

Pipistrellus subflavus. By Marty S. Fujita and Thomas H. Kunz

Published 14 November 1984 by The American Society of Mammalogists

Pipistrellus subflavus (F. Cuvier), 1832
Eastern Pipistrelle

[*Vespertilio*] *subflavus* F. Cuvier, 1832:17. Type locality eastern United States, probably Georgia. Restricted by Davis (1959a) to Le Conte Plantation, 3 mi SW Riceboro, Liberty County, Georgia.

Vespertilio erythroductylus Temminck, 1835-1841:238. Type locality vicinity of Philadelphia, Pennsylvania.

Vespertilio monticola Audubon and Bachman, 1842:281. Type locality Grey Sulphur Springs, Virginia.

Vesperugo veraecrucis Ward, 1891:745. Type locality Las Vigas, Canton of Jalapa, Veracruz.

CONTEXT AND CONTENT. Order Chiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Genus *Pipistrellus*. The genus *Pipistrellus* includes 48 species (Honacki et al., 1982). Four subspecies of *P. subflavus* are recognized (Davis, 1959a):

P. s. clarus Baker, 1954:585. Type locality 2 mi W Jimenez, 850 ft, Coahuila, Mexico.

P. s. floridanus Davis, 1957:213. Type locality Homosassa Springs, head Homosassa River, Citrus County, Florida.

P. s. subflavus (F. Cuvier, 1832:17), see above (*erythroductylus* Temminck, *monticola* Audubon and Bachman, and *obscurus* Miller are synonyms).

P. s. veraecrucis (Ward, 1891:745), see above.

DIAGNOSIS. *Pipistrellus subflavus* (Fig. 1) can be distinguished readily from smaller species of *Myotis*, with which it is most easily confused, by its distinctly tricolored hairs that are dark at the base, lighter and yellowish-brown in the middle band, and dark at the tip (Barbour and Davis, 1969; Nason, 1948). *Pipistrellus s. subflavus* varies from pale yellow-orange to dark reddish-brown dorsally, and from pale yellow-orange to dark mahogany ventrally (Davis, 1959a). *Pipistrellus s. subflavus* is the most widely distributed race; its range borders those of the other three subspecies. It can be distinguished from *P. s. clarus* in being smaller and darker; from *P. s. veraecrucis* in being larger and paler, and from *P. s. floridanus* in being slightly smaller (Davis, 1959a). In the southeastern part of its range, *P. s. subflavus* can be distinguished from *P. s. floridanus* in being slightly smaller in size and by having guard hairs that are orange (Davis, 1959a). Guard hairs of *P. s. floridanus* are silvery (Davis, 1959a). One female specimen of *P. s. subflavus* collected in Texas was white over most of its dorsal and ventral areas but had brown appendages (Blair, 1948). A few instances of melanism have been reported (Osgood, 1936; Trapido and Crowe, 1942) in which the typical tricolor banding of hairs was distinct but not as striking as in normal-colored individuals; the specimens were sooty black on both dorsum and venter with darkly pigmented wing membranes. A skewbald bat (white wingtips) was reported by Goslin (1942).

The congeners, *P. subflavus* and *P. hesperus*, have ranges that meet but do not overlap. Hall and Dalquest (1950) listed 15 morphological differences that may be used to distinguish these two species, including color (*subflavus* predominantly brown; *hesperus* predominantly grey), length of hindfoot (*subflavus* foot more than half as long as tibia; *hesperus* foot less than half as long as tibia), length of thumb (*subflavus* thumb greater than 4.9 mm; *hesperus* thumb less than 4.9 mm), and skull profile (*subflavus* dish-faced; *hesperus* nearly straight).

GENERAL CHARACTERS. Measurements (in mm) summarized from Davis, (1959a) are: total length, 77 to 89; length of tail, 34 to 41; length of hindfoot, 7.3 to 9.9; length of ear, 12.4 to 14.1; length of forearm, 31.4 to 34.1; length of third metacarpal, 29.7 to 32.1; length of fifth metacarpal, 28.1 to 31.2; length of

tibia, 13.1 to 14.1; greatest length of skull, 12.4 to 13.1; zygomatic breadth, 7.3 to 8.0; breadth of cranium, 6.3 to 6.7; height of skull, 5.7 to 6.0; alveolar length of maxillary toothrow, 3.9 to 4.2 (Fig. 2). Davis (1959a) listed separate means for males and females of the four named subspecies. The dental formula is: i 2/3, c 1/1, p 2/2, m 3/3, total 34. Fitch (1966) reported a mean weight for adult males as 7.5 g, and adult females as 7.9 g in September, and 4.6 and 5.8, respectively, in April. Females are consistently heavier than males (LaVal and LaVal, 1980; Myers, 1978). The anterior third of the interfemoral membrane is furred and the calcar is without a keel (Barbour and Davis, 1969).

FOSSIL RECORD. *Pipistrellus subflavus* has been found in at least 17 Pleistocene deposits. Three sites are known from Florida (Martin, 1974a, 1974b; Martin and Webb, 1974), one from Kentucky (Guilday et al., 1971), four from Missouri (Hawksley et al., 1973; Hood and Hawksley, 1975; Parmalee and Oesch, 1972; Parmalee et al., 1969), two from Pennsylvania (Guilday et al., 1964, 1966), two from Tennessee (Guilday et al., 1969, 1978), two from Texas (Dalquest et al., 1969; Roth, 1972), two from Virginia (Guilday, 1962; Guilday et al., 1977), and one from West Virginia (Guilday and Hamilton, 1978). The earliest occurrences are late Irvingtonian (Kurtén and Anderson, 1980).

DISTRIBUTION. *Pipistrellus subflavus* occurs throughout most of eastern North and Central America and in parts of the midwestern United States (Fig. 3). The eastern border of the range of the subspecies *subflavus* follows the Atlantic seaboard from Georgia north to Nova Scotia. The northern border extends eastward along the extreme southeastern portions of Quebec and Ontario to central Minnesota. Marginal records from Michigan, not reported in Hall (1981), are known from the western Upper Peninsula. Although Hall's (1981) range map indicates that *P. s. subflavus* extends into southeastern Michigan, the only known marginal record from the Lower Peninsula of Michigan is from the southwest corner (Kurta, 1982). The westernmost border extends to the Edwards Plateau of Texas south to Tamaulipas, Mexico (Davis, 1959a). The Gulf of Mexico along the Florida panhandle marks the southernmost border. *Pipistrellus s. floridanus* occurs throughout peninsular Florida north to southeastern Georgia. The range of *P. s. clarus* extends from northern Coahuila in Mexico to adjacent parts of Texas and is separated from *P. s. subflavus* by the Rio Grande Valley that may serve as an ecological barrier (Davis, 1959a). *P. s. veraecrucis* is known from the tropical lowland and mountainous regions of eastern Mexico, and the northeastern portion of Honduras (Davis, 1959a).



