MAMMALIAN SPECIES No. 632, pp. 1–4, 3 figs.

Nycteris grandis.

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Published 12 May 2000 by the American Society of Mammalogists

Nycteris grandis Peters, 1865

Large Slit-faced Bat

Nycteris grandis Peters, 1865:358. Type locality "Guinea."
Nycteris marica Kershaw, 1923:534. Type locality "Tindiga, Kilosa, Tanganyika."
Nycteris proxima Lönnberg and Glydenstolpe, 1925:2. Type locality "Kartousi, Semiliki Valley."

CONTEXT AND CONTENT. Order Chiroptera, suborder Microchiroptera, family Nycteridae, genus *Nycteris*. Two subspecies were recognized by Koopman (1994):

N. g. grandis Peters, 1865:358, see above (*proxima* and *baikii* are synonyms, but see Remarks).
N. g. marica Kershaw, 1923:534, see above.

DIAGNOSIS. Bats of the genus *Nycteris* can be distinguished from all other bats by their tails, which terminate in a Y- or T-shaped piece of cartilage (Kingdon, 1974; Rosevear, 1965). *Nycteris grandis* can be distinguished from all other nycterids except *N. hispida* by its trifid upper incisors (upper incisors are bifid in other species of *Nycteris*—Rosevear, 1965). *N. grandis* can be distinguished from *N. hispida* (and all other *Nycteris* species) by its large size (forearm length, 57–66 mm—Hayman and Hill, 1971).

GENERAL CHARACTERS. Dorsal pelage of *N. grandis* is reddish brown to gray, and ventral surface is paler and grayer (Rosevear, 1965). A female from Zambia had a slight yellow tinge around neck and shoulders (Ansell, 1986). The face of *N. grandis* is dominated by large ears connected by a membrane at the base and a deep trench, which contains the noseleaf and is surrounded by a series of fleshy lobes and flanges (Fig. 1; Kingdon, 1974; Rosevear, 1965). Although the term noseleaf typically is used to describe this structure, it differs markedly in morphology (and perhaps in function) from noseleaves of the Phyllostomidae (Bogdanowicz et al., 1997).

Ranges of measurements for external or skeletal characters are as follows: body mass, 23–36 g; length of forearm, 57–66 mm; length of tibia, 29.5–33.5 mm; length of ear, 28–35 mm; length of tail, 65–75 mm; and length of head and body, 63–93 mm. Skull measurements are as follows: total skull length, 26–27 mm; breadth of brain case, 10.6 mm; condylocanine length, 23.6–23.7 mm; zygomatic breadth, 16–17 mm; length of maxillary tooth row (C–M3), 9.1–9.7 mm; and maxillary width (M3–M3), 10.4–11.1 mm (Fig. 2; Ansell, 1986; Hayman and Hill, 1971; Kingdon, 1974; Rosevear, 1965; Verschuren, 1976). *N. grandis* is not sexually dimorphic in size.

DISTRIBUTION. *Nycteris grandis* is restricted to Africa and has been recorded from Guinea, Liberia, and Cameroon in the west; eastward to Zaire, Uganda, Kenya, and Tanzania; and south to Zimbabwe, Malawi, and Mozambique (Fig. 3; Ansell, 1986; Kingdon, 1974; Rosevear, 1965; Verschuren, 1976). It also occurs on the offshore islands of Zanzibar and Pemba (Kingdon, 1974; Rosevear, 1965).

FORM AND FUNCTION. Facial area of *N. grandis* is dominated by a deep frontal groove from which the family vernacular name (slit-faced bats) is derived (Kingdon, 1974; Rosevear, 1965). The groove houses the noseleaves and extends from the nostrils to a line joining the base of the ears (Fig. 1; Rosevear, 1965). The groove is deeper and wider towards the rear and is divided by a longitudinal septum arising from the floor of the cavity (Rosevear, 1965). Paired noseleaves consist of a thin membrane thickened at anterior and posterior ends. The rounded posterior thickening lies in a deep rearward depression, whereas the anterior thickening is kidney shaped and lies above and to the rear of the nostrils (Rosevear, 1965). Exact function of the noseleaf is unknown; nycterids emit echolocation calls through their nostrils, and the noseleaf may play a role in echolocation (Rosevear, 1965).

