

Otomops martiensseni. By Jennifer K. Long

Published 23 June 1995 by The American Society of Mammalogists

Otomops Thomas, 1913

Otomops Thomas, 1913:90. Type species *Nyctinomus wroughtoni* Thomas, 1913, by original designation.

CONTEXT AND CONTENT. Order Chiroptera, Family Molossidae. The genus *Otomops* contains six known species. Key characters used here were taken primarily from Dorst (1953), Freeman (1981), and Kitchener et al. (1992).

- 1 Size large (forearm 63-66 mm) 2
Size smaller (forearm usually <60 mm) 3
- 2 Found in Africa and Madagascar; rostrum delicate; diastema present between canine and first upper premolar
..... *O. martiensseni* Indian species; rostrum less delicate than that of *O. martiensseni*; first upper premolar confined between canine and second premolar
..... *O. wroughtoni*
- 3 Size smaller (forearm usually <59 mm); New Guinean species 4
Size larger (forearm usually >58 mm); not located in New Guinea 5
- 4 NE New Guinea, collar well defined and pale; forearm >54 mm *O. secundus*
W New Guinea, collar barely defined; forearm <54 mm
..... *O. papuensis*
- 5 Pelage on head dark (same color as lower back); Alor Island *O. johnstonei* Pelage on head lighter than that of lower back; W. Java *O. formosus*

Otomops martiensseni (Matschie, 1897)

Giant Mastiff Bat

Nyctinomus martiensseni Matschie, 1897:84. Type locality "Plantago Magrotto unweit Tanga" (Magrotto Plantation, southeast Usambara Mountains, Tanzania).

Otomops icarus Chubb, 1917:433. Type locality "Durban, Natal, South Africa."

Otomops madagascarensis Dorst, 1953:236. Type locality "Cave P. Saboureaux in reservation No. 8 in Namoroka, Madagascar."

CONTEXT AND CONTENT. Context as in generic summary. Currently, some authors recognize three subspecies of *O. martiensseni* (Freeman, 1981; Hayman and Hill, 1971). However, due to possible misidentification of several specimens, the distribution of *icarus* is unclear. Several authors express doubt regarding the validity of *icarus* as a subspecies (Hill and Carter, 1941; not seen, cited in Meester et al., 1986).

O. m. icarus (Chubb, 1917:433), see above.

O. m. madagascarensis (Dorst, 1953:236), see above.

O. m. martiensseni (Matschie, 1897:84), see above.

DIAGNOSIS. *Otomops martiensseni* is the only African member of its genus. It is also the largest member of the genus (length of forearm 62-73 mm). The ears are very large and long (about 40 mm, Fig. 1); they are attached along the whole length of the head and conjoined on the extended snout. There is a very prominent vertical projection on the zygomatic protuberance, and a diastema separating the first and second upper premolars (Dorst, 1953). This diastema is not present in any other species of *Otomops*. The muzzle of *O. martiensseni* is less bulky and wide than that of *O. wroughtoni*; the rostrum is more delicate and appears less raised in profile (Dorst, 1953).

GENERAL CHARACTERISTICS. The fur of *O. martiensseni* is relatively short, fine and velvety. The dorsal pelage is dark brown with a pale or whitish band across the shoulders in most

specimens, although there is some variation among individuals and/or possible subspecies (Harrison, 1957). Ventral pelage is similar to the dorsal in most specimens; it ranges from pale brown to dark black-brown. A very thin band of white fur borders the body from the shoulder to the knee on the dorsal side (Skinner and Smithers, 1990).

The body is streamlined; proportions are slender compared to other molossids. The tail extends distally from the interfemoral membrane and ranges from 33-42 mm in length (\bar{x} = 36.5 mm, n = 10; males and females; Skinner and Smithers, 1990). The pinnae are rigid and have small spines along their anterior borders. The tragus and antitragus are both absent. A moveable lobe or flange behind the antitragal position runs from the back to the middle of the ear. The upper lips are very finely wrinkled and form into flaps on either side. A gular gland is present in both sexes; it is marked by a conspicuous circular skin pocket on the throat (Kingdon, 1974).

