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Hypsignathus monstrosus.

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Hypsignathus H. Allen, 1861

Hypsignathus H. Allen, 1861:156. Type species *Hypsignathus monstrosus* H. Allen, 1861, by monotypy.

Sphyrocephalus Murray, 1862:8. Type species *Sphyrocephalus labrosus* Murray, 1862, by monotypy. Preoccupied by *Sphyrocephala* Westwood, 1848, a dipteran; and by *Sphyrocephalus* Schmarda, 1859, a turbellarian.

Zygaenocephalus Murray, 1862:pl.1. Type species *Zygaenocephalus labrosus* Murray, 1862, by monotypy. This name was attached to the plate illustrating Murray's description of *Sphyrocephalus* and serves as a replacement for *Sphyrocephalus* Murray, 1862.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Megachiroptera, Family Pteropodidae, Subfamily Pteropodinae, Tribe Epomophorini, Genus Hypsignathus, which includes only *H. monstrosus.*

Hypsignathus monstrosus H. Allen, 1861

Hammerhead Bat

Hypsignathus monstrosus H. Allen, 1861:157. Type locality "Western Africa" (Gabon).

Sphyrocephalus labrosus Murray, 1862:8. Type locality "Old Calabar River" (Nigeria).

Zygaenocephalus labrosus Murray, 1862:pl.1. Replacement name attached to the illustration of *Sphyrocephalus labrosus* noted above.

Epomophorus macrocephalus Peters, 1876:474. Type locality "Dongila" (Gabon).

Hypsignathus haldemani: Matschie 1899:29. Not *Pteropus haldemani* Halowell, 1846.

CONTEXT AND CONTENT. Context noted in generic summary above. *H. monstrosus* is monotypic.

DIAGNOSIS. *Hypsignathus monstrosus* is the largest bat in Africa and is distinguished by its size (Fig. 1). The forearm is >118 mm in the adult. The species shows marked sexual dimorphism; the mass of males can be almost twice that of females and males possess an enlarged rostrum and larynx (Fig. 2). The second premolar and molars are markedly lobed. This is unique among African fruit bats and is diagnostic of the genus (Andersen, 1912). Other bats that might be confused with *H. monstrosus* are the smaller genera *Epomophorus* and *Epomops* (Wickler and Seibt, 1976).

GENERAL CHARACTERS. Males have a large, square, truncated head (Tate, 1942) with enormous pendulous lips, ruffles around a warty snout and a hairless, split chin (Lang and Chapin, 1917). Females do not have such an elevated rostrum and consequently have a more fox-shaped muzzle (Fig. 1; Bradbury, 1977*a*). The pelage is generally grey-brown or slaty-brown, with a whitish collar extending from shoulder to shoulder. The dark brown ears have a white tuft at their base. Facial hairs are dark brown and short except for a few long, stiff whiskers near the mouth. Minute hairs may be found on the black-brown wing membranes (Allen, 1861; Murray, 1862). The dental formula is i 2/2, c 1/1, p 2/3, m 1/2, total 28 (Andersen, 1912). Range of measurements (in mm) for males and females (when available), respectively, are: total length, 220–280, 195–225; length of forearm, 120–140, 118–128; wingspan, 686–970, 840; length of pollex, 128–137, 118–127; digit II—length of metacarpal, 62.0–75.5, 62.0–66.5; length of phalanx I, 13.0–14.5, 12.0; length of phalanx II, 15.0–16.5, 13.5–16.0; digit III—length of metacarpal, 85.0–101.0, 82.0–88.5; length of phalanx I, 60.0–66.5, 58.0–60.0; length of phalanx II, 81.0–85.0, 70.0–82.0; digit IV—length of metacarpal, 79.0–98.5, 79.0–87.5; length of phalanx I, 43.5–46.0, 40.5–43.0; length of phalanx II, 45.5–47.5, 45.0; digit V—length of metacarpal, 82.0–95.0, 79.0–87.5; length of phalanx I, 41.0–46.0, 40.5–42.5; length of phalanx II, 40.5–42.5, 37.0–39.5; length of ear, 32.0, 27.0; length of tibia, 54.0–60.0, 52.0–55.0; length of foot, 33.0–38.0, 33.5–35.5; skull—total length, 69.5–73.0, 65.0; width of braincase at zygomata, 22.5–23.7, 22.0; width of zygomata, 34.5–38.5, 32.0–34.8; interorbital width, 12.5–14.0, 12.0–12.5; width of cranium, 22.7, 21.0; distance between C1 and M1, 22.6–24.2, 19.7–21.5; length of mandible, from condyle, 54.4–62.0, 47.4–53.0; length of maxillary toothrow, 23.2, 24.6 (Fig. 3); weight (in g), 228–450, 218–377 (Allen, 1861; Allen et al., 1917; Andersen, 1912; Bergmans, 1979; Feiler, 1986; MacNamara et al., 1980; Murray, 1862).

