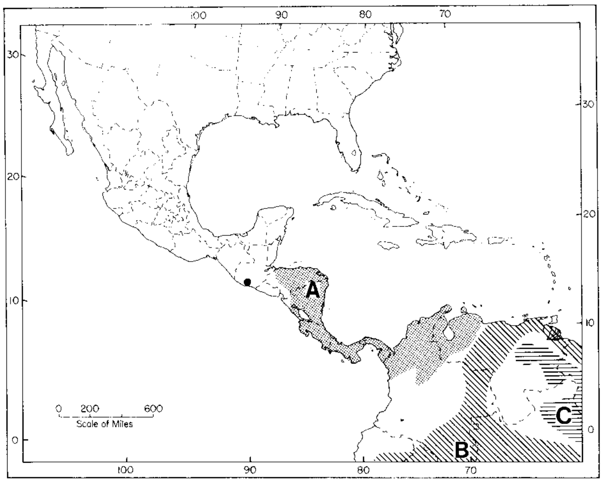

FIGURE 2. Geographic distribution of *Noctilio albiventris* in Central America. Solid circle represents the range extension reported by Dolan and Carter (1979).

ranges for adult weights from Rio Coco (between Honduras and Nicaragua) for 15 males as 31.2 (22.2 to 40.3) g; and for 12 females as 24.5 (18.1 to 30.8) g. In a sample from Peru, the means and ranges for 12 males were 37.1 (30.5 to 44.0) g, and for 16 females, 31.4 (22.0 to 36.3) g.

The pelage is extremely short; coloration varies considerably between individuals and over geographic localities. Dunn (1934) found two distinct color phases (in both sexes) in a study in Panama. Upperparts ranged from bright to russet to dark brown, with bright yellowish-brown to buffy-white underparts. A pale, whitish mid-dorsal stripe extends from the interscapular region to the rump. Davis (1976) noted color variation between males and females and among geographical races. The darkest individuals were found to be assigned to the subspecies *N. albiventris affinis*. In a sample from Peru, both dorsum and underparts of males varied from chocolate to brownish orange. Other geographic races are generally paler; in a sample of *N. a. minor* from Rio Coco, the dorsum of males was dull brown to rich mahogany with underparts from yellowish through buff to bright rufous. In females, the dorsum varied from dull brown to reddish brown with underparts buff to yellowish, tinged with rusty red (Davis, 1976). Davis (1976) also noted that the mid-dorsal stripe was barely discernible in many individuals; there seemed to be considerable variation in this characteristic.

DISTRIBUTION. *Noctilio albiventris* is found north to Honduras, south through Central America to Argentina and Paraguay, and east to the coast of Brazil (Davis, 1976). Dolan and Carter (1979) extended the known range northwest into northwestern Guatemala along the Pacific Coast of Central America and suggested that the distribution is discontinuous along the Pacific Coast from Guatemala to Rivas, Nicaragua. Dickerman et al. (1981) confirmed this distributional record by collecting six additional specimens from the Pacific lowlands of Guatemala. Figures 2 and 3 show the distribution of the four subspecies recognized by Davis (1976).

Noctilio albiventris primarily inhabits mesic tropical forest habitats, foraging over rivers, streams, and marshes (Davis, 1976; Davis et al., 1964; Dickerman et al., 1981; Dolan and Carter, 1979). The altitudinal range of the species extends up to 1,100 m (Davis, 1976). No fossils have been reported.

FORM AND FUNCTION. Smith (1972) gave details on features of the postcranial skeleton, especially regarding the elbow and shoulder articulations. The functions of the proximal and distal ends of the humerus were discussed by Miller (1907) and Smith (1972). Wing morphometrics were presented in Smith and Starrett (1979). The wings are described as having a high aspect ratio; however, Smith and Starrett (1979) cautioned about making direct correlations with swift flight because *N. albiventris* is able to maneuver dense vegetation. Brandon (1977, 1979) compared flight mechanics of *N. albiventris* and *Tadarida brasiliensis* using cinematography. These species differed in the use of tail membrane for pitch control and landing.

Dental formula is: i 2/1, c 1/1, p 1/2, m 3/3, total 28. Phillips and Jones (1969) examined seven specimens for dental abnormalities. No developmental abnormalities were found but one adult male had lost the right upper first and second incisors.