The skull has moderately well developed sagittal and lambdoidal crests; the top of the braincase is domed (Fig. 2). The permanent dentition consists of 30 teeth: i 1/2, c 1/1, p 2/2, m 3/3 (Dorst, 1953). The first upper premolar is smaller than the second; premolars are not molariform. Molars possess a W-shaped loph pattern (Freeman, 1981).

Ranges and means of external measurements for males (n = 4) and females (n = 6), respectively (in mm) are: head and body,

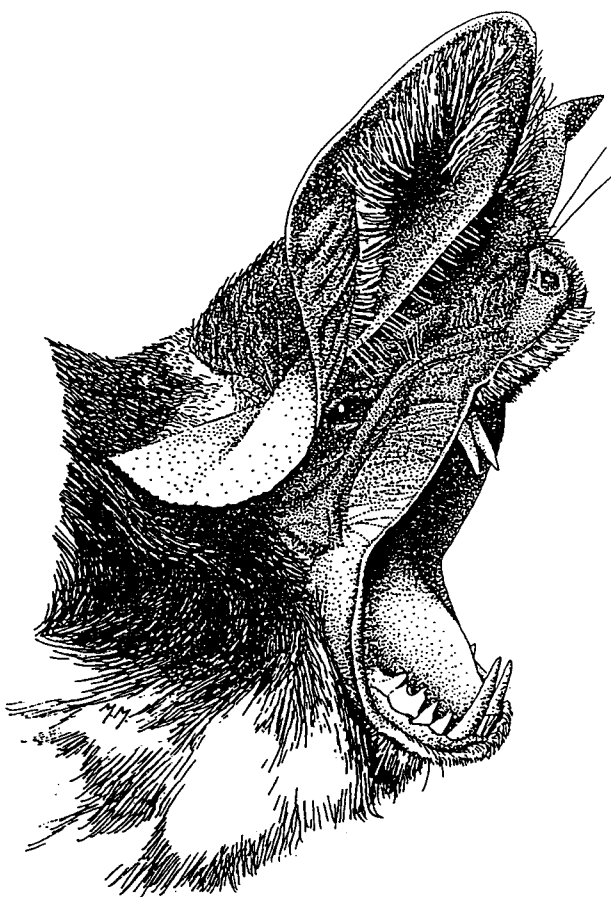


FIG. 1. Giant mastiff bat, *Otomops martiensseni*. Drawing by Mark Marcuson (from Freeman, 1983).