DISTRIBUTION. *Hypsignathus monstrosus* is found in central Africa (Fig. 4). It occurs in forest regions from Senegal to extreme southern Sudan, south through Uganda and western Tanzania to northern Angola (Feiler, 1986; Koopman, 1975; Koopman et al., 1978; Novick, 1960; Robbins, 1980; Verschuren, 1976, 1986; Wolton et al., 1982). There is no fossil record for this species.

FORM AND FUNCTION. In males, much of the face is taken up by large cheek pouches that begin at the midline of the skull, near the ears, and continue down and around the front of the eyes to the lower jaw. These pockets store food and may be involved in sound production (Allen et al., 1917; Dobson, 1881; Mertens, 1938). The most noticeable anatomical features of the male involve sound production. The larynx is one-half the length of the vertebral column and fills most of the thoracic cavity, pushing the heart, lungs and alimentary canal backward and sideways. The large larynx is due to the enlarged and ossified thyroid, arytenoid, and cricoid cartilages (Fig. 2, Allen et al., 1917; Zeller, 1984). The larynx is almost three times larger in males than females and may have resulted from intraspecific selection due to the specialized mating

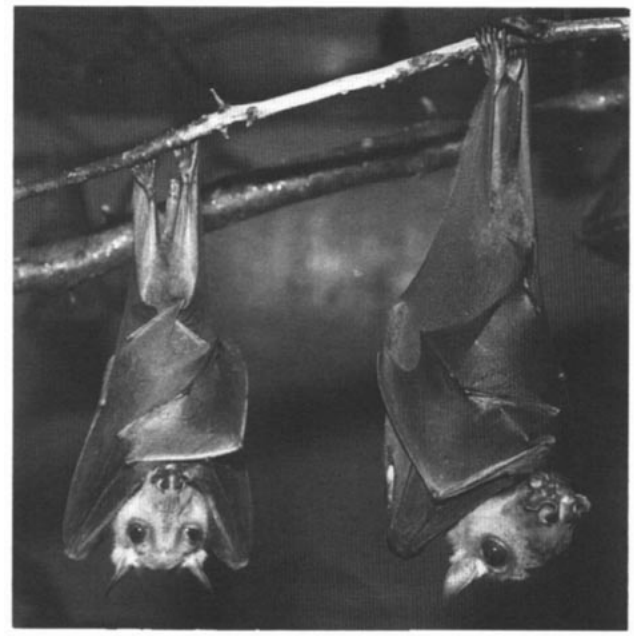

FIG. 1. Adult female (left) and male (right) *Hypsignathus monstrosus.* Note the size dimorphism and enlarged snout of the male. Photograph courtesy of J. Cohen, National Zoological Park, Washington, D.C.

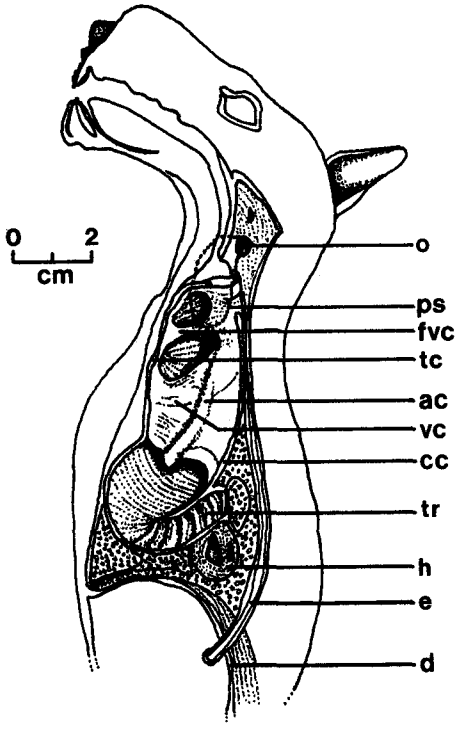

FIG. 2. Diagram of a sagittal section illustrating the larynx of a male *Hypsignathus monstrosus*: ac, arytenoid cartilage; cc, cricoid cartilage; d, diaphragm; e, esophagus; fvc, false vocal cord; h, heart; o, orifice of pharyngeal sac; ps, right pharyngeal sac; tc, thyroid cartilage; tr, trachea; vc, vocal cord (redrawn from Lang and Chapin, 1917).

behavior (Zeller, 1984). The function of this specialization is to produce loud calls to attract females (Wickler and Seibt, 1976).