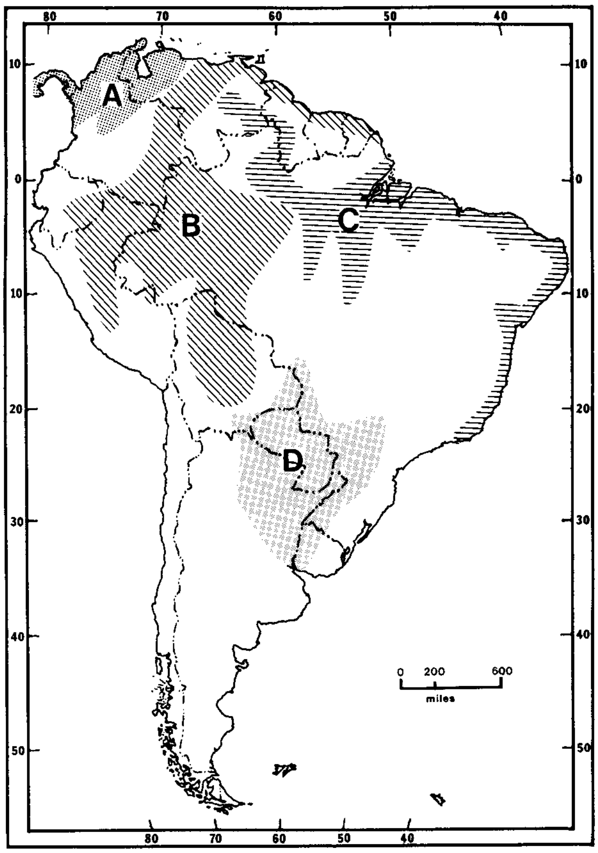

FIGURE 3. Geographic distribution of *Noctilio albiventris* in South America. Subspecies are: A, *N. a. minor*; B, *N. a. affinis*; C, *N. a. albiventris*; D, *N. a. cabrerai*. Maps adapted from Davis (1976).

External morphology of the facial region, including the lips, nose pad, and chin were given in Smith (1972) with comparison to the Mormoopidae and Phyllostomidae. Smith (1972) described and illustrated the tragus. Murry and Strickler (1975) noted the presence of cheek pouches formed by posterolateral expansions of the buccinator muscle in *N. albiventris* as identical in structure to those of *N. leporinus*. Murray and Strickler (1975) hypothesized that cheek pouches evolved as an adaptation to a piscivorous habit, but with the discovery of well-developed pouches in *N. albiventris* (primarily an insectivore, see below), they concluded that pouches arose as an adaptation to a diet other than fish. Stomach morphology and histochemistry of *N. albiventris* are generally similar to that found in other carnivorous bats (Forman, 1972, 1973). There is a distinct cardiac sphincter formed at the gastroesophageal junction; this sphincter has a distinct muscular component and is unique for bats. Forman (1973) described an even more dramatic anatomical sphincter in *N. leporinus* and discussed implications for the evolution of piscivory in this species. Features of the gastric system of *N. albiventris* shared with an insectivorous bat, *Pteronotus parnellii*, are: extensive pylo-fundic transition zone, pyloric glands occupying narrow region near sphincter, narrow oxynitic glands, limited distribution of zymogenic cells with fundic tubules, no reduction of mucosae in caecum (Forman, 1972).

McNab (1969) provided information on general physiology and temperature regulation. Relationships between metabolic rate (measured as oxygen consumption) and body temperature in *N. albiventris* was typical of other Neotropical bats; however, McNab (1969) found that peripheral cooling did not seem to affect heat loss.

ONTOGENY AND REPRODUCTION. *Noctilio albiventris* is monovular and ovulation occurs in either ovary (Anderson and Wimsatt, 1963; Rasweiler, 1977*a*, 1978). Anderson and Wimsatt (1963) likened the breeding cycle to that of other Microchiroptera in being annual and of short duration. Based on their limited material from Panama, they suggested that breeding begins as early as late November or December with pregnancy through the spring and parturition in April or May. Litter size appears to be one young per mating per year (Anderson and Wimsatt, 1963). Rasweiler (1977*a*) reported a single case of twinning in 72 pregnant bats he examined. In a study of 112 females from Colombia, Rasweiler (1977*a*) confirmed a highly synchronous breeding cycle with fertilization and early embryonic development in late February and March. Hooper and Brown (1968) reported that 13 of 15 females from Costa Rica were pregnant (embryos ranged from 3 to 5 mm, crown to rump) in February. Additional reproductive data were given by LaVal and Fitch (1977) for bats from Costa Rica, where pregnancy was noted in 10 of 40 females collected in February, one in April, and one in August. Davis et al. (1964) reported collections from Costa Rica with one of two females pregnant in March and two pregnant in April. They also reported females from Honduras that were reproductively active in a period from February to May (15 of 21 females pregnant with embryos ranging 25 to 33 mm, crown to rump). In Nicaragua, Jones et al. (1971) noted 26 of 31 females pregnant in April (embryos ranged 5 to 26 mm, crown to rump). A reproductively inactive female was recorded in July by Dolan and Carter (1979) from Guatemala. Tuttle (1970) reported a collection from Peru with two of three females pregnant in July (embryos were 14 and 16 mm, crown to rump). Jones et al. (1971) reported the following average testis sizes for males from Nicaragua (measurements in mm): April (n = 15), 4.6 (2 to 7); June (no sample size given), 5.2 (4 to 6). Tuttle (1970) collected two males in Peru during July with testis measurements of 7 by 4 mm and 5 by 8 mm, and Dickerman et al. (1981) noted one inactive male in April from Guatemala.