FIGURE 1. Photograph of an alert *Pipistrellus subflavus* roosting on the wall of a cave in Kansas. Photograph by Thomas Henry Kunz.

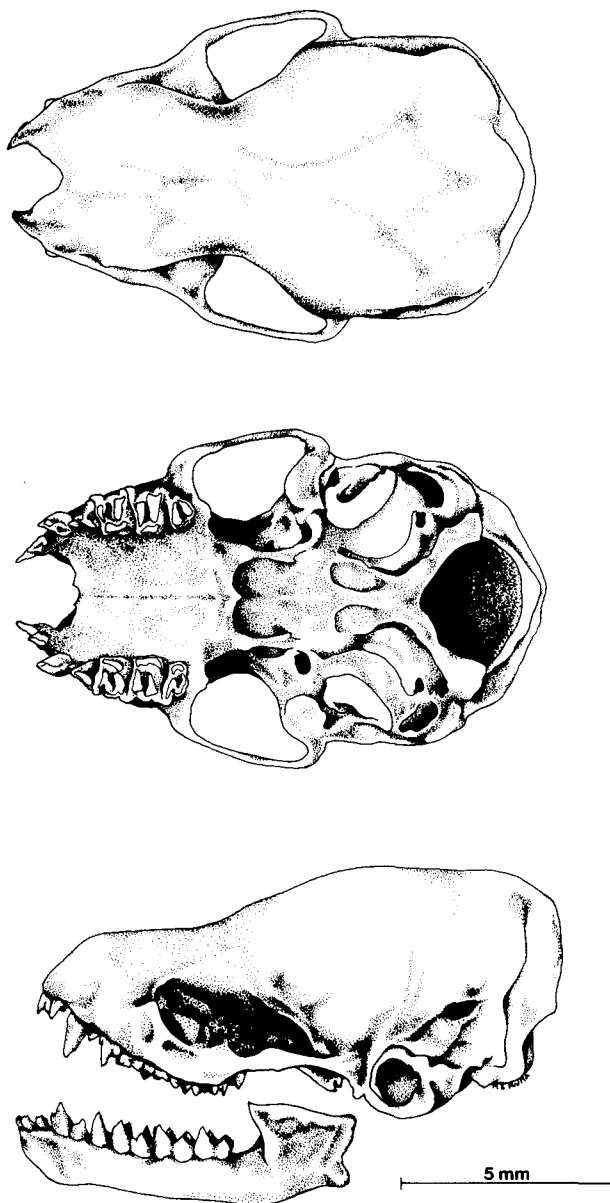


FIGURE 2. The skull of *Pipistrellus subflavus* (MCZ 41944), Museum of Comparative Zoology, Harvard University. In order from the top, dorsal view, ventral view, and lateral view of skull and lateral view of mandible. Drawings by Marty S. Fujita.

FORM AND FUNCTION. Nason (1948) found that the overhairs of *P. subflavus* were approximately 10 mm long and 15 μm in diameter; the underhairs ranged from 5 to 8 mm long and were 10 to 12 μm in diameter. Hair scales were, in general, of the imbricate type, elongated at the base, elongated and ovate at the midsection, crenated at the widest diameter, and ovate at the tip (Nason, 1948).

Poole (1936) reported a wing area from both alar membranes of approximately 59 cm^2 and a ratio of body mass (using 4.3 g) to wing area of 13.9. Based on 40 specimens, Farney and Fleharty (1969) reported a wing-loading value (July and August body mass) of 0.06 (0.05 to 0.08) g/cm^2 and an aspect ratio of 6.9 (6.5 to 7.6). In addition, they found the wing span to be 23.6 (22 to 25) cm, area of the tail membrane to be 11.9 (9 to 14.6) cm^2 , and the wing area, based on the measurement of the lower surface area of the wings, head, and body, to be 81.2 (71 to 92) cm^2 .

The muzzle and facial areas contain sebaceous glands with hair follicles, large nests of sebaceous glandular cells divided by connective tissue, and large, coiled sudiferous gland tubules; histo-

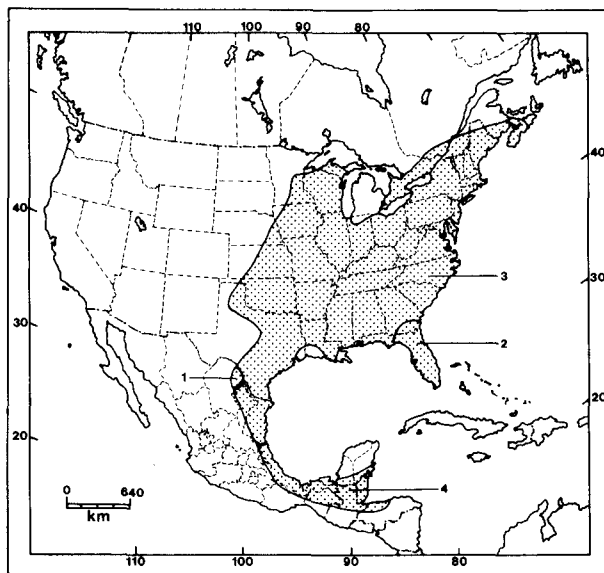


FIGURE 3. The distribution of *Pipistrellus subflavus*: 1, *P. s. clarus*; 2, *P. s. floridanus*; 3, *P. s. subflavus*; 4, *P. s. veraecrucis* (modified after Hall, 1981).

logically, the region is most similar to that of *Myotis grisescens* (Dalquest and Werner, 1954).

Larger size of females in *P. subflavus* reportedly was related to the high cost of lactation and to the relatively large embryo mass of pregnant bats, and was not explainable on the basis of sexual selection (Myers, 1978).

Jennings (1958b) noted that 1 young female from a sample of 306 pipistrelles was found to be polydactylous, having six digits on both hindlimbs and two thumbs on each manus.