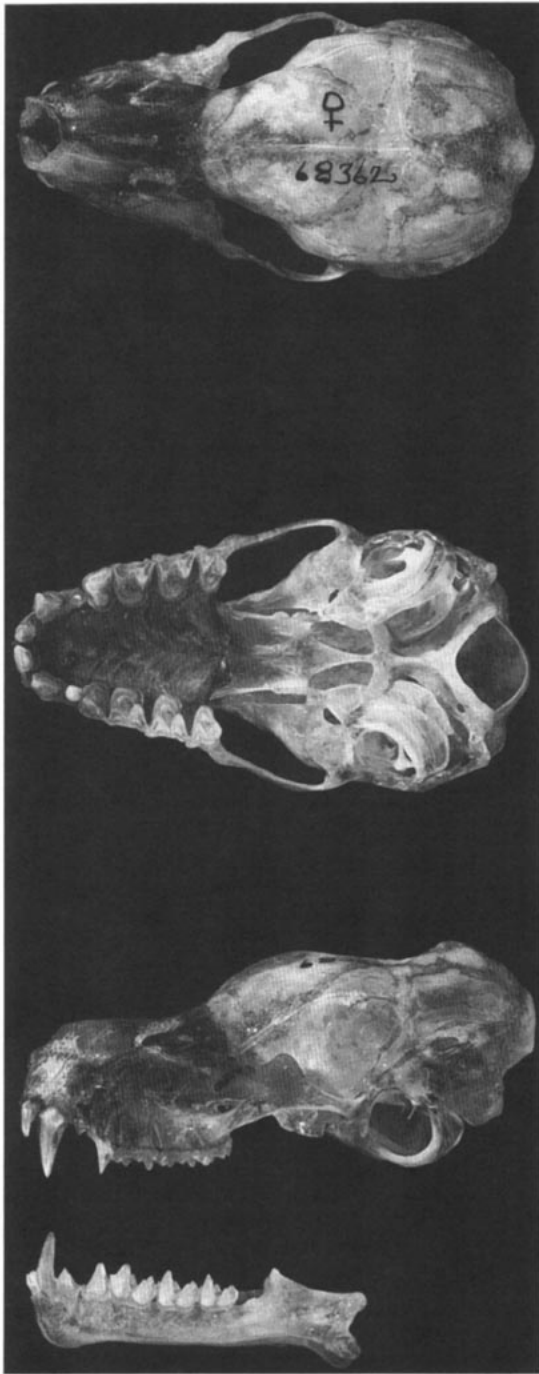


FIG. 2. Dorsal, ventral and lateral views of cranium and lateral view of mandible of a female *Otomops martiensseni* (Royal Ontario Museum, 68362) from Kenya. Photos taken by Brian Boyle, Royal Ontario Museum.

78–93 (\bar{x} = 84), 94–103 (\bar{x} = 98); tail, 35–37 (\bar{x} = 36), 33–42 (\bar{x} = 37); length of forearm, 52–58 (\bar{x} = 55), 62–64 (\bar{x} = 63; Skinner and Smithers, 1990). Mass ranges from 22.2–37.2 (\bar{x} = 29.1) in males and 30.1–33.4 (\bar{x} = 31.9) in females (Skinner and Smithers, 1990). Means and ranges (n = 16) of skull measurements from Kenya are (in mm; Long, unpubl. data): greatest length of skull, 27.6 (26.7–29); condylobasal length, 25.7 (24.5–27.6); palatal length, 11.4 (10.8–12.4); length of maxillary tooththrow, 10.5 (10–11.3); zygomatic breadth, 14.3 (13.9–14.9); mastoid breadth, 13.7 (13–14.3); breadth of braincase, 13.2 (12.7–13.6); depth of cranium, 9.25 (9.0–9.6); mandibular length, 18.7 (17.9–19.8); length of mandibular tooththrow, 11.0 (10.3–11.8).

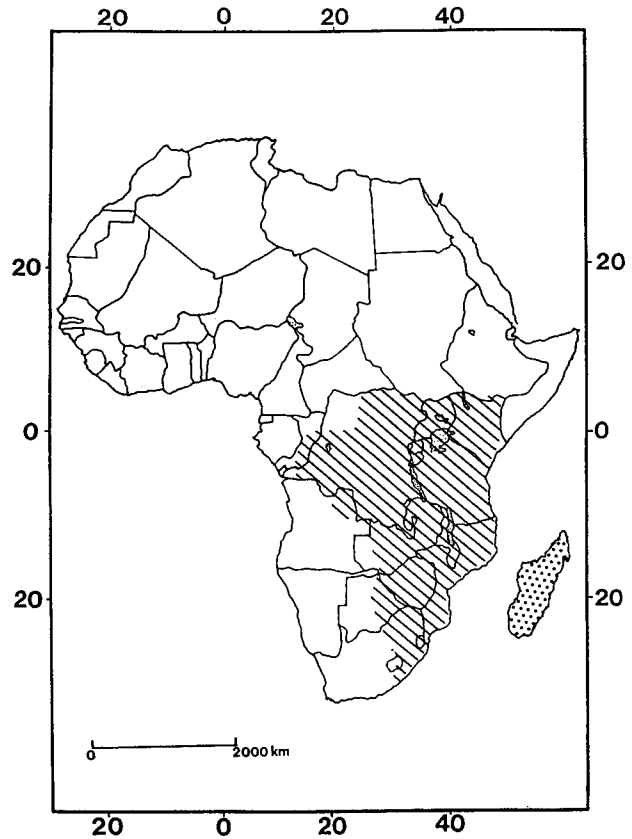


FIG. 3. Distribution of *Otomops martiensseni* showing distribution of subspecies *martiensseni* (striped) and *madagascarensis* (stippled). Due to uncertainty of the validity of the subspecies *icarus* and therefore its distribution, continental range has been assigned completely to *martiensseni* (from Kingdon, 1974).

DISTRIBUTION. *Otomops martiensseni* is a southeast African species, occurring from the Congo east to include Zaire, Uganda, Kenya, Tanzania and south to Angola, Zambia, Mozambique, Zimbabwe, Botswana and eastern South Africa (Fig. 3). This species was once considered rare, with wide gaps in distribution, but collecting has demonstrated local abundance in several areas. The giant mustiff bat also occurs on Madagascar (Hayman and Hill, 1971). It has been reported from sea level to altitudes of up to 2,000 m (Kingdon, 1974). No fossils are available for this species.