Rasweiler (1977*a*) described fertilization and early embryonic development in *N. albiventris*. Ova are fertilized in the oviduct where they develop to an advanced state compared to most other families of bats (Rasweiler, 1979). Unilateral oviductal and uterine reactions may mediate this prolonged preimplantation development by way of local vascular pathways (Rasweiler, 1978). The well-developed blastocyst implants in a ridge formed in the hypertrophied antimesometrial wall of the uterine horn. The definitive chorioallantoic placenta is of the endotheliochorial type (Anderson and Wimsatt, 1963).

Dunn (1934) described an unusual sac-like fold of skin associated with the scrotum. He noted that when testes descended into the scrotum (in reproductive males), this fold everted to present a ridge of wart-like projections. This structure may be involved in breeding, but observations on breeding behavior have not been reported.

ECOLOGY AND BEHAVIOR. Studies of food habits have shown that unlike *N. leporinus*, *N. albiventris* is primarily insectivorous (Davis et al., 1964; Fleming et al., 1972). Dunn (1934) observed individuals dipping for water, but found only insect parts in guano samples. Attempts to experimentally test the fishing habit of *N. albiventris* have resulted in only limited success; in some cases bats refused to take fish as food, even to the point of starvation (Bloedel, 1955). However, fish parts and scales were found in stomach contents by Howell and Burch (1974). Several reports document that lesser bulldog bats feed over water and scoop insects from water surfaces (Brown, 1968; Davis et al., 1964; Hooper and Brown, 1968; Suthers and Fattu, 1973). In a fecal analysis, Whitaker and Findley (1980) found Coleoptera (Dytiscidae, Carabidae), Hemiptera (Lygaeidae), Homoptera (Cercopidae), Lepidoptera, and Diptera. The predominence of dytiscids (22.5% by volume) in this sample of four individuals suggests aquatic feeding because these beetles spend a majority of their life cycle in water. Hooper and Brown (1968) examined 34 stomachs of Costa Rican *N. albiventris* and found Coleoptera, Lepidoptera, Hemiptera, Hymenoptera, Diptera, Orthoptera, and Homoptera; similar results were reported in bats from Colombia (Tamsitt and Valdivieso, 1963) and Nicaragua (Jones et al., 1971). Howell and Burch (1974) observed *N. albiventris* feeding on a moraceous tree (*Brosimum*: Moraceae) and found pollen from *Ceiba* (Bombacaceae), lepidopterans, and fish parts in the stomachs of two individuals; Dobson (1878) reported seeds of the genus *Morus* in the stomachs of several bats.

Activity patterns of *N. albiventris* include an early activity peak (dusk to 1900 h) and a secondary activity peak after midnight (Brown, 1968; Davis et al., 1964; Dunn, 1934). This pattern differs from that of *N. leporinus*. Hooper and Brown (1968) suggested that this temporal separation contributes to differences in diet and reproduction and thus facilitates sympatry of the two species. *N. albiventris* has been captured in association with *Rhynchonycteris naso*, *Uroderma bilobatum*, *U. magnirostrum*, *Myotis fortidens*, *Lasiurus ega*, *Molossus ater*, and *M. molossus* (Dolan and Carter, 1979), and has an activity pattern similar to that of *Molossus ater* (Brown, 1968).

FIGURE 4. Karyotype of male *Noctilio albiventris* (TTU 9032) from Leticia, Colombia.

Hunting behavior includes foraging in small groups over rivers and streams (Davis et al., 1964; Dunn, 1934; Tuttle, 1970). Lesser bulldog bats roost in hollow trees and buildings and have been found in large numbers with *Molossus coibensis* (Dunn, 1934) and *Molossus* sp. (Goodwin, 1946). *Noctilio leporinus* differs in roosting behavior, being found in rock crevices and dark caves near bodies of water; however, *N. leporinus* also has been found in hollow trees (Bloedel, 1955; Goodwin, 1946).