Large ears of *N. grandis* greatly amplify sounds at frequencies below 15 kHz, achieving pinna gains of about 15 dB at 15 kHz. The ears contribute to localization of prey-generated sounds (Obrist et al., 1993).

Low aspect ratio (5.2) and moderate wing loading (11.4 N/m^2) of *N. grandis* permit slow maneuverable flight (Norberg and Rayner, 1987). This type of flight, in combination with a relatively large head (Fenton, 1989), allows *N. grandis* to eat prey that weigh >20% of their body mass (Fenton et al., 1987, 1990, 1993).

Skin temperatures of *N. grandis* varied from 33.5°C to 38°C at ambient temperatures of 23–35°C, but ambient temperature did not significantly influence skin temperature (Fenton et al., 1993).

ONTOGENY AND REPRODUCTION. Little is known about reproduction and ontogeny of *N. grandis*. In Zimbabwe, Fenton et al. (1987) captured females with young that were estimated to be 1–7 days old on 1 December. A single female captured on 18 December in Liberia had a 5-mm embryo (Verschuren, 1976). Seven females collected on 22 September 1972 in Zambia each had a single fetus with crown–rump lengths of 24–27 mm and head lengths of 17–18 mm (Ansell, 1986); Brosset (1966) recorded fetuses or young from Gabon in April, August, and November.

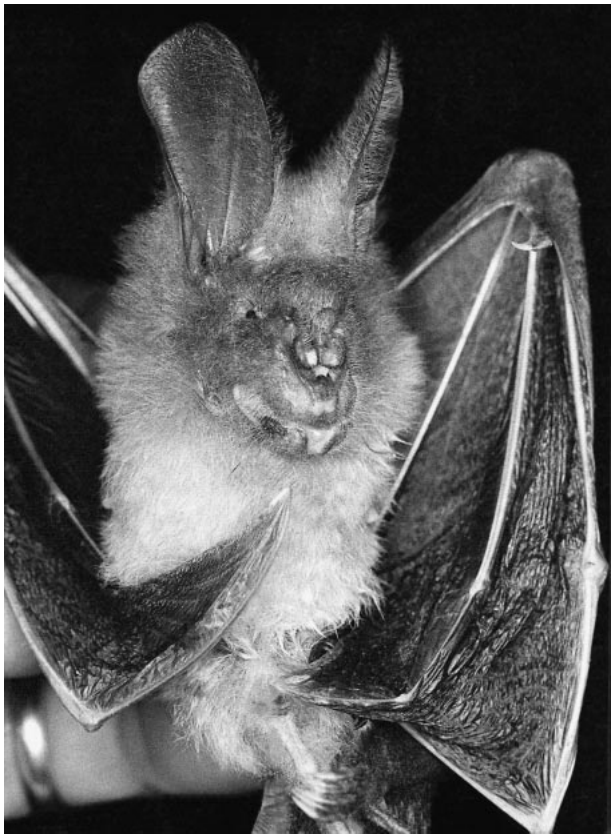

FIG. 1. *Nycteris grandis*. Photograph by M. B. Fenton.

