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Lavia frons.

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Lavia Gray, 1838

Lavia Gray, 1838:490. Type species *Megaderma frons* E. Geoffroy, by original designation.
Livia L. Agassiz, 1846:6. Misspelling of *Lavia.*

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Megadermatidae. The genus *Lavia* contains one recent species.

Lavia frons (Geoffroy 1810)

African Yellow-winged Bat

La *feuille* Daubenton, 1759:388. Invalid name, not a binomial.
Megaderma frons Geoffroy, 1810:192. Type locality Senegal.
Lavia rex Miller, 1905:227. Type locality "Taveta, German East Africa (Tanzania)."

CONTEXT AND CONTENT. Context as above. No subspecies are currently recognized (Koopman, 1993).

DIAGNOSIS. *Lavia frons* (Fig. 1) is distinguished from all other African bats except *Cardioderma cor* in having a large, erect noseleaf, a divided tragus, and large ears that are basally united across the top of the head. *Lavia frons* differs from *Cardioderma cor* by having a long (ca. 20 mm) noseleaf that is bluntly truncated at its tip and a tragus with the inner lobe sharply pointed and the outer lobe pointed and >0.5 the length of the ear. *Cardioderma* has a shorter noseleaf, <15 mm, and a tragus with the inner lobe quadrate or rounded and the outer lobe pointed but <0.5 the length of the ear (Hayman and Hill, 1971). *Lavia* also has distinctive coloration, with yellowish ears and flight membranes and blue to slaty gray fur.

GENERAL CHARACTERS. Fur is long and is blue gray, pearl gray, or slaty gray, often greenish-yellow posteriorly in males and on the underparts. Fur extends sparsely onto the upper arms both above and below, but otherwise membranes are naked. Ears and flight membranes are variegated bright yellow, reddish- to orange-yellow, or light brown. Ears are enormous with large, bifid tragi. Ears are joined to form a high band across the forehead. Both lobes of the tragus are pointed, and the outer lobe is relatively long. The noseleaf is long, broad, and bluntly truncated at the tip. The eyes are very large. *L. frons* has a well-developed interfemoral membrane but no external tail.

Ranges of measurements (in mm) for 31 females, 25 males, and 41 adults of unknown sex are as follows: length of head and body, 60–80; length of forearm, 53.1–64.3; length of metacarpal III, 39.5–48; length of first phalanx, 21.5–26; length of second phalanx, 36–45; length of metacarpal IV, 41–50; length of first phalanx, 14–17; length of second phalanx, 13.5–18; length of metacarpal V, 42.5–51.5; length of first phalanx, 13.5–18; length of second phalanx, 14.5–20.5; length of ear, 33–47; length of interior lobe of tragus, 11.5–14.5; length of exterior lobe of tragus, 22.5–27; length of noseleaf, 16–23; breadth of noseleaf, 10–16; length of tibia, 29–37; length of foot, 15–20 (Allen et al., 1917; Andersen and Wroughton, 1907; Miller, 1905; Poché, 1975; Rosevear, 1965). Body mass is 28–36 g (Kingdon, 1974). *Lavia frons* shows little sexual dimorphism, but males have glands on the lower back which exude a yellowish secretion that discolors the fur of that area and probably causes the sweet, spicy smell of males (Bergmans, 1977; Rosevear, 1965).

Frontal expansion of the skull of *L. frons* is well developed and has prominent postorbital processes (Fig. 2). Interorbital region is noticeably concave. Upper canines project noticeably forward, each having a large secondary cusp in addition to the main shaft. Mesostyles of upper molars are well developed. The following are skull measurements (in mm) from 31 females, 25 males, and 41 adults of unknown sex: greatest length of skull, 21.3–26.1; postorbital breadth, 7.3–8.0; greatest palatal width including molars, 8.2–9.2; zygomatic breadth, 13.5–15.5; mastoid breadth, 12.0–12.4; breadth of brain case, 10–11; length of maxillary tooth row, 8.2–10; length of mandibular tooth row, 8.9–11; breadth across upper canines, 4–5.4; breadth across m3–m3, 16.2–16.5 (Allen et al., 1917; Andersen and Wroughton, 1907; Miller, 1905; Poché, 1975; Rosevear, 1965). Dental formula is i 0/2, c 1/1, p 1/2, m 3/3, total 26 (Koopman, 1994).