FORM AND FUNCTION. A gular gland is present in both sexes of *O. martiensseni*, but only reaches full development in the male. This gland forms a shallow circular pocket on the lower throat and is about 9 mm in diameter (Harrison, 1957). Thickened lips surround the pocket; some soft hairs may be present, but no actual tuft is formed. Hemotoxylin-eosin stained sections prepared from a male specimen show that these lips contain many deep sebaceous glands. The sac is lined with stratified squamous epithelium. Ducts of the glands penetrate the epithelium and are often associated with hair roots. The glands extend through the dermis to the muscle; they are diffusely scattered throughout the sac. Sudoriparous glands are thought to be represented by masses of tissue located basally in the sac (Harrison, 1957).

The large number of microscopic wrinkles on the upper lips of *O. martiensseni* allow the lips to flap-like when expanded. Flaps such as this may have several functions (Freeman, 1981; Kingdon 1974). Their expandability may play a role in the direction of echolocation calls; most molossids are known to be oral emitters. Some species are known to hold food items in their lips and then process the mass as a whole. Alternatively, the lips may hold the inedible parts of prey during processing; these inedible parts are then spit out (Freeman, 1981).

The external ear of *O. martiensseni* has a specialized design (Valdivieso et al., 1979). The ears project forward and the pinnae

are quite rigid, perhaps to prevent folding or excessive vibration during flight (Fig. 1; Kingdon, 1974). The flange or flap on the lateral margin of the ear may be closed, creating a funnel and thereby functioning in a manner similar to the tragus and antitragus. An alternative hypothesis is that this margin serves to close the auditory meatus, protecting the ear from intense noises (Valdivieso et al., 1979). Additionally, the increased streamlining may aid in flight efficiency by deflecting air that would eddy in the meatus (Kingdon, 1974).

The basisphenoid pits of *O. martiensseni* are very deep and well-defined (Valdivieso et al., 1979). These pits are located posteriorly in the nasal pharynx. They are, on average, 3 mm long and 1.5 mm wide, are deep posteriorly (1.5–1.6 mm) and become more shallow anteriorly (1.0–1.2 mm). They are separated by a posteriorly tapering septum. Histological study of the pits shows three distinct layers of tissue. These include a layer of loose connective tissue immediately internal to the bone, containing large adipose cells (28–30 μm) and other irregularly shaped cells; lymphocytes and polymorphonuclear leukocytes were also present. Next is a layer containing cartilage cells, elastic fibers, mucous glands, and lymphatic nodules. The most internal layer contains pseudo-stratified, ciliated, columnar epithelial cells with large nuclei. This arrangement of tissues does not differ significantly from the normal mammalian pharyngeal histological pattern (Valdivieso et al., 1979).

In species lacking these pits, communication between the middle ear cavity and the pharynx occurs via the auditory tube. However, in species such as *O. martiensseni*, which have these deep pits, the auditory tube and pharynx communicate via the lumen of the pits. Like most species of Microchiroptera, the auditory tube is quite large in *O. martiensseni*; diverticula of the tube have been seen in this species. The middle ear cavity is essentially enclosed by the tympanic bone, which terminates in a lobular structure. The sensor tympani muscle is well developed as in other Microchiroptera. It is possible that the pits may act as resonating chambers for the sound produced by the larynx, and perhaps in conjunction with the large ears and flanged lips of this bat, play a role in echolocation. Hunting strategy and prey type may be found to correlate with this system of echolocation (Freeman, 1981; Peterson, 1969; Valdivieso et al., 1979).

The height of the cochlea of *O. martiensseni* is 2.8 mm; there are five half-turns (Pye, 1973). The width of the basilar membrane increases from the base to the apex. The cells of Claudius have an average height of 55 μm at the base; this decreases to 25–30 μm at the apex. The spiral ligament has a greatest height of about 520 μm and a greatest width of about 200 μm .