The gross morphology of spermatozoa of *P. subflavus* (Hirth, 1960) can be summarized as follows: sperm head slightly obovate, with a blunter apex than in *Myotis* sp.; basal margin of the head somewhat concave and midpiece swollen at the anterior end; sperm tail tapers gradually to a narrow end-piece. Forman (1968) noted that, in general, *P. subflavus* sperm were similar to those of *Eptesicus fuscus*, but could be distinguished from other vespertilionids in that the midpiece in those of *P. subflavus* was longer and the head shorter than in *E. fuscus*. The baculum of *P. subflavus* is Y-shaped with prongs at the proximal position, sufficiently different from that of *P. hesperus* to suggest generic or subgeneric differences between the two species (Hamilton, 1949). Dawson (1980), in a comparative study of the femoral structure of *P. subflavus*, *Blarina brevicauda*, and *Myotis lucifugus*, found that the external morphology of the two bat species differed from the shrew in such a way as to increase flight efficiency and resistance to mechanical stress. He also noted that radiographic measurements of the length, transverse width, and anterior-posterior width of the femur of *P. subflavus* were significantly less than those of *Myotis lucifugus*.

Except for rennin (not present in bats) and aminopeptidase (bat tissues not tested), *P. subflavus*, *Myotis grisescens*, *Scalopus aquaticus*, and *Rattus norvegicus* reportedly possess the same digestive enzymes (Bucholz, 1958).

Among 34 species of small mammals for which various blood variables were determined, blood of *P. subflavus* had the highest oxygen-carrying capacity and hemoglobin concentration (Sealander, 1964). Baer (1966) noted that blood samples obtained from the orbital sinus produced less mortality than samples obtained by cardiac puncture in small bats such as pipistrelles.

Ploskey and Sealander (1979) reported that fat-free dry mass remained relatively constant throughout the hibernation period; fat content varied seasonally, with the highest fat index occurring in October and the lowest in May. Females had significantly larger fat deposits that may provide the extra energy necessary for gestation or may simply reflect differences in metabolism or hormonal balance between the sexes.

During the hibernal period, male *P. subflavus* steadily decrease in mass from September to April, and females from September to March (Fitch, 1966). Total loss in mass was significantly different for females (29%) and males (39%) (Fitch, 1966). Body temperatures, monitored during this period, revealed a sharp decrease among males from January to February, whereas among females the decrease was rapid from November to January after which their body temperatures remained constant until April (Fitch, 1966). In a series of laboratory experiments in which ambient temperature was changed from 5 to 10 to 15°C, Davis and Reite (1967) found that hibernating *P. subflavus* responded by spontaneously and rapidly increasing heart rate. Furthermore, they report that arousal occurred when the bats were subjected to ambient temperatures below 0°C.

Because of its small size and propensity for hibernating singly rather than in clusters, *P. subflavus* can successfully hibernate in Florida caves in which relatively high ambient temperatures exclude other bat species (McNab, 1974). In Florida, *P. subflavus* is an obligate hibernator, even though food supplies are nearly continuous throughout the year (McNab, 1974). The inability to escape hibernation was attributed to its reproductive requirements, most notably the long period of torpor required for successful sperm storage in the female (McNab, 1974).

REPRODUCTION AND ONTOGENY. Copulation and insemination of females occurs in autumn (Guthrie, 1933a; LaVal and LaVal, 1980) and again at the time of ovulation in spring (Guthrie, 1933a). Spermatozoa are stored in the uterus of hibernating females until spring ovulation (Guthrie, 1933a). Although two to seven ova may be shed, only two usually implant in each uterine horn. The ova grow equally for a time but the pair implanted medially later lag behind in development and finally are resorbed (Wimsatt, 1945). The gestation period, as measured from implantation to parturition, lasts at least 44 days (Wimsatt, 1945) after which two young are usually born (Allen, 1921; Brimly 1923; Cope and Humphrey, 1972; Lane, 1946; Wimsatt, 1945). Newborn twins can constitute up to 52% of the mother's total postpartum mass (Hoying, 1983), although Barbour and Davis (1969) and Wimsatt (1945) indicated that the average mass of newborn twins was approximately one-third of the maternal mass.

In Florida, parturition occurs during the last week of May and first 3 weeks of June (Jennings, 1958a). In Missouri, pregnant females were trapped from 7 May to 20 June and lactating bats netted from 5 June through 24 July, suggesting that the parturition period may extend from early June to early July (LaVal and LaVal, 1980). Cope and Humphrey (1972) indicated that parturition in southern Indiana occurred during the last week of June and the first week of July. Lane (1946) reported that the arrival of bats at one parturition site in Pennsylvania occurred in late May, and the parturition period occurred from 13 June to 10 July. Hoying (1983) reported that most young were born between 14 June and 23 June in eastern Massachusetts. In Vermont, Davis (1963) noted that young pipistrelles were born in early July. These few reports suggest that parturition may occur later and is more highly synchronized in more northern populations. As in most temperate vespertilionids, sexes typically are segregated at the spring and summer maternity colonies (Lane, 1946).

Young are born hairless and pink with eyes closed and pinnae folded (Hoying, 1983; Lane, 1946). Newborn pipistrelles are capable of making loud audible clicking sounds that may aid their mothers in retrieving them (Hoying, 1983). Young begin to fly at 3 weeks of age (Hoying, 1983; Lane, 1946) and achieve adult-like flight and foraging abilities about 1 week later (Hoying, 1983). Rapid postnatal growth, as determined by changes in forearm length, occurs during the first 18 days after birth (Hoying, 1983). Complete closure of the epiphyseal gap in the fourth metacarpal occurs at approximately 45 days of age (Hoying, 1983).

LaVal and LaVal (1980) reported that subadult pipistrelles were first observed to arrive at hibernacula by 5 August in eastern Missouri. Davis (1963) observed that subadults in Vermont, Ontario, and Quebec had not undergone first molt and the epiphyses had not closed by the time they entered hibernation. No apparent growth occurred during hibernation as epiphyses were still open and subadults were easily distinguished from adults on the basis of coat color by the time of arousal in May and April. In contrast, subadults from more southern populations in West Virginia, Kentucky, and Florida molted in autumn and the epiphyses were closed by the

time young entered hibernation. Based on the recapture of one known-age banded female that returned to its place of birth and subsequently gave birth to two normal-sized young, Hoying (1983) estimated that sexual maturity in this individual was attained between 3 and 11 months of age. Attainment of sexual maturity in the first year, however, may not be characteristic of *P. subflavus* throughout its entire range.