DISTRIBUTION. *Lavia frons* is the only megadermatid in west Africa. *Lavia frons* is typically found in low-lying savannah and open woodland <2,000 m in elevation (Koopman, 1994; Nowak, 1994; Vaughan, 1987; Vaughan and Vaughan, 1986) and is probably absent from undisturbed rainforest (Koopman, in litt.). *Lavia frons* occurs south of the Sahara from Gambia and Senegal in the west through Guinea Bissau, Guinea, Sierra Leone, Burkina-Faso, southern Niger, Togo, Benin, Nigeria, Cameroon, Chad, Central African Republic, southern and central Sudan, western and eastern Ethiopia, western Eritrea, and northern Somalia in the east (Fig. 3). Its range continues south along the east African coast through Kenya and Tanzania, and west through Rwanda, Burundi, Zaire, Congo, and Gabon (Anderson and Wroughton, 1907; Ansell, 1978; Ansell and Dowsett, 1988; Happold, 1987; Hayman, 1967; Hayman and Hill, 1971; Hayman et al., 1966; Kingdon, 1974; Koopman, 1994; Koopman et al., 1978; Rosevear, 1965). The southern extent of the distribution is defined by two localities in northern Zambia (Ndola—Ansell 1978) and Malawi (Karonga—Ansell and Dowsett, 1988). Although *L. frons* appears to occur in Africa between 15°N and 15°S, the geographical distribution is imperfectly known with few documented precise localities, especially in west Africa (Koopman, personal communication). In east Africa, *L. frons* is conspicuously absent from the Machakos District, Kenya, despite the availability of *Acacia*-woodland (O'Shea and Vaughan, 1980). No fossils of *L. frons* are known.

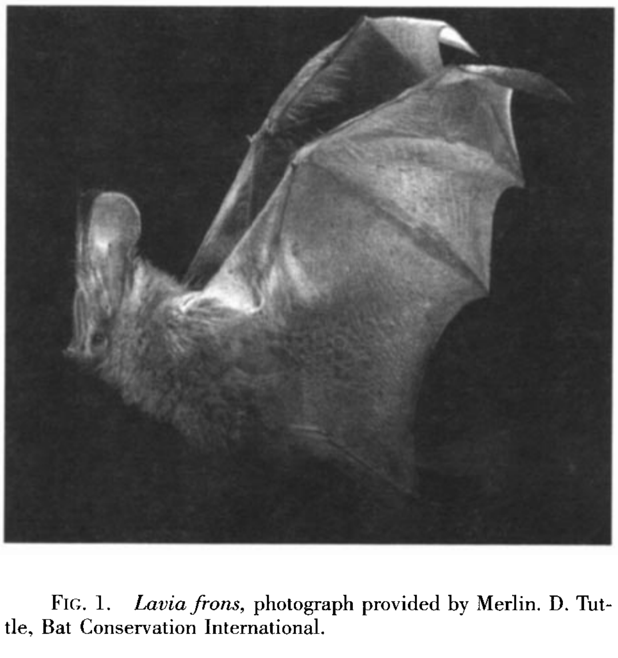

FIG. 1. *Lavia frons*, photograph provided by Merlin. D. Tuttle, Bat Conservation International.

