Noctilio albiventris Desmarest, 1818
Lesser Bulldog Bat

Noctilio albiventris Desmarest, 1818:15. Type locality Rio Sao Francisco, Bahia, Brazil.
Noctilio albiventris Spix, 1823:58, an emendation.
Noctilio affinis D'Orbigny, 1836:10. 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.

DIRUS irix Thomas, 1920:273. Type locality Rio Irizi, 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 (irix Thomas a synonym).
N. a. affinis D'Orbigny, 1836:10. 10. Fig. 1. see above zaparo Cabrera a synonym.
N. a. minor Osgood, 1919:30, see above.
N. a. cabrera Davis, 1976:704. Type locality Fuerte Olimpo Dep.-to. 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 tail 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 tail 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 excrecences but with strongly projecting nose pad. Lips are full and swollen; chin has well-developed crest ridges, giving these bats a “bulldog-like” appearance. Internal cheek pouches are present. Ears are separate, narrow, and pointed; tragus is pinnae lobed with finger-like projections. Tail is more than half as long as femur, extending 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. Calcars is well developed and bony. Humerus is trochanter smaller than trochoh; articulation with scapula is slight; proximally, epiphysis and spinous process are well developed and capitulum is in line with humeral shaft. Seventh cervical vertebra is not fused with first thoracic; pelvis has ischial fused and in contact with laterally compressed, urostylar-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 sagittal crest (greatly developed in males). Rostrum is only half as long as braincase, highly arched; maxilla near ankle and open forward with a slight posterior dim out. 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 large 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 long as high, and cusp is 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 hypcone 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 cranial and 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, 10 to 16; length of ear, 22 to 34; 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 sagittal 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.
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 (30.3 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 dorsal 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.

**DISTRICTION.** *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 flight speed 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: 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.

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. Murray and Strickler (1975) noted the presence of cheek pouches formed by postero-lateral 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-juvenile transition zone, pyloric glands occupying narrow region near sphincter, narrow oxyntic glands, limited distribution of zymogenic cells with fundic tubules, no reduction of mucosa 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; Rasmussen, 1977a, 1978). Anderson and Wimsatt (1963) likened the breeding cycle to that of other Microchi-
roptera 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 nesting and parturition in April or May. Litter size appears to be one young per mating per year (Anderson and Wimsatt, 1963). Rasweiler (1977a) reported a single case of twinning in 72 pregnant bats he examined. In a study of 112 females from Colombia, Rasweiler (1977a) 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: 6.0 ± 2.0 (n= 15), 4.6 ± 0.2 (n= 15), 5.2 (n= 4). 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 (1977a) 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 prematuration 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 endodochorial type (Anderson and Wimsatt, 1963).

Dunn (1934) described an unusual sac-like fold of skin associated with the scrotum. He noted that when teses descended into the scrotum (in reproductive males), this fold evverted 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 and 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 they 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; Sutters and Fattu, 1973). In a fecal analysis, Whitaker and Findley (1980) found Coleoptera (Dytiscidae, Carabidae), Hemiptera (Lygaeidae), Homoptera (Cercopidae), Lepidoptera, and Dipitera. The predominance 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 (Bombaceae), lepidopterans, and fish parts in the stomachs of two individuals; Dolson (1878) reported seeds of the genus Morus in the stomachs of several bats.

Genome 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 in different ways to reproduction and thus facilitates sympatry of the two species. N. albiventris has been captured in association with Rhynchopteryx naso, Uroderma bilobatum, U. magnumstro, Myotis foridens, Lasius ega, Molossus ater, and M. molossus (Dolan and Carter, 1979), and has an activity pattern similar to that of Molossus ater (Brown, 1968).

N. albiventris 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 cobensis (Dunn, 1934) and Mo- losus sp. (Goodwin, 1946).

In order to test the incidence of infection by Trypanosoma cruzi and a number of bloodsucking insects of the subfamily Triatominae in N. albiventris, Bats were captured in 123 villages, the area of which was nearly 100% of the total area of the state (Yunker and Radovsky, 1980). Eggs of M. nocotilo were found on the inner surface of the pinnae and nasal cavities. Yunker and Radovs- ky (1980) believed that M. nocentilo was restricted to N. albiventris.

Bat flies (family Streblidae) occurring on N. albiventris include Parahyracaius carparia, P. parulaeae, Nictinolobracteinae, and N. maee. Nictinolobracteinae is apparently restricted to noctilious bats (Wenzel et al., 1966). Fairchild et al. (1966) reported a tick, Ornithodoros haselis (family Argasidae), on N. albiventris. O. haselis also has been reported from N. leporinus, Uroderma bilobatum, Vampyrops helleri, and Tonatius silicola.

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

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

GENETICS. The standard karyotype of Nocitilo 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-banding analysis indicated that heterochromatin is restricted to the centromeric region in all chromosomes except chromosome 29. On the basis of banding homologies, N. albiventris and Peromyscus parvus share all elements of their respective karyotypes except for three of their chromosome rearrangements. Additional studies on morbilloids reveal that noctuid snails and morbilloids have experienced the least amount of chromosomal differentiation thus far documented between two families of bats (Baker and Beckham, 1980; Sites et al., 1981).

Genetic relationships of N. albiventris and N. leporinus, morbilloids, and phyllodonts 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 species 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. albitarsis Desmarest, 1818.

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

LITERATURE CITED


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