ECOLOGY AND BEHAVIOR. Winter hibernacula and summer maternity sites generally are at separate locations (Griffin, 1934, 1936; Guthrie, 1933b). During winter, males and females are not segregated (Griffin, 1940a) and hibernate in relatively small numbers in caves, mines, and other man-made structures, often in association with *Myotis lucifugus*, *M. keenii*, *M. sodalis*, *M. austroriparius*, *M. grisescens*, or *Eptesicus fuscus* (Davis, 1964; Fenton, 1970; Folk, 1940; Goehring, 1954; Griffin, 1940a; Guthrie, 1933b; Hall, 1962, 1963; Hitchcock, 1949; Jennings and Layne, 1957; Mumford and Whitaker, 1975; Myers, 1960; Swanson and Evans, 1936). *Pipistrellus subflavus* normally does not hibernate in clusters, but usually roosts singly (Guthrie, 1933b; Hall, 1962; Hitchcock, 1949; McNab, 1974). It selects deeper parts of caves where ambient temperatures usually are relatively constant (Fitch, 1966; Hall, 1962; Hitchcock, 1949). Disproportionate sex ratios in hibernating populations were reported (Davis, 1959b; Hall, 1962; Hitchcock, 1949; Mohr, 1942; Sealander and Young, 1955) and were attributed to higher survival rates of males (Davis, 1959b) and differences in male and female selection of hibernacula (Jones and Pagels, 1968). LaVal and LaVal (1980) noted that the large number of bats captured at cave hibernacula in Missouri in late April and May, and again in late July and August, suggested that individuals of this species were among the first bats to enter hibernacula in autumn and the last to leave in spring. The large number of marked bats recaptured during the August swarming period demonstrated strong fidelity to specific hibernacula.

In spring, pipistrelles disperse from hibernacula and migrate to maternity roosts. Maternity colonies are found most frequently in barns (Hoying, 1983; Lane, 1946; Poole, 1938) and other man-made structures (Allen, 1921; Jones and Pagels, 1968; Jones and Suttkus, 1973). Trees, caves, and rock crevices (Allen, 1921; Humphrey, 1975; Humphrey et al., 1976) also may serve as maternity sites. During the maternity period, sexes are segregated (Hamilton, 1943) and males are presumed to be solitary (Lane, 1946). Solitary bats were reported to roost in trees (Findley, 1954).

Allen (1921) banded four adult female *P. subflavus* in central New York, and recovered them 3 years later when they returned to the summer roost where they were banded originally; this marked the first attempt to use banding techniques to study migration in North American bats. Since then, thousands of bats of many species including *P. subflavus* have been banded to yield valuable information on movement, migration distance, homing ability, and longevity (Davis, 1966; Griffin, 1936, 1945). The longest migration distance recorded for *P. subflavus* was of a female bat banded in April at Sheffield, Massachusetts, and recovered at Katonah, New York, indicating that it had flown at least 52.8 km to its winter hibernaculum (Griffin, 1940b). Also, *P. subflavus* exhibited a marked homing instinct in that individuals returned to the same summer roosts year after year (Griffin, 1934).

The greatest longevity record for *P. subflavus*, is for a male, captured in Illinois 14.8 years after it was banded (Walley and Jarvis, 1972). Other records include ages of approximately 11 years (Paradiso and Greenhall, 1966), 10 years (Mohr, 1953), 7 years (Cockrum, 1952) and 6 years (Hitchcock, 1965). Davis and Hitchcock (1965) showed that high mortality among juvenile *P. subflavus* occurred during the second summer and that males had a higher probability of survival than females. Davis (1966) noted that survivorship curves did not approximate an exponential decay curve that might be expected if constant mortality rates were assumed for each age class. Rather, he stated that high mortality exists between the first and second hibernation season, most probably during winter and not during the second summer as previously thought. Survivorship during the third and fourth years was exceptionally high, but decreased afterward and fell sharply as individuals approached maximum life span. However, Baker (1978) argued that, because survivorship was based on returns of banded individuals to a specific location, variation in survivorship observed by Davis (1966) could not be distinguished from that caused by "removal migration" of individuals to different home ranges. Baker (1978) noted that re-

moval migration observed in *P. subflavus* was most frequent during the first 2 years of life, minimal at 4 years, and slowly increased with age and was more frequent in females than in males—a pattern that tracks changes in recaptures attributed to survivorship by Davis (1966).

Failure to store sufficient fat reserves may cause significant mortality among subadults during the first hibernation season (Davis, 1966). Mortality may be especially high during the preflight period when initial flight attempts are made by young incapable of returning to the roost and are not retrieved by their mothers (Hoying, 1983). Mortality from predation, accidents, disturbance, and inclement weather have been documented, although no consistent predators or causes of mortality were found (Gillette and Kimbrough, 1970). Predators included a vole (*Microtus ochragaster*; Martin, 1961), a leopard frog (*Rana pipiens*; Creel, 1963), and a hoary bat (*Lasiurus cinereus*; Bishop, 1947). High losses in populations from flooding of caves (DeBlase et al., 1965) and from severe snow storms (Rysgaard, 1941) were recorded.

Most accounts of feeding ecology indicate that *P. subflavus* forages most commonly over waterways and at forest edges (Barley, 1923; Blair, 1935; Bowles, 1975; Davis and Mumford, 1962; LaVal et al., 1977; Paradiso, 1969; Rausch, 1946; Schmidly et al., 1977). This species has a characteristically slow (approximately 18.7 km/h in an open field; Patterson and Hardin, 1969), erratic, and fluttery flight while foraging (Hahn, 1908; Hoying, 1983; Lewis, 1940; Paradiso, 1969) and is among the earliest species to feed in the evening (Hamilton, 1943). Gould (1955) reported that in a 30-min foraging bout, pipistrelles acquired 1.4 to 1.7 g of food or one food item every 2 s. Analyses of stomach contents revealed that the diet of *P. subflavus* included species of Coleoptera (primarily carabids), Homoptera (primarily cicadillids), Diptera (primarily culicids and chironomids), Hymenoptera (primarily formicids), and Lepidoptera (Ross, 1967; Sherman, 1939; Whitaker, 1972). Prey items generally consist of small insects ranging from 4 to 10 mm in length (Ross, 1967).