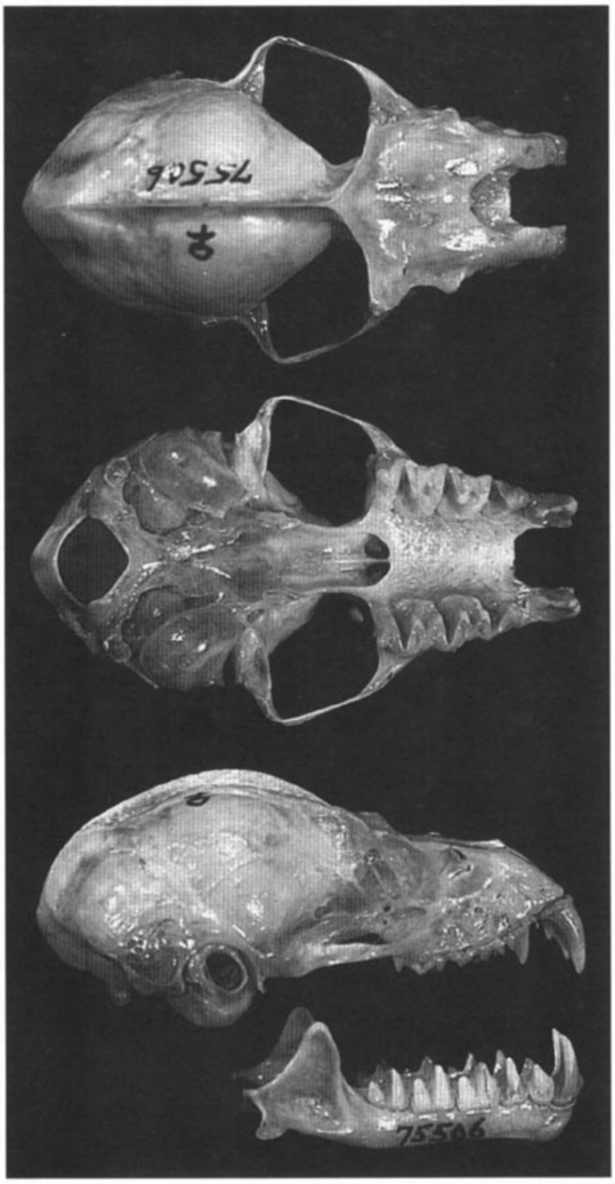

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Lavia frons* from Lake Baringo, Kenya (female, Royal Ontario Museum specimen 75506). Greatest length of cranium is 24.2 mm. Photographs by M. B. Fenton.

FORM AND FUNCTION. Females have two nonfunctional nipples, ca. 5 mm in length immediately above the anus. These are common in other megadermatids and in bats of some other families (Allen et al., 1917; Rosevear, 1965). Nonfunctional nipples are used by young *L. frons* to hold onto their mothers (Vaughan and Vaughan, 1987). Males have glands on the lower back which secrete a yellowish substance of unknown function (Rosevear, 1965). The scrotal sac of *L. frons* males is unusually prominent and pendulous, a condition which is unique within the Chiroptera, and the scrotal skin is heavily pigmented, which is unique among megadermatids (Kermott and Timm, 1988). Brown pigmentation is restricted to the epidermis and lighter pigmentation occurs at the base of the dermis. Underlying tissues of the testes and epididymis, as well as the tunica albuginea and vaginalis, are not pigmented (Kermott and Timm, 1988). Pigmentation may be an adaptation to protect germinal tissue from ultraviolet radiation in a species which roosts in locations exposed to direct sunlight. In *L. frons*, pigmentation may also function in social or reproductive communication (Kermott and Timm, 1988). *Lavia frons* does not enter torpor during daylight (Vaughan and Vaughan, 1986).

The eyes of *L. frons* are the largest (ca. 3 mm in diameter in adults) of any African microchiropteran except *Cardioderma cor* (Vaughan and Vaughan, 1986). Large eyes may be related to the fact that *L. frons* is often very active during the day (Rosevear, 1965). The tail is reduced to a coccyx and is not visible externally, but the interfemoral membrane is well developed (Allen et al., 1917). Zharova (1990) found no microflora in the esophagus of *L. frons*. Griffiths et al. (1992) describes the hyoid musculature in great detail in a systematic context.