Echolocation calls of *O. martiensseni* are within the range of human hearing, with a lowest frequency of 10 kHz, and a greatest frequency of 17 kHz (Fenton and Bell, 1981). The frequency with the greatest energy was 13 kHz. Two harmonics were present. Duration of search calls averaged 5 ms, but calls over 30 ms in duration were noted (Fenton and Bell, 1981).

The mandible of the giant mastiff bat is long and delicate; mean dentary thickness is 1.6 mm, and the associated musculature is not excessively developed (Freeman, 1981). The coronoid process, the mandibular condyle and the angular process are all relatively small (3.5 mm in height, 1.8 mm in length, 3.4 by 3.4 mm in length by width, respectively). These features are thought to give the bat its wide gape, which can exceed 90° (Freeman, 1984). This gape is a characteristic threat posture in molossid bats. In addition, it might allow *O. martiensseni* to eat relatively large insects. Because of the presence of such thin jaws, and the slight development of the sagittal and lambdoidal crests, it is predicted that the prey items are soft-bodied insects such as moths (Freeman, 1981).

The cervical vertebrae of *O. martiensseni* have a shallow angle of articulation between anterior and posterior zygapophyses, 41.9°, which allows little dorso-ventral flexibility of the head in roosting (Crerar, 1983; Fenton and Crerar, 1984). The degree of flexion is related to roosting posture.

The wings of the giant mastiff bat have an aspect ratio of 10.04 (Norberg, 1976). Wing area is 0.0218 m²; wing span is 0.467 m. The third, fourth, and fifth digits are: 126.4 mm, 94.2 mm, and 68 mm long, respectively (Freeman, 1981). Comparable wing characteristics are found in other molossids and indicate an ability for fast, strong flight (Freeman, 1981).

The mean number of erythrocytes was 14.42×10^6 and 12.46×10^6 cells/ml of blood for males and females, respectively (Kinoti, 1973). The erythrocytes are spherical, biconcave discs having a mean diameter of 5.3 μm , a mean thickness of 1.8 μm , and a mean

volume of 40.7 μm^3 . Mean level of hemoglobin was 20.70 g/ml for females, and 18.15 g/ml for males. Number of leukocytes ranged from 1,360–5,200 cells/ml (Kinoti, 1973). The high number of red blood cells accounts for the thick nature of *O. martiensseni*'s blood, and along with high hemoglobin levels and a highly vascularized liver, suggests that this bat has a high metabolic rate and is capable of sustained flight. The low leukocyte count may indicate relative freedom from infection (Kinoti, 1973). Total protein ranged from 4.4–5.7 g/100 ml blood; albumin, 3.1–3.8 g/ml; globulin, 1.0–2.0 g/ml; and the albumin/globulin (A/G) ratio ranged from 1.6–3.1 g/ml. Electrophoresis separated the proteins into six fractions which were identified as albumin and α_1 , α_2 , β_1 , β_2 , and γ globulins. These values are within the normal mammalian range, but the separation into six fractions is unusual in a mammal that is considered to be primitive (Kinoti, 1973).

There were no important histological differences observed between the bladder of the giant mastiff bat and that of other mammals (Epelu-Opio, 1974). The wall of the bladder is divided into three layers, a tunica mucosa, a tunica muscularis, and a tunica adventitia. The epithelial cells are divided into superficial and basal layers. Examination of the ultrastructure revealed numerous fusiform vesicles, which perhaps play some role in the secretion of mucopolysaccharides. Low quantities of rough endoplasmic reticulum were also noted, but not discussed in detail (Epelu-Opio, 1974).

Testes have a low volume of Leydig cells and little connective tissue stroma; peritubular lymphatic sinusoids are extensive and occupy a large part of the intertubular area. The seasonal increase in testis mass seems to reflect an increase in the size of the interstitial cells of the seminiferous tubules; there is no significant increase in the number of cells (Kayanja and Mutere, 1978).

In nonbreeding bats, the Leydig cells contain a large quantity of lipid droplets and although mitochondria are numerous, the number of cristae present is quite low (Kayanja and Mutere, 1978). In breeding males, the number of lipid droplets is greatly reduced and a notable increase in smooth endoplasmic reticulum is seen. The number of cristae on mitochondria also increases greatly. The proliferation of smooth endoplasmic reticulum is evidence for increased steroid production during the breeding season. The lymphatic sinusoids are thought to play a role in the distribution of hormones and metabolites to the epithelial cells of the seminiferous tubules (Kayanja and Mutere, 1978).