No virus or antibodies of eastern equine encephalitis (EEE) were detected in a small sample of *Pipistrellus subflavus*, although *Myotis lucifugus* and *Eptesicus fuscus* were found to harbor antibodies to EEE (Daniels et al., 1960; Main, 1979). The incidence of rabies infection has been relatively low in *P. subflavus* (Constantine, 1967; Daniels et al., 1960; Whitaker and Miller, 1974; Wiseman et al., 1962). Tesh and Schneidan (1967) tested samples of tissue and feces from *P. subflavus* for the presence of histoplasmosis; among eight North American bat species, only *P. subflavus* and *Tadarida brasiliensis* were negative.

Endoparasites recorded from *P. subflavus* include the trematodes, *Acanthatrium pipistrelli* (Macy, 1940), *A. macyi*, *Prosthodendium oligolecithum*, and *Plagiorchis micracanthos* (Jones, 1957). Infection by trematodes in males was almost twice that in females and the helminth burden was lowest after hibernation, increased in spring and reached a peak in autumn (Nickel and Hansen, 1967). Oocysts of the coccidian, *Eimeria macyi*, were first described from cecal contents of *P. subflavus* (Wheat, 1975). Chute and Covalt (1960) found that the development of experimental infections of *Trichinella spiralis* in *P. subflavus* was inhibited when the body temperature of the host was decreased.

Ectoparasites include chiggers (*Euscongastia pipistrelli*; Sealander and Young, 1955; Whitaker and Mumford, 1971), with infestation rates of 23.2% and 23.8% reported (Whitaker, 1973; Whitaker and Loomis, 1979). *Euscongastia staffordi*, *E. pipistrelli*, and a new genus and species record for *Perissopalla flagil-lesutata* were recorded from pipistrelles (Brennan and White, 1960). *Macronyssus crosbyi* and *M. unidens* collected from *P. subflavus* represent host records for these acarids (Reisen et al., 1976). Sealander and Young (1955) noted that spinturnicid mites were frequently occurring ectoparasites. Yunker (1958) found myobiid mites (*Neomyobia caudata*) on one specimen of *P. subflavus*.

Griffin and Welsh (1937) reported persistent, well defined 24-h activity rhythms regardless of the various light and dark regimes to which individuals were subjected. *Pipistrellus subflavus* was included in a study of the cochlear potentials elicited by ultrasounds (Galambos, 1942); this was the first demonstration that bats could perceive supersonic sounds, thus supporting the auditory theory of obstacle avoidance in flying bats.

GENETICS. The diploid number of chromosomes of *P. subflavus* is 30, with a fundamental number of 56 (Baker and Patton, 1967). Autosomes consist of 10 large to medium metacen-

tric and submetacentric pairs and 4 small submetacentric pairs. The X-chromosome is a medium-sized submetacentric; the Y-chromosome is small and acrocentric. Baker and Patton (1967) noted that the large chromosomal discrepancies between *P. hesperus* and *P. subflavus* were not typical of most other vespertilionid genera. Bickham (1979) noted that an exceptionally large amount of variation was evident in the karyotypes of Old and New World pipistrelles, and that *Pipistrellus* may be a more specialized genus of vespertilionids by virtue of its lower chromosome number with respect to more primitive but related genera.

REMARKS. Various vernacular names have been applied to *Pipistrellus subflavus* including Georgian bat, pigmy bat, and southern pipistrel. The most frequently used name is the eastern pipistrelle.

The generic name is derived from the Italian word, "pipistrello," meaning bat. The specific name is derived from the two Latin roots, "sub," meaning somewhat, and "flavus" meaning yellow.

We would like to thank Allen Kurta and Elaine Anderson for editorial comments, Stephen Bartz for providing technical assistance in the preparation of the skull illustrations, and Maria Rutzmoser for providing access to specimens at the Museum of Comparative Zoology, Harvard University.

LITERATURE CITED

- ALLEN, A. A. 1921. Banding bats. *J. Mamm.*, 2:53-57.
- AUDUBON, J. J., AND J. BACHMAN. 1842. Descriptions of new species of quadrupeds inhabiting North America. *Philadelphia Acad. Nat. Sci. J.*, 8:280-323.
- BAER, G. M. 1966. A method for bleeding small bats. *J. Mamm.*, 47:340.
- BAKER, R. H. 1954. A new bat (genus *Pipistrellus*) from north-eastern Mexico. *Univ. Kansas Publ., Mus. Nat. Hist.*, 7:583-586.
- BAKER, R. J., AND J. L. PATTON. 1967. Karyotypes and karyotypic variation of North American vespertilionid bats. *J. Mamm.*, 48:270-286.
- BAKER, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier, New York, 1012 pp.
- BARBOUR, R. W., AND W. H. DAVIS. 1969. *Bats of America*. Univ. Press of Kentucky, Lexington, 286 pp.
- BARLEY, V. 1923. Mammals of the District of Columbia. *Proc. Biol. Soc. Washington*, 36:103-138.
- BICKHAM, J. W. 1979. Chromosomal variation and evolutionary relationships of vespertilionid bats. *J. Mamm.*, 60:350-363.
- BISHOP, S. C. 1947. Curious behavior of a hoary bat. *J. Mamm.*, 28:293-294.
- BLAIR, W. F. 1935. The mammals of a Florida hammock. *J. Mamm.*, 16:271-277.
- . 1948. A color pattern aberration in *Pipistrellus subflavus subflavus*. *J. Mamm.*, 29:178-179.
- BOWLES, J. B. 1975. Distribution and biogeography of mammals of Iowa. *Spec. Publ. Mus., Texas Tech Univ.*, 9:1-184.
- BRENNAN, J. M., AND J. S. WHITE. 1960. New records and descriptions of chiggers (Acarina:Trombiculidae) on bats in Alabama. *J. Parasitol.*, 46:346-350.
- BRIMLEY, C. S. 1923. Breeding dates of small mammals of Raleigh, North Carolina. *J. Mamm.*, 4:263-264.
- BUCHOLZ, R. H. 1958. Digestive enzymes of mole, bat and rats. *J. Mamm.*, 39:452-454.
- CHUTE, R. M., AND D. B. COVALT. 1960. The effect of body temperature on the development of *Trichinella spiralis* in bats. *J. Parasitol.*, 46:855-858.
- COCKRUM, E. L. 1952. Longevity in the pipistrelle, *Pipistrellus subflavus subflavus*. *J. Mamm.*, 33:491-492.
- CONSTANTINE, D. G. 1967. Bat rabies in the southwestern United States. *Publ. Health Rept.*, 82:867-888.
- COPE, J. B., AND S. R. HUMPHREY. 1972. Reproduction of the bats *Myotis keenii* and *Pipistrellus subflavus* in Indiana. *Bat Res. News*, 13:9-10.
- CREEL, G. C. 1963. Bats as a food item of *Rana pipiens*. *Texas J. Sci.*, 15:104.
- CUVIER, F. 1832. *Essai de classification naturelle des vespertili- lions, et description de plusieurs espèces de ce genre*. *Nouv. Ann. du Mus. Hist. Nat.*, 1:1-21.
- DALQUEST, W. W., AND H. J. WERNER. 1954. Histological as-