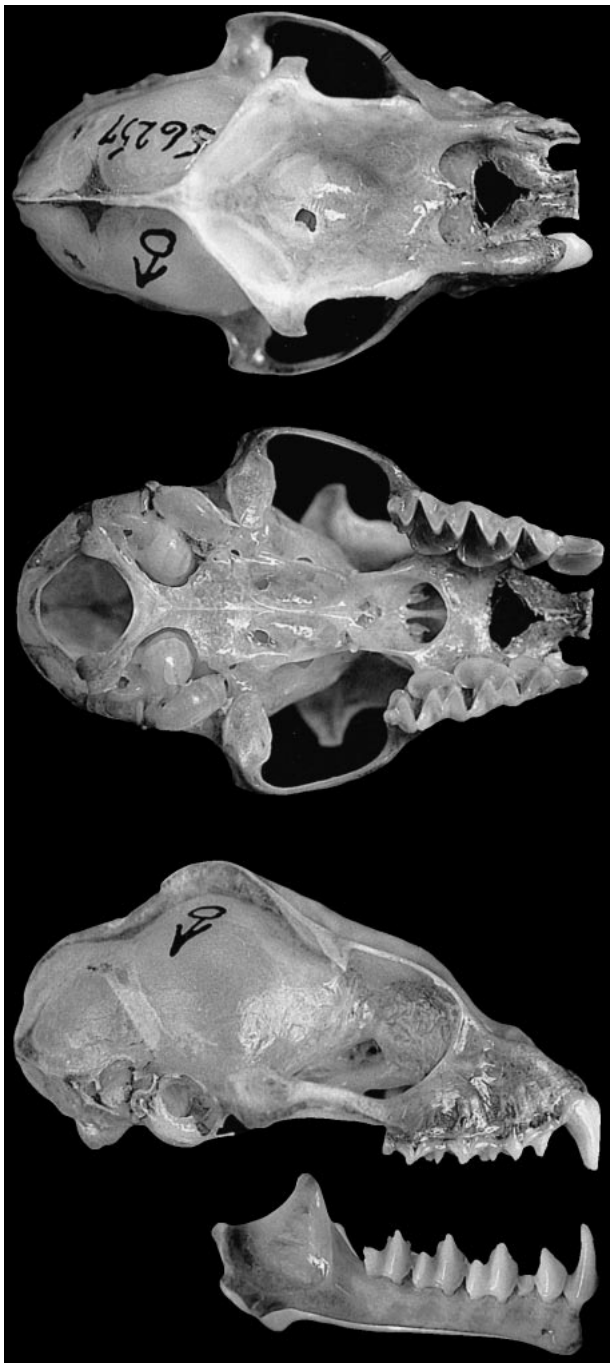

FIG. 2. Dorsal, ventral, and lateral view of the skull and lateral view of the mandible of *Nycteris grandis* (Royal Ontario Museum, Toronto, Canada 56257). Greatest length of skull is 27 mm.

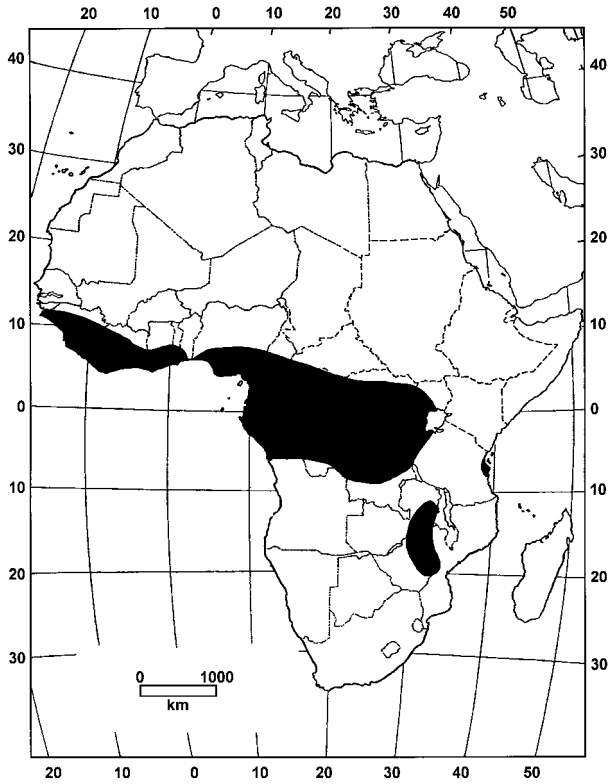

FIG. 3. Distribution of *Nycteris grandis* in Africa. *N. g. marica* occurs from southeastern Kenya south to Zimbabwe and Mozambique including Pemba and Zanzibar, and *N. g. grandis* occupies the remaining range.