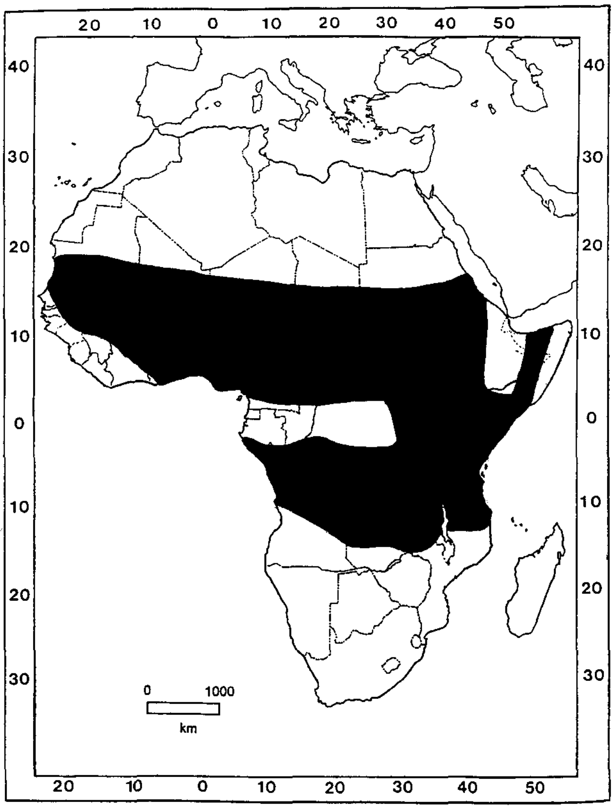

FIG. 3. Distribution of *Lavia frons* in Africa, modified from Kingdon (1974).

Lavia frons produces search-phase echolocation calls and at least three social calls that are audible to humans (Wickler and Uhrig, 1969). The echolocation call is a short, low-intensity, broadband call that yields information about close objects (Vaughan and Vaughan, 1986). The presence of large eyes and a tapetum lucidum suggest that night vision may augment echolocation (Vaughan and Vaughan, 1986) for perception of prey and allow *L. frons* to perceive silhouetted insects, as is done by some nightjars (Caprimulgidae—Mills, 1986). Social calls are of three main types and are heard before or during aggression, copulation, or interactions between mother and offspring (Wickler and Uhrig, 1969). The latter call has highest energy at ca.10 kHz (Wickler and Uhrig, 1969). *Lavia frons* does not appear to have a territorial song as heard in *Cardioderma cor* (Csada, 1977).

ONTOGENY AND REPRODUCTION. In different parts of its range *L. frons* may or may not reproduce synchronously. In Zambia, *L. frons* gives birth at the end of the dry season in October, although no data were available from other times of the year (Happold and Happold, 1990). At Lake Baringo in Kenya, *L. frons* is seasonally monoestrous (Happold and Happold, 1990) and typically gives birth in April at the beginning of the "long rains" that extend until June (Vaughan and Vaughan, 1986). At Cella in southern Upper Volta (Burkina-Faso), from March 11 to 14, Koopman et al. (1978) collected females with embryos ranging in size from 13 to 33 mm. In Garamba National Park, in extreme northeastern Zaire, a defined breeding season occurs with births starting in April (Kingdon, 1974). Pregnancies from Zaire, Uganda, and Sudan are more numerous in the months from January to April, but scattered records exist for other months (Kingdon, 1974). In Belgian Congo (Zaire), Verschuren (1957) captured five pregnant females and a juvenile in March and April, and Allen et al. (1917) collected one large fetus and five young between October and April.

Gestation lasts ca. 3 months, as with other megadermatids (Kingdon, 1974), and in all parts of its range *L. frons* gives birth to a single young. For several weeks after birth the young clings tenaciously to its mother, even when she forages (Allen et al., 1917; Vaughan and Vaughan, 1987). The young is then left at the roost for about a week and begins flying alone. Before the young begins flying, it practices flapping its wings while clinging with its feet to its mothers neck (Vaughan and Vaughan, 1987). Weaning occurs 20 days after the first solo flight, when the young is ca. 55 days old, but it continues to share its parents' territory and roost for at least another 30 days (Vaughan and Vaughan, 1987).