- pects of the faces of North American bats. *J. Mamm.*, 35: 147-160.
- DALQUEST, W. W., E. ROTH, AND F. JUDD. 1969. The mammal fauna of Schulze Cave, Edwards County, Texas. *Bull. Florida State Mus.*, 13:206-276.
- DANIELS, J. B., ET AL. 1960. A search for encephalitis and rabies in bats of eastern Massachusetts. *New England J. Med.*, 263: 516-520.
- DAVIS, W. H. 1957. A new subspecies of the eastern pipistrelle from Florida. *Proc. Biol. Soc. Washington*, 70:213-216.
- . 1959a. Taxonomy of the eastern pipistrel. *J. Mamm.*, 40:521-531.
- . 1959b. Disproportionate sex ratios in hibernating bats. *J. Mamm.*, 40:16-19.
- . 1963. Aging bats in winter. *Trans. Kentucky Acad. Sci.*, 24:28-30.
- . 1964. Winter awakening patterns in the bats *Myotis lucifugus* and *Pipistrellus subflavus*. *J. Mamm.*, 45:645-647.
- . 1966. Population dynamics of the bat *Pipistrellus subflavus*. *J. Mamm.*, 47:383-396.
- DAVIS, W. H., AND H. B. HITCHCOCK. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. *J. Mamm.*, 46:296-313.
- DAVIS, W. H., AND R. E. MUMFORD. 1962. Ecological notes on the bat, *Pipistrellus subflavus*. *Amer. Midland Nat.*, 68:394-398.
- DAVIS, W. H., AND O. B. REITE. 1967. Responses of bats from temperate regions to changes in ambient temperature. *Biol. Bull.*, 132:320-328.
- DAWSON, D. L. 1980. Functional interpretations of the radiographic anatomy of the femora of *Myotis lucifugus*, *Pipistrellus subflavus* and *Blarina brevicauda*. *Amer. J. Anat.*, 157:1-15.
- DEBLASE, A. F., S. R. HUMPHREY, AND K. S. DRURY. 1965. Cave flooding and mortality in bats in Wind Cave, Kentucky. *J. Mamm.*, 46:96.
- FARNEY, J., AND E. D. FLEHARTY. 1969. Aspect ratio, loading, wing span, and membrane areas of bats. *J. Mamm.*, 50:362-367.
- FENTON, M. B. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. *Life Sci. Contrib. Royal Ontario Mus.*, 77:1-34.
- FINDLEY, J. S. 1954. Tree roosting of the eastern pipistrelle. *J. Mamm.*, 35:433.
- FITCH, J. H. 1966. Weight loss and temperature response in three species of bats in Marshall County, Kansas. *Search*, 6: 17-24.
- FOLK, C. E., JR. 1940. Shift population among hibernating bats. *J. Mamm.*, 21:306-315.
- FORMAN, G. L. 1968. Comparative gross morphology of spermatozoa of two families of North American bats. *Univ. Kansas Sci. Bull.*, 67:901-928.
- GALAMBOS, R. 1942. Cochlear potentials elicited from bats by supersonic sounds. *J. Acoust. Soc. Amer.*, 14:41-49.
- GILLETTE, D. D., AND J. D. KIMBROUGH. 1970. Chiropteran mortality. Pp. 262-283, in *About bats* (R. H. Slaughter and D. W. Walton, eds.). Southern Methodist Univ. Press, Dallas, 339 pp.
- GOEHRING, H. H. 1954. *Pipistrellus subflavus obscurus*, *Myotis keenii*, and *Eptesicus fuscus* hibernating in a storm sewer in central Minnesota. *J. Mamm.*, 35:434-435.
- GOSLIN, R. 1942. A bat with white wingtips. *J. Mamm.*, 28:62.
- GOULD, E. 1955. The feeding efficiency of insectivorous bats. *J. Mamm.*, 36:399-407.
- GRIFFIN, D. R. 1934. Marking bats. *J. Mamm.*, 15:202-207.
- . 1936. Bat banding. *J. Mamm.*, 17:235-239.
- . 1940a. Notes on the life histories of New England cave bats. *J. Mamm.*, 21:181-187.
- . 1940b. Migrations of New England bats. *Bull. Mus. Comp. Zool.*, 86:217-246.
- . 1945. Travels of banded cave bats. *J. Mamm.*, 26:15-23.
- GRIFFIN, D. R., AND J. H. WELSH. 1937. Activity rhythms in bats under constant external conditions. *J. Mamm.*, 18:337-342.
- GUILDAY, J. E. 1962. The Pleistocene local fauna of the Natural Chimneys, Augusta County, Virginia. *Ann. Carnegie Mus.*, 36: 87-122.
- GUILDAY, J. E., AND H. W. HAMILTON. 1978. Ecological significance of displaced boreal mammals in West Virginia caves. *J. Mamm.*, 59:176-181.
- GUILDAY, J. E., H. W. HAMILTON, AND A. D. MCCRADY. 1966. The bone breccia of Bootlegger Sink, York County, Pennsylvania. *Ann. Carnegie Mus.*, 38:145-163.
- . 1969. The Pleistocene vertebrate fauna of Robinson Cave, Overton County, Tennessee. *Paleovertebrata*, 2:25-75.
- . 1971. The Welsh Cave peccaries (*Platygonus*) and associated fauna, Kentucky Pleistocene. *Ann. Carnegie Mus.*, 43:249-320.
- GUILDAY, J. E., P. S. MARTIN, AND A. D. MCCRADY. 1964. New Paris No. 4: a Pleistocene cave deposit in Bedford County, Pennsylvania. *Bull. Nat. Speleol. Soc.*, 26:121-194.
- GUILDAY, J. E., P. W. PARMALLEE, AND H. W. HAMILTON. 1977. The Clark's Cave bone deposit and the late Pleistocene paleoecology of the central Appalachian Mountains of Virginia. *Bull. Carnegie Mus. Nat. Hist.*, 2:1-88.
- GUILDAY, J. E., H. W. HAMILTON, E. ANDERSON, AND P. W. PARMALLEE. 1978. The Baker Bluff Cave deposit, Tennessee, and the late Pleistocene faunal gradient. *Bull. Carnegie Mus. Nat. Hist.*, 11:1-67.
- GUTHRIE, M. J. 1933a. The reproductive cycles of some cave bats. *J. Mamm.*, 14:199-216.
- . 1933b. Notes on the seasonal movements and habits of some cave bats. *J. Mamm.*, 14:1-19.
- HAHN, W. L. 1908. Some habits and sensory adaptations of cave-inhabiting bats. *Biol. Bull.*, 15:135-193.
- HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1-600+90.
- HALL, E. R., AND W. W. DALQUEST. 1950. A synopsis of the American bats of the genus *Pipistrellus*. *Univ. Kansas Publ. Mus. Nat. Hist.*, 1:591-602.
- HALL, J. S. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. *Reading Public Mus. and Art Gallery Sci. Publ.*, 12:1-68.
- . 1963. Notes on *Plecotus rafinesquii* in central Kentucky. *J. Mamm.*, 44:119-120.
- HAMILTON, W. J., JR. 1943. The mammals of eastern United States. Comstock Publ. Co., Ithaca, New York, 432 pp.
- . 1949. The bacula of some North American vespertilionid bats. *J. Mamm.*, 30:97-102.
- HAWKSLEY, O., J. E. REYNOLDS, AND R. L. FOLEY. 1973. Pleistocene vertebrate fauna of Bat Cave, Pulaski County, Missouri. *Bull. Natl. Speleol. Soc.*, 35:61-87.
- HIRTH, H. F. 1960. The spermatozoa of some North American bats and rodents. *J. Morphol.*, 106:77-83.
- HITCHCOCK, H. B. 1949. Hibernation of bats in southeastern Ontario and adjacent Quebec. *Canadian Field-Nat.*, 63:47-59.
- . 1965. Twenty-three years of bat banding in Ontario and Quebec. *Canadian Field-Nat.*, 79:4-14.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press Inc. and The Association of Systematic Collections, Lawrence, Kansas, 694 pp.
- HOOD, C. H., AND O. HAWKSLEY. 1975. A Pleistocene fauna from Zoo Cave, Taney County, Missouri. *Missouri Speleol.*, 15:1-42.
- HOYING, K. 1983. Growth and development of the eastern pipistrelle bat, *Pipistrellus subflavus*. Unpubl. M.A. thesis, Boston Univ., Boston, 148 pp.
- HUMPHREY, S. R. 1975. Nursery roosts and community diversity of nearctic bats. *J. Mamm.*, 56:321-346.
- HUMPHREY, S. R., R. K. LAVAL, AND R. L. CLAWSON. 1976. Nursery populations of *Pipistrellus subflavus* (Chiroptera, Vespertilionidae) in Missouri. *Trans. Illinois State Acad. Sci.*, 69:367.
- JENNINGS, W. L. 1958a. The ecological distribution of bats in Florida. Unpubl. Ph.D. dissert., Univ. Florida, Gainesville, 126 pp.
- . 1958b. Polydactyly in the eastern pipistrel. *J. Mamm.*, 39:437-438.
- JENNINGS, W. L., AND J. N. LAYNE. 1957. *Myotis sodalis* in Florida. *J. Mamm.*, 38:259.