ECOLOGY. *Nycteris grandis* is most common in rainforests, where it often selects swampy sites (Rosevear, 1965); however, it also occurs in drier savannah habitat (Fenton et al., 1990). *N. grandis* roosts in hollow trees such as *Acacia albida* (Fenton et al., 1990), *Adansonia digitata* (Ansell, 1986), *Ceibia pentendra* (Adam and Hubert, 1976), and *Mitragyna stipulosa* (Verschuren, 1957). It also roosts in artificial structures such as houses (Ansell, 1986; Fenton et al., 1990, 1993), disused water towers (Fenton et al., 1990, 1993), and culverts (Rosevear, 1965). These bats also may use hollow fallen logs and holes or small caverns in rocks (Rosevear, 1965). Some day roosts also are used as night roosts (Fenton et al., 1990).

Nycteris grandis roosts alone, in pairs, or in small groups (Kingdon, 1974). Individuals return predictably to the same roost each day but may abandon the roost in response to disturbance or capture, sometimes returning to the original roost after a few days (Fenton et al., 1993). Emergence times of *N. grandis* are variable, ranging from 1900 to 2100 h, and emergence patterns among individuals are not consistent (Fenton et al., 1993). Females leave their young behind when they leave the roost to forage (Fenton et al., 1993).

Nycteris grandis is an opportunistic forager, and its large body size allows it to eat prey ranging from small vertebrates to medium-size and large insects (Fenton et al., 1990, 1993). Prey remains collected from beneath feeding perches in northern Zimbabwe included parts of insects (Lepidoptera, 46 species; Orthoptera: Tettigoniidae and Acrididae; Mantoidea, two genera; Coleoptera; Neuroptera), other arthropods (Solpugida), bats (Vespertilionidae, Rhinolophidae, and Nycteridae), frogs (*Ptychadena anchietae, P. mascariensis, Chiromantis xerampelina, Hemisus, Xenopus muelleri, X. laevis,* and *Tomopterna cryptotis*), fish (*Tilapia rendalli*), and birds (Fenton et al., 1987, 1990, 1993).

Diet of *N. grandis* varies seasonally within years (Fenton et al., 1990), and seasonal patterns vary among years (Fenton et al., 1993). Remains of prey collected each month from beneath feeding perches between March 1987 and April 1988 (Fenton et al., 1990) suggested that frogs were the most common prey (total numbers) in March, April, May, August, and September, bats were most common in June and July, and arthropods were most common in December, January, and February. Because of their low mass compared with frogs and bats, arthropods usually accounted for <20% (by mass) of the diet of *N. grandis* (Fenton et al., 1990). The seasonal pattern that was apparent in 1987–1988 was absent in a longer study conducted at the same site from 1987 to 1990. For example, the high incidence of remains of bats beneath feeding perches in 1987 was not evident in 1990, even though small bats were in the vicinity of feeding perches used by *N. grandis* (Fenton et al., 1993).

In captivity, *N. grandis* preferred katydids and beetles over moths. They culled wings from moths as well as wings and posterior legs from katydids (Fenton et al., 1983). They also ate frogs (*Hyperolius marmoratus, Ptychadena anchietae,* and *Chiromantis xerampelina*) and small bats, but unlike *Trachops cirrhosus* (Tuttle

and Ryan, 1981), they did not use the calls of male frogs to locate their prey (Fenton et al., 1983).

Little information is available regarding parasites of *N. grandis*. Keymer (1971) reported "broad trypanosomes" from four of six specimens collected from Zambia.

BEHAVIOR. *Nycteris grandis* produces echolocation calls during attacks, increasing the rate of calling as it approaches prey (Fenton et al., 1983). Large prey (e.g., bats and birds) are grasped in the mouth and immobilized by a strong bite to the head (Fenton et al., 1983). Prey, except for small prey, are consumed while hanging from a perch. Typically *N. grandis* hangs from a perch with one foot while using wings to position prey, sometimes taking up to 1 h to position prey before eating. Hind legs of large frogs (larger than *H. marmoratus*) and skin, fur, and wings of bats sometimes are discarded (Fenton et al., 1983). Average prey-handling times were 5.3 ± 1 min (± *SD*; $n = 11$) for *H. marmoratus* (1 g) and 18 min ($n = 3$) for *P. anchietae* (3–5 g). *N. grandis* took 3 h and 26 min to eat a 7-g bat (*Hipposideros ruber*), but actual eating consisted of only eight bouts 4–10 min in length (total time = 59 min—Fenton et al., 1983).