The left ovary of *O. martiensseni* is consistently atrophic (Kayanja and Mutere, 1975). The right ovary is enclosed in a well-developed ovarian bursa with average dimensions of 1.5 by 1.0 by 0.5 mm. The germinal epithelium is well developed; cells tend to be more columnar near the mesovarium and several layers of epithelium can be distinguished here. Beneath the germinal epithelium lies the tunica albuginea and ovarian cortex, which contains the follicles and the interstitial gland tissue. The interstitial gland tissue is more apparent during anestrus; antral follicles greater than 250 μm in diameter are often atretic at this time. The authors believe the interstitial gland tissue may be derived from the atretic follicles. The cells in the interstitial gland tissue have well-developed smooth endoplasmic reticulum, which suggests that a main function is steroidogenesis. The granulosa cells in atretic follicles contain lipid droplets, and undergo disintegration in the later stages of atresia. Cells of the theca interna come to resemble interstitial gland cells as they accumulate lipid during atresia. The corpus luteum is formed mainly from granulosa cells. At its full development, the corpus luteum takes up most of the ovary; the cells are densely packed and highly vascularized. The gland degenerates early in pregnancy (Kayanja and Mutere, 1975).

ONTOGENY AND REPRODUCTION. No detailed information is available on fertilization or implantation in *O. martiensseni*. In all pregnant bats observed, the fetus was located in the right horn of the uterus (Kayanja and Mutere, 1975; Mutere, 1973). The gestation period appears to be about 3 months; females give birth to a single young. The corpus luteum degenerates early in pregnancy in *O. martiensseni* although the exact stage of the embryo's development at which this deterioration begins is unknown (Kayanja and Mutere, 1975). Breeding is limited to one season per year; pregnant bats were found from October through January at two cave sites in Kenya (Mutere, 1973). On very rare occasions a pregnant bat was netted in May or June, but researchers did not consider it evidence for a second breeding season. Most births occurred in December. The young are hairless and occur in groups

or patches, often apparently surrounded by mothers. Young bats do not cling to the mother after birth (Mutere, 1973).

Adult males of *O. martiensseni* had the greatest testicular mass in August, with a mean mass of 0.16 ± 0.04 g ($n = 2$) and 0.18 ± 0.05 g ($n = 44$) at two cave sites in Kenya (Ithundu and Mt. Suswa). Lowest mean testicular mass occurred in May/June and December (Mutere, 1973).

Male giant mastiff bats reach sexual maturity at about 1 year of age (Mutere, 1973). At this time, the bats weigh approximately 25 g and have forearm lengths of about 70 mm. The appearance of the gular sac is also indicative of male maturity. Females attain maturity at about the same mass and body size as males; presence of a fetus or evidence of lactation is confirmation of female reproductive maturity (Mutere, 1973).

ECOLOGY AND BEHAVIOR. This species inhabits a variety of ecological zones from semi-arid regions to montane forests; it has been recorded from sea level to altitudes of 2,000 m (Kingdon, 1974). The habitats occupied by *O. martiensseni* can be extremely dry and barren during the dry season and may not contain sufficient food for the population. The bats may make long distance foraging flights or migrate to find richer patches of food during the dry season (Kingdon, 1974).

Otomops martiensseni usually dwells in caves. Two of the best known roosts are in lava caves in Kenya (Mts. Suswa and Ithundu), although the giant mastiff bat may also occur in other caves in this region (Mutere, 1973). In these roosts, the bats occur in groups of several hundred, and they pack together tightly. They tend to favor the darker parts of the caves, where ventilation is relatively poor (Kingdon, 1974; Mutere, 1973). *O. martiensseni* was the only species of bat found in the cave at Mt. Suswa. *Rhinolophus* sp. and *Triaenops afer* were also found in the cave at Ithundu (Mutere, 1973).

The sex ratio of *O. martiensseni* at the two caves investigated by Mutere (1973) appears to fluctuate; however, these data represent only two sites over a period of one year. Among juveniles at one site (Ithundu), the ratio shifted from 1:1 (male : female) in 1971 to 1:4 in 1972; the 1:1 ratio held stable at Mt. Suswa in 1971 and 1972. Among adults, the ratio at Ithundu remained at 1:2 from 1971 to 1972; at Mt. Suswa, the ratio changed from 1:2 in 1971 to 3:1 in 1972 (Mutere, 1973).