- JONES, C., AND J. PAGELS. 1968. Notes on a population of *Pipistrellus subflavus* in southern Louisiana. *J. Mamm.*, 49:134-139.
- JONES, C., AND R. D. SUTTKUS. 1973. Colony structure and organization of *Pipistrellus subflavus* in southern Louisiana. *J. Mamm.*, 54:962-968.
- JONES, J. K., JR. 1957. Type hosts of the bat trematodes *Prosthodendrium oligolecithum* (Manter and Debus, 1945) and *Acanthatrium macyi* (Sogandareberrel, 1956). *J. Parasitol.*, 43:185.
- KURTA, A. 1982. A review of Michigan bats: seasonal and geographic distribution. Michigan Academician, 14:295-312.
- KURTÉN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia Univ. Press, New York, 442 pp.
- LANE, H. K. 1946. Notes on *Pipistrellus subflavus subflavus* (F. Cuvier) during the season of parturition. *Proc. Pennsylvania Acad. Sci.*, 20:57-61.
- LAVAL, R. K., AND M. L. LAVAL. 1980. Ecological studies and management of Missouri bats with emphasis on cave-dwelling species. *Terrestrial Ser. Missouri Dept. Conserv.*, 8:1-53.
- LAVAL, R. K., R. L. CLAWSON, M. L. LAVAL, AND W. CLAIRE. 1977. Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. *J. Mamm.*, 58:592-599.
- LEWIS, J. B. 1940. Mammals of Amelia County, Virginia. *J. Mamm.*, 21:422-428.
- MACY, R. W. 1940. Description of three new trematodes with notes on other species of *Acanthatrium* (Lecithodendriidae) and a key to the genus. *J. Parasitol.*, 26:279-286.
- MAIN, A. J. 1979. Virologic and serologic survey for eastern equine encephalomyelitis and certain other viruses in colonial bats of New England. *J. Wildl. Dis.*, 15:455-466.
- MARTIN, R. A. 1974a. Fossil mammals from the Coleman IIA fauna, Sumter County. Pp. 35-99, in *Pleistocene Mammals of Florida* (S. D. Webb, ed.). Univ. Florida Presses, Gainesville, Florida, 270 pp.
- . 1974b. Fossil vertebrates from the Haile XIVA fauna, Alachua County. Pp. 100-113, in *Pleistocene mammals of Florida* (S. D. Webb, ed.). Univ. Florida Presses, Gainesville, Florida, 270 pp.
- MARTIN, R. A., AND S. D. WEBB. 1974. Late Pleistocene mammals from the Devil's Den fauna, Levy County. Pp. 114-145, in *Pleistocene mammals of Florida* (S. D. Webb, ed.). Univ. Florida Presses, Gainesville, Florida, 270 pp.
- MARTIN, R. L. 1961. Vole predation on bats in an Indiana cave. *J. Mamm.*, 42:540-541.
- MENNAB, B. K. 1974. The behavior of temperate cave bats in a subtropical environment. *Ecology*, 55:943-958.
- MOHR, C. E. 1942. Bat tagging in Pennsylvania turnpike tunnels. *J. Mamm.*, 23:375-379.
- . 1953. A survey of bat banding in North America, 1932-1951. *Amer. Caver Bull.*, 14:3-13.
- MUMFORD, R. E., AND J. O. WHITAKER, JR. 1975. Seasonal activity of bats at an Indiana cave. *Proc. Indiana Acad. Sci.*, 84:500-507.
- MYERS, P. 1978. Sexual dimorphism in size of vespertilionid bats. *Amer. Nat.*, 112:701-711.
- MYERS, R. F. 1960. *Lasiurus* from Missouri caves. *J. Mamm.*, 41:114-117.
- NASON, E. S. 1948. Morphology of hair of eastern North American bats. *Amer. Midland Nat.*, 39:345-361.
- NICKEL, P. A., AND M. F. HANSEN. 1967. Helminths of bats collected in Kansas, Nebraska and Oklahoma. *Amer. Midland Nat.*, 78:481-486.
- OSGOOD, F. L. 1936. Melanistic pipistrelles. *J. Mamm.*, 17:64.
- PARADISO, J. L. 1969. Mammals of Maryland. *N. Amer. Fauna*, 66:1-193.
- PARADISO, J. L., AND A. M. GREENHALL. 1966. Longevity records for American bats. *Amer. Midland Nat.*, 78:251-252.
- PARMALEE, P. W., AND R. D. OESCH. 1972. Pleistocene and Recent faunas from the Brynjulfson Caves, Missouri. *Illinois State Mus. Rep. Invest.*, 25:1-52.
- PARMALEE, P. W., R. D. OESCH, AND J. E. GUILDAY. 1969. Pleistocene and Recent vertebrate faunas from Crankshaft Cave, Missouri. *Illinois State Mus. Rep. Invest.*, 14:1-37.