Typically, *Nycteris* searched for prey by hanging by one foot with its head elevated, scanning with ear and head movements and 180° body rotations. When prey were detected, scanning ceased, and the bat oriented its head toward the prey and rapidly moved its ears backwards and forwards. *N. grandis* captured prey either from the ground or air. When capturing prey on the ground, *Nycteris* uses its wings to envelope the prey (Fenton et al., 1983).

In captivity, *N. grandis* relied on prey-generated sounds to locate targets and responded to low-frequency sounds such as fluttering of insects and irritation vocalizations of smaller bats but not to echolocation calls of *Rhinolophus landeri* or *Eptesicus capensis* (Fenton et al., 1983). When presented with pithed frogs, *N. grandis* responded immediately only if frogs were accompanied by noise (a scratching sound made with a stick); no response to stationary *Hyperolius marmoratus* was observed (Fenton et al., 1983). If the scratching sound was >10 cm from the dead frog, attacks were unsuccessful (Fenton et al., 1983). *N. grandis* captured bats in the air (*H. ruber* and *E. capensis*) or while they were crawling (*Pipistrellus nanus*). *Nycteris* tracked and intercepted prey rather than following them from behind (Fenton et al., 1983).

In flight cages, *N. grandis* reacted to chewing sounds of conspecifics and often tried to steal food. Typically, the aggressor would grab the prey and try to back away while the "owner" held on. If unsuccessful, the aggressor would hit its opponent with its wrists, eliciting the same response from the owner. Eventually, bats in the colony learned to stop chewing when one of its roost mates had finished its prey and would wait until the other bat resumed eating (Fenton et al., 1983).

Echolocation calls of *N. grandis* vary from a complex overlay of harmonics to steep frequency-modulated pulses as they approach prey. Spectra of calls early in the feeding sequence have four peaks (20–112 kHz), whereas those later in the approach have a single peak at approximately 73–91 kHz. Minimum and maximum frequencies are 17 and 114 kHz early in the approach sequence and 61 and 110 kHz in the terminal phase of the approach. Pulse duration varies from from 0.6 to 2.8 ms, and interpulse interval varies from 6.0 to 17.8 ms (Fenton et al., 1983).

Nycteris grandis hunts during continuous flight or by making short flights from a hunting perch to attack passing prey (Fenton et al., 1987, 1990, 1993). They forage in a variety of habitats including over large rivers and in woodland (Fenton et al., 1990, 1993). Their flight behavior varies among individuals on the same night and within individuals on different nights (Fenton et al., 1990, 1993). The degree to which bats rely on either foraging strategy (i.e., continuous flight or sallying from a perch) depends on habitat and prey availability (Fenton et al., 1987, 1990, 1993). *N. grandis* often forages on concentrations of flying insects attracted to lights (Kingdon, 1974).

REMARKS. Taxonomy of this group is relatively unstable. Distinguishing *N. major* from *N. arge* is difficult, and because *N. major* is relatively rare and the measurements of these two species often overlap, care must be taken. Rosevear (1965) stated that *N. major* has relatively shorter ears than *N. arge*, and Eisentraut (1956) suggested the claws of the thumbs and toes of *N. major* are shorter and more blunt than those of *N. arge*. These questionable differences have caused some authors to suggest that *N. major* is only a large representative of *N. arge*. Koopman (1994) recognized these forms as distinct but did not indicate on what grounds. Differences among *N. intermedia*, *N. arge*, and *N. nana* are faint, particularly between *N. intermedia* and *N. arge*. Therefore, many authors treat *N. intermedia* as a small form of *N. arge* (Van Cakenburghe and De Vree, 1985).

The name *baikii* was used presumably by Gray, but no publication of his exists that corresponds to this name. Peters (1867) considered *baikii* to be the second specimen of *N. grandis* (Rosevear, 1965).

The generic name *Nycteris* is derived from the Greek *nykteros*, meaning 'nocturnal', and the specific name *grandis* is derived from the Latin *grandis*, meaning 'magnificent' (Brown, 1991; Jaeger, 1978).

We are grateful to A. M. Surch, J. Flaro, J. Lawson, and M. B. Fenton, who provided valuable comments on earlier versions of the manuscript.

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