Hypsignathus monstrosus has a large, powerful tongue with a trifoiled tip. An oval patch of backwardly pointing tridentate papillae is adapted for rasping fruit tissue so juices may be extracted (Lang and Chapin, 1917). The stomach and intestine are long and narrow, with many folds in the interior wall to permit digestion of plant matter (Allen et al., 1917; Murray, 1862). The cervical vertebrae have little flexibility due to neural spines and planes of articulation that restrict dorso-ventral movement. This restricts the head to a ventral position when the bat is roosting (Fenton and Crerar, 1984).

Body temperature during flight ranges from 37 to 41°C. They tolerate higher ambient temperatures during flight than other megachiropterans due to their high thermal conductance. Low ambient temperatures, however, cause a loss in coordination and flight endurance is severely reduced below an ambient temperature of 11°C. This is likely due to cooling of the flight muscles. At a flight speed of 5.5 m/s, heart rate is 620 beats/min and respiration rate is 293/min. Respiration is coupled to the wing beat at the minimum power input velocity (5 m/s). Wing beat frequency ranges from 301 to 318/min at flight speeds of 4–8 m/s. Mean respiratory quotient in flight is 0.79. The mass specific oxygen consumption ranges from 15.8 to 17.5 l O_2 kg^{-1} h^{-1} at flight speeds of 4–8 m/s and the corrected power input ranges from 87 to 97 Watts/kg. The cost of transport is from 1.13 to 2.46 Watts (Carpenter, 1986).

ONTOGENY AND REPRODUCTION. Breeding takes place during the dry seasons, which vary geographically. For instance, Wolton et al. (1982) found the breeding seasons at Mt. Nimba, Liberia, to be from August to September and from December to January. Usually, there are two breeding seasons with peaks of activity during February and July (Bradbury, 1977*a*). The onset of a dry season does not seem to be the only trigger that initiates the breeding season; *H. monstrosus* in captivity maintain the same breeding seasons (June to August and December to January) as they do in the wild (MacNamara et al., 1980), even though climatic cues, such as precipitation, are absent.

Females have a postpartum estrus and are capable of reproducing twice a year. Females produce one infant/pregnancy and the sex is of even distribution (Allen et al., 1917; MacNamara et al., 1980). Females mature faster than males, are sexually mature after 6 months, and reach full size after 9 months. Males take up to 18 months to mature sexually. Until males are about 12 months old, they are difficult to differentiate from females in external morphology (Bradbury, 1977*a*).

FIG. 3. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a male *Hypsignathus monstrosus* from Soumou River, Cameroon (Royal Ontario Museum 56169). Greatest length of skull 65.5 mm.

ECOLOGY. Hammerhead bats live in lowland (<1,800 m elevation) riverine forests, swamps, mangroves, and palm forests. The diet include juice and soft pulp of mangoes (*Mangifera*), bananas (*Musa*), guavas (*Psidium*), and soursops (*Annona*), but figs (*Ficus*) make up most of the food consumed (Allen et al., 1917; Andersen, 1912; Bradbury, 1977*a*; Koopman et al., 1978; Rosevear, 1965). Fruit may be eaten in situ or picked and taken to a nearby tree, where it is chewed, the juice squeezed out, and the pulp discarded (Lang and Chapin, 1917). *H. monstrosus* has been reported to scavenge meat scraps and attack chickens (Van Deusen, 1968). In captivity, *H. monstrosus* has been observed to drink by scooping water with its mouth while flying low over a bowl (Bergmans, 1978).