ECOLOGY. *Lavia frons* generally inhabits riparian habitats in low-lying woodland and savannah throughout its range. *Lavia frons* can be found in forest or open habitat, usually in low branches of acacia trees and thorn bushes along rivers, swamps, and lakes (Kulzer, 1962; Nowak, 1994), and it flies close to and over rivers and open water (Happold, 1987). In acacia-savannah woodland of East Africa, *L. frons* is associated with acacia trees, which attract many insects during the flowering period in the dry season when insect availability is low (Vaughan and Vaughan, 1986). *Lavia frons* prefers habitats in which it can observe its surroundings and is therefore found where vegetation is not very dense (Nowak, 1994).

Lavia frons is characterized as a tree-roosting bat (Kulzer, 1962) that roosts singly in small trees and shrubs (Happold, 1987). In Kenya, *L. frons* typically occurs in *Acacia tortillis* or *A. elatior* at heights of 5–10 m (Delany and Happold, 1979; Vaughan and Vaughan, 1986). In Burundi, *L. frons* typically occurs in patches of dry bush below *Hyphaene benguellensis* (Verschuren, 1980). *Lavia frons* also roosts in tree cavities and buildings (Rosevear, 1965). Roosting habits are similar throughout the species range and resemble those of *Nycteris hispida*, which also spends the day on low branches in the bushland and in the savanna, protected under thick shady bushes (Kulzer, 1962). The manner in which *L. frons* hangs pendant from branches <1 cm in diameter (Vaughan and Vaughan, 1986) has been compared with that of megachiropterans (Kulzer, 1962).

Lavia frons uses primary and peripheral roost trees with the primary roost tree being the roost to which bats return in the morning and meet before foraging in the evening (Vaughan and Vaughan, 1986). During the day, short flights (<2 m) are made between primary and peripheral roost trees. Short flights between roosts are made throughout the day on hot days, presumably because bats are looking for shade, whereas long flights are less common than short flights and are often made in the heat of midday (Vaughan and Vaughan, 1986).

Lavia frons feeds solely on insects, unlike other members of the family Megadermatidae that often feed on small vertebrates. *Lavia frons* hunts soft- and hard-bodied insects (Hollister, 1918; Kingdon, 1974; Vaughan and Vaughan, 1986). Termites (*Macrotermes falciger*), scarabid beetles, orthopterans, lepidopterans, and dipterans have been recorded as prey (Kingdon, 1974; Rosevear, 1965; Vaughan and Vaughan, 1986). The size of insects captured appears to vary from "very small to relatively large" (Kingdon, 1974), however only prey >2 mm were captured by *L. frons* in Kenya (Vaughan and Vaughan, 1986). Vaughan and Vaughan (1986) suggest that *L. frons* occupies an exclusive feeding niche because of its unique foraging style and because the time and place of foraging do not overlap with those of other bats in the area.

Predation pressure on *L. frons* is probably high because of its conspicuous coloration, roosting habits, and activity during both day and night. However *L. frons* does not seem to have a consistent predator, perhaps because it remains alert during the day. Predators of *L. frons* include mambas (*Dendroapsis angusticeps*), night tree vipers (*Boiga blandingii*), and bat hawks (*Machaerhamphus anderssoni*) in Tanzania (Wickler and Uhrig, 1969), and diurnal European kestrels (*Falco tinunculus*) in Kenya (Vaughan and Vaughan, 1986). In Kenya, *L. frons* flew away when approached by hornbills (*Tockus*), white-browed coucals (*Centropus superciliosus*), and grey-headed bush shrikes (*Malacotus blanchoti*—Vaughan and Vaughan, 1986).

No interference competition occurs between members of a *L. frons* male-female pair when foraging in close proximity (Vaughan and Vaughan, 1986). *Lavia frons* may compete for prey with some birds. Nightjars (Caprimulgidae), that have similar foraging styles, have occasionally been chased by male *L. frons* (Vaughan and Vaughan, 1986). On more than one occasion, *L. frons* has been seen pursuing the same insect as a drongo (*Dicrurus adsimilis*), which also forages from acacia branches (Vaughan and Vaughan, 1986).