- PATTERSON, A. P., AND J. W. HARDIN. 1969. Flight speeds of five species of vespertilionid bats. *J. Mamm.*, 50:152-153.
- PLOSKEY, G. R., AND J. A. SEALANDER. 1979. Lipid deposition and withdrawal in *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). *Southwestern Nat.*, 24:71-78.
- POOLE, E. L. 1936. Relative wing ratios of bats and birds. *J. Mamm.*, 17:412-413.
- . 1938. Notes on the breeding of *Lasiurus* and *Pipistrellus* in Pennsylvania. *J. Mamm.*, 19:249.
- RAUSCH, R. 1946. Collecting bats in Ohio. *J. Mamm.*, 27:275-276.
- REISEN, W. K., M. L. KENNEDY, AND N. T. REISEN. 1976. Winter ecology of ectoparasites collected from hibernating *Myotis velifer* (Allen) in southwestern Oklahoma (Chiroptera: Vespertilionidae). *J. Parasitol.*, 62:628-635.
- ROSS, A. 1967. Ecological aspects of the food habits of insectivorous bats. *Proc. Western Found. Vert. Zool.*, 1:205-263.
- ROTH, E. L. 1972. Late Pleistocene mammals from Klein Cave, Kerr County, Texas. *Texas J. Sci.*, 24:75-84.
- RYSCGAARD, G. N. 1941. Bats killed in a severe storm. *J. Mamm.*, 22:452-453.
- SCHMIDLY, D. J., K. T. WILKINS, R. L. HONEYCUTT, AND B. C. WEYNAND. 1977. The bats of east Texas. *Texas J. Sci.*, 28:127-143.
- SEALANDER, J. A. 1964. The influence of body size, season, sex, age and other factors upon some blood parameters in small mammals. *J. Mamm.*, 45:598-616.
- SEALANDER, J. A., AND H. YOUNG. 1955. Preliminary observations of the cave bats of Arkansas. *Proc. Arkansas Acad. Sci.*, 7:21-31.
- SHERMAN, H. B. 1939. Notes on the food of some Florida bats. *J. Mamm.*, 20:103-104.
- SWANSON, G., AND C. EVANS. 1936. The hibernation of certain bats in southern Minnesota. *J. Mamm.*, 17:39-43.
- TEMMINCK, C. J. 1835-1841. Monographies de mammalogie; ou, Description de quelques genres de mammifères dont les espèces ont été observées dans les différents musées de l'Europe. C. C. van der Hoeck, Leiden, 2:1-329+45 plates.
- TESH, R. B., AND J. D. SCHNEIDAN, JR. 1967. Naturally occurring histoplasmosis among bat colonies in the southeastern United States. *Amer. J. Epidemiol.*, 86:545-551.
- TRAPIDO, H., AND P. E. CROWE. 1942. Color abnormalities in three genera of northeastern cave bats. *J. Mamm.*, 23:303-305.
- WALLEY, H. D., AND W. L. JARVIS. 1972. Longevity record for *Pipistrellus subflavus*. *Trans. Illinois State Acad. Sci.*, 64:305.
- WARD, H. L. 1891. Descriptions of three new species of Mexican bats. *Amer. Nat.*, 25:743-753.
- WHEAT, B. E. 1975. *Eimeria macyi* sp. n. (Protozoa: Eimeriidae) from the eastern pipistrelle, *Pipistrellus subflavus* from Alabama. *J. Parasitol.*, 61:920-922.
- WHITAKER, J. O., JR. 1972. Food habits of bats from Indiana. *Canadian J. Zool.*, 50:877-883.
- . 1973. External parasites of bats of Indiana. *J. Parasitol.*, 59:1148-1150.
- WHITAKER, J. O., JR., AND R. B. LOOMIS. 1979. Chiggers (Acarina: Trombiculidae) from the mammals of Indiana. *Proc. Indiana Acad. Sci.*, 88:426-433.
- WHITAKER, J. O., JR., AND W. A. MILLER. 1974. Rabies in bats of Indiana, 1968-1972. *Proc. Indiana Acad. Sci.*, 83:469-472.
- WHITAKER, J. O., JR., AND R. E. MUMFORD. 1971. Notes on a collection of bats taken by mist-netting at an Indiana cave. *Amer. Midland Nat.*, 85:277-279.
- WIMSATT, W. A. 1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. *J. Mamm.*, 26:23-33.
- WISEMAN, J. S., B. L. DAVIS, AND J. E. GRIMES. 1962. Rabies infection in the red bat, *Lasiurus borealis borealis* (Muller), in Texas. *J. Mamm.*, 43:279-280.
- YUNKER, C. E. 1958. The parasitic mites of *Myotis lucifugus* (Le Conte). *Proc. Helminth. Soc.*, 25:31-34.

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