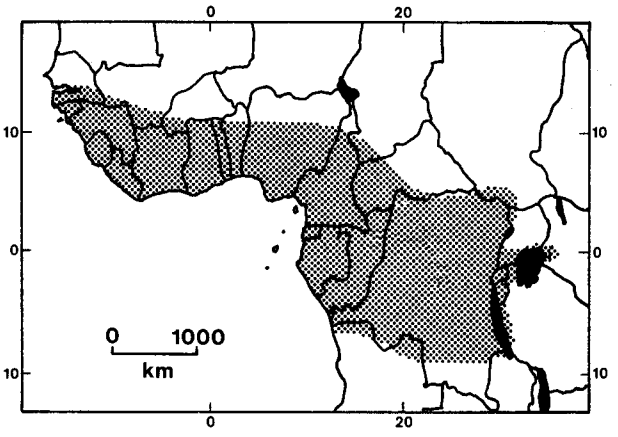

FIG. 4. Distribution of *Hypsignathus monstrosus* in Africa.

Hammerhead bats roost 20–30 m up in the forest canopy, usually on exposed branches beneath a dense cover of vegetation (Bradbury, 1977*a*). They hang quietly during the day, relying on camouflage for protection. There is no selection of a particular species of tree. *H. monstrosus* has been found roosting among rocks (Sanderson, 1940). A roost may have up to 25 individuals, but the average size is 4.4 bats (Bradbury, 1977*a*). Although all age classes and both sexes will roost together, only a female and her dependent young will roost closer than 10–15 cm to each other. Bradbury (1977*a*) found individuals changed roosts every day, while Thomas (1988) discovered that a group would use a roost for long periods if undisturbed. Although males may roost with females, during the breeding season the males set up separate territories. The territories may be close (<1 km) or far (>10 km) from the calling arena, while females roost in the intermediate area (Bradbury, 1977*a*, 1977*b*).

Males and females show different foraging strategies. Females use a trap-line strategy, relying on a constant but moderate-quality food supply. They apparently establish a regular route through the forest, feeding on dependable food sources, even if the food is not of the highest quality. Males tend to search for rich food patches, flying up to 10 km to feed on a particularly rich food supply (Bradbury, 1981).

Infection by parasites appears to be common among adult *H. monstrosus*, which hosts the following mites: *Mycteronyssus polli* (Fain, 1959), *Teinocoptes auricularis* (Fain, 1967), *Ancystropus aethiopicus* (Dusbabek and Bergmans, 1980). This bat hosts its own specific hepatoparasite, *Hepatocystis carpenteri* (Miltgen et al., 1980). In at least some populations, nearly all individuals are infected (Ayala et al., 1981).

BEHAVIOR. The most studied behavior of *H. monstrosus* is the lek or arena mating system that occurs for the 1–3 month breeding season. A lek is formed when males gather at night in an area to advertise themselves to females. This occurs along stream or river beds where a group of 20–135 males gather in a long (400–1,600 m) narrow (ca. 40 m) assembly. The males are spaced regularly at 10 m intervals and defend locations within the arena. Males attract females using loud guttoral honks or croaks (Allen et al., 1917; Wickler and Seibt, 1976) and wing flapping. Females fly through the arena, pick a mate, and land on a branch next to the male. Having been chosen, males emit a "staccato buzz" call and, without prelude, a short (30–60 s) copulation follows. Usually a few males, located in the geometric center of the lek, are responsible for the majority of matings. Calling activity is bimodal with peaks at 1900 and 0400 h. Males spend about 4 h at the lek before leaving to forage. The early evening session is most important for copulations, while the late night period is taken up with male–male agonistic behavior as individuals try to establish territories. As the breeding season progresses, the late-night session becomes less important (Bradbury, 1977*a*, 1977*b*, 1981). When in the singing assemblage, males show a lack of fear and seem oblivious to talking, rapping, banging of pots, or gunfire (Allen et al., 1917). *H. monstrosus* males have been known to reply to calls of Franquet's fruit bat (*Epomops franqueti*) and the croaks of the western tree dassie (*Dendrohyrax dorsalis*; Brosset, 1966).

GENETICS. Female *H. monstrosus* have a diploid number of 36 chromosomes and a fundamental number of 68 (Bogart et al., 1977; Haiduk et al., 1980). The standard karyotype is indistinguishable from that of *Epomops franqueti* (Haiduk et al., 1980). G-band and C-band karyotypes also have been reported (Haiduk et al., 1981). The Y chromosome has not been found; males have the unusual chromosome combination of XO (Bogart et al., 1977).

REMARKS. *Hypsignathus monstrosus* also is called hammerheaded bat, hammer bat, and big lipped bat.

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