Funayama (1973) studied the incidence of infection by *Trypanosoma cruzi* and a number of bloodsucking insects of the subfamily Triatominae in *N. albiventris*. Bats were captured from Sao Paulo, Brazil, and injected with *T. cruzi*. During peak infection, 10,000 *T. cruzi* per mm^3 were found in the blood. The incidence of death of bats was 83.3%. A second experiment involved infecting bats with five triatomine species and studying the incidence of infection. *Noctilio albiventris* was most heavily infested by *Panstrongylus megistus* (100%) followed by *Triatoma infestus* (83.3%), *Rhodinus neglectus* (80.0%), and *Triatoma sordida* (50.0%).

McDaniel (1972) reported two species of labidocarpid mites (*Parakosa tadarida* and *P. maxima*) parasitizing *N. albiventris*. The latter species was also reported on individuals taken in Nicaragua (McDaniel, 1972). McDaniel (1972) remarked that these labidocarpid mites are common parasites of New World bats occurring from southern United States through Central America and into Venezuela. Ectoparasites of a new genus, *Mitonyssus*, were found infesting *N. albiventris* in Venezuela, Suriname, and Bolivia (Yunker and Radovsky, 1980). Eggs of *M. noctilio* were found on the inner surface of the pinnae and nasal cavities. Yunker and Radovsky (1980) believed that *M. noctilio* was restricted to *N. albiventris*.

Bat flies (family Streblidae) occurring on *N. albiventris* include *Paradyschiria parvula*, *P. parvuloides*, *Noctilionstrebla aitkeni*, and *N. maae*. *Noctiliostrebla* is apparently restricted to noctilionid bats (Wenzel et al., (1966). Fairchild et al. (1966) reported a tick, *Ornithodoros hasei* (family Argasidae), on *N. albiventris*. *O. hasei* also has been reported from *N. leporinus*, *Uroderma bilobatum*, *Vampyrops helleri*, and *Tonatia silvicola*.

Echolocation sounds of *N. albiventris* begin with constant frequency cries of about 70 kHz that are frequency modulated down to 40 kHz after several milliseconds (Griffin and Novick, 1955; Suthers and Fattu, 1973). Repetition rates as high as 200 per s have been measured during pursuit of food. Griffin and Novick (1955) found a similar pattern of ultrasonic cries in other insectivorous microchiropteran families. Foraging behavior of *N. albiventris* consists of briefly scooping or dipping the feet into the water as well as employing the interfemoral membrane to catch insects. Suthers and Fattu (1973) suggested that this behavior may represent an early stage in the evolution of piscivory.

Noctilio albiventris has been maintained in captivity and has proven to be a good research animal for a variety of studies (Nellis, 1969; Rasweiler, 1977*b*; Suthers and Fattu, 1973).

GENETICS. The standard karyotype of *Noctilio albiventris* (Fig. 4) was originally reported (Baker and Jordan, 1970) to possess a diploid number (2n) of 34 and a fundamental number (FN) of 58. The X was described as a medium-sized metacentric and the Y as a small acrocentric chromosome. Patton and Baker (1978) reported the results of G- and C-banding studies and revised the fundamental number to 62; C-band analysis showed that heterochromatin is restricted to the centrometric region in all chromosomes except chromosome 29. On the basis of banding homologies, *N. albiventris* and *Pteronotus parnellii* share all elements of their respective karyotypes except for three chromosomal rearrangements. Additional studies on mormoopids reveal that noctilionids and mormoopids have experienced the least amount of chromosomal differentiation thus far documented between two families of bats (Baker and Bickham, 1980; Sites et al., 1981).

Genic relationships of *N. albiventris* and *N. leporinus*, mormoopids, and phyllostomids have been assessed using protein electrophoretic and albumin immunological data by Arnold et al. (1982).

REMARKS. There has been some confusion regarding the specific epithet for *N. albiventris*. For many years, *N. labialis* was considered the correct name for the lesser bulldog bat (Hershkovitz, 1949). However, Davis (1976) and Hershkovitz (1975) presented convincing evidence that the name *N. labialis* was based on a specimen referable to *N. leporinus*. With *N. labialis* assigned as a subjective synonym of *N. leporinus*, the earliest valid name for the lesser bulldog bat is *N. albiventris* Desmarest, 1818.

Evolutionary relationshps of the family Noctilionidae have been discussed by many authors. Some workers have emphasized primitive features of noctilionids, and propose phylogenetic relationships with emballonurids. Such interpretations have led to the placement of noctilionids in the superfamily Emballonuroidea (Dobson, 1875; Miller, 1907; Simpson, 1945; Trouessart, 1897). Other workers have specified a close association of noctilionids with mormoopids and phyllostomids, and place the three families in a monophyletic superfamily Phyllostomatoidea (Arnold et al., 1982; Patton and Baker, 1978; Smith, 1972; Walton and Walton, 1968; Winge, 1892).

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