Large deposits of guano have been noted at two cave sites in Kenya, Suswa and Ithundu (Glover et al., 1964, not seen, cited by Mutere, 1973; Mutere, 1973). In one case, this guano was covered with fleas. At the Ithundu site, carnivorous beetles, especially *Vil-liersia trivalis*, covered the floor and their larvae were thought to help churn the guano to a fine powdery consistency. The caves have been mined by the Kenya Guano Company, and the guano sold as fertilizer to tea and coffee farmers. In 1973, almost all of the guano was said to have been removed from these two sites. Mining activities may disturb the bat populations and perhaps alter the physical characteristics and microclimate of the cave to the point that the bats abandon them, at least temporarily. A decrease in recruitment percentage from 11% to 2% (from 1971 to 1972) at Ithundu may reflect this disturbance (Mutere, 1973).

Recruitment of juveniles into the adult populations at the two sites was 14% and 11% in one year and 50% and 2% in the next year (Mutere, 1973). These significant changes in recruitment may be because of either changes in natality or changes in adult emigration. The drop from 11% to 2% occurred in a cave that had been mined for guano, and it is possible that the microclimate was altered, making the cave less suitable for the bats. Overall, recruitment rate is described as slow, especially for a monotocous (one young per brood) species such as this one.

The giant mastiff bat flies rapidly and in a straight line (Kingdon, 1974). *O. martiensseni* uses sideslips (to the left and right, alternately) to decrease altitude quickly while entering a roost cave (Norberg, 1976). A sideslip is a maneuver in which one wing is pronated (rotated forward and down) while the other is supinated (rotated upward and back), causing the bat to lose altitude; it is referred to as 'fishtailing' by pilots. The bat observed in this study had a flight speed of about 5 m/s and a stroke frequency of 8.8 strokes/s. The bat holds its wings in a strongly flexed position and then pronates the right wing and supinates the left, resulting in a rotation of the body into the roll plane, then the sideslip to the right occurs. Body (parasite) drag increases, which is due to friction between the surface of the body and the air. The equilibrium gliding angle becomes steeper, allowing a rapid descent (Norberg, 1976).

GENETICS. *O. martiensseni* has a diploid number of 48 and a fundamental number of 56 or 58 (Dulic and Mutere, 1973; Warner et al., 1973). Among the 23 autosomal pairs, there is one large metacentric pair, 3 pairs of smaller submetacentrics, 2 pairs of subtelocentrics (1 medium and 1 small), and a graded series of 17 acrocentric pairs (Warner et al., 1973). The resulting fundamental number is 58 in this case. Dulic and Mutere (1973) list 3 metacentric pairs, 1 submetacentric pair, 1 subtelocentric pair, and 18 acrocentric pairs, giving a fundamental number of 56. The X chromosome is a medium submetacentric; the Y is a small acrocentric.

REMARKS. Because several species of the genus *Otomops* are known only from type specimens, construction of a useful key is difficult. All of the known species are very similar in appearance; differences in ecology and behavior are virtually undocumented (Dorst, 1953). The subspecies *icarus* and *madagascarensis* were originally regarded as valid species, but comparisons of morphological characters make it clear that the two do not differ significantly from *martiensseni* (Harrison, 1957). There is some variation in coat color and definition of the collar between subspecies, but little else. The generic name *Otomops* was first used in 1913 when Oldfield Thomas decided that features possessed by *O. wroughtoni* and *O. martiensseni* justified the establishment of a new genus separate from *Nyctinomus*. The generic name *Otomops* consists of two separate components, *oto*, which is derived from a Greek word meaning large or long ear, and *mops*, which is reported to be a Malaysian word for bat (J. L. Eger, pers. comm.). *O. martiensseni* was named in honor of a "Herr Martienssen of the Königlich Museum für Naturkunde"; he found the type specimen described by Matschie (1897).

I would like to thank the Mammalogy Department at the Royal Ontario Museum (ROM) for allowing me access to their collections of both bats and reference materials, and ROM photographer Brian Boyle for taking the skull photos. Their assistance is greatly appreciated.

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