The effects of human activity on the population dynamics of *L. frons* are unknown. There is also no record of population change over time. *Lavia frons* is not listed as threatened or endangered by any national or international organization, but is probably uncommon. A close association may occur between populations of *L. frons* and *A. tortillis* in the acacia-savanna areas of East Africa (Vaughan and Vaughan, 1986). *Acacia tortillis* lacks synchrony in blooming and provides growth of new leaves in the dry season which is accompanied by bursts of insect abundance that may be important for *L. frons* (Vaughan and Vaughan, 1986).

BEHAVIOR. *Lavia frons* is behaviorally monogamous (Vaughan and Vaughan, 1986). As no genetic data on paternity are available for *L. frons*, extra-pair copulations cannot be precluded. Pair bonds are established and maintained during the breeding season and pairs maintain exclusive foraging territories (Vaughan and Vaughan, 1986). Behavior of pairs is predictable with respect to foraging route, roosting tree, and roosting twig (Vaughan and Vaughan, 1986).

While roosting, bats are usually 5–10 m above the ground and the male and female of a pair are <1 m apart (Vaughan and Vaughan, 1986). *Lavia frons* is alert throughout the day, moves between roosts during the day, and begins foraging earlier than other bats (Happold, 1987; Hollister, 1918; Vaughan and Vaughan, 1986). Movement between roosts may facilitate behavioral thermoregulation which involves moving into a basking site in the sun or a cooling site in the shade on cool and warm days, respectively (Kingdon, 1974; Loveridge, 1922; Vaughan, 1987). Wing fanning and shivering have not been observed.

Pairs of *L. frons* have exclusive feeding territories (0.6–0.95 ha), with the distance between pairs of bats always >20 m (Vaughan and Vaughan, 1986). During the day, one member of the male-female pair is vigilant and has a characteristic swivel, through an arc of 225°, in which the head is held up and the ears are pinned against the back to track the sources of disturbance (Vaughan and Vaughan, 1986). Upon returning from foraging in the morning (10 min before sunrise) and before foraging in the evening (30–40 min before sunset), males visit the peripheral roost trees and defend them against conspecifics (Vaughan and Vaughan, 1986).

Before foraging in the evening, males and females meet at the primary roost tree for a period of grooming, stretching, and social interaction (Vaughan and Vaughan, 1986). *Lavia frons* is a sit-and-wait predator that scans for insects (>2 cm) and then swoops to intercept the insects before returning to the roost site to eat its prey (Happold, 1987; Vaughan and Vaughan, 1986). *Lavia frons* does not glean insects from the ground and can be found foraging from 1 m to 20–30 m above the ground (Vaughan and Vaughan, 1986). Foraging behavior differs between wet and dry seasons. During the dry season, foraging is biphasic, with an initial search phase when *L. frons* visits a number of trees with few foraging flights, and a subsequent feeding phase when *L. frons* forages from the same tree for 15–20 min, presumably until the patch is depleted (Vaughan and Vaughan, 1986). During the wet season, when prey is constantly available, *L. frons* selectively forages at canopy level for insects of 1–2 cm, and feeding frequency appears to be limited by handling time (Vaughan and Vaughan, 1986). Some form of information transfer (Wilkinson, 1992), such as close range vocal communication, is likely to occur between members of a foraging pair because one member of a pair (usually the female) joins the other at foraging patches (Vaughan and Vaughan, 1986).

The most common male-female interaction, most often initiated by the male in the morning, involves one member of the pair swooping up to its partner and hovering, which may or may not be accompanied by vocalizations (Vaughan and Vaughan, 1986). After the period of interaction, the pair separates for the day and does not interact until shortly before foraging in the evening (Vaughan and Vaughan, 1986). Male-female interactions peak in May and June when rains are frequent, insects are abundant, and juveniles are learning to forage (Vaughan and Vaughan, 1986). During this time, males and females interact at midday as well as dawn and dusk (Vaughan and Vaughan, 1986). Apparent courtship flights (during which males attempt to mount perched females) occur during this period of peak interaction (Vaughan and Vaughan, 1986).

REMARKS. *Lavia* comes from *lavo* which means fine, elegant, or splendid; *frons* refers to either leaf or forehead. Thus, the scientific name refers either to the "splendid leaf" that is a prominent feature of this species or to the striking frontal appearance of the skull (Rosevear, 1965).

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