MAMMALIAN SPECIES No. 394, pp. 1–4, 3 figs.

Epomophorus wahlbergi.

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Published 5 June 1992 by The American Society of Mammalogists

Epomophorus wahlbergi (Sundevall, 1846)

Wahlberg's Epauletted Fruit Bat

Pteropus wahlbergi Sundevall, 1846:118. Type locality "Prope Port-Natal et in Caffraria interiore occisus" (Durban, Natal, South Africa).

Pteropus haldemani Hallowell, 1846:52. Type locality "Western Africa."

Epomophorus wahlbergi: Peters, 1868:869. First use of current name combination.

Epomophorus zenkeri Matschie, 1899:46. No type originally designated. Type locality restricted to "Chinchoxo, Cabinda" (Angola) by Anderson (1912:524).

Epomophorus neumanni Matschie, 1899:50. No type originally designated. Type locality restricted to "Mombasa, British East Africa" (=Kenya) by Andersen (1912:524).

Epomophorus stuhlmanni Matschie, 1899:50. No type originally designated. Type locality restricted to "Vikindo, Usaramo, German East Africa" (=Tanzania) by Andersen (1912:527).

CONTEXT AND CONTENT. Order Chiroptera, Suborder Megachiroptera, Family Pteropodidae, Subfamily Pteropodinae, Genus *Epomophorus*. Six species are recognized (Bergmans, 1988); a key is presented in Boulay and Robbins (1989). Andersen (1912) recognized two subspecies of *E. wahlbergi*:

E. w. haldemani Hallowell, 1846:52, see above (*zenkeri* Matschie and *neumanni* Matschie are synonyms).

E. w. wahlbergi Sundevall, 1846:118, see above (*stuhlmanni* Matschie is a synonym).

The two subspecies differ in size; this difference is most evident in the skulls of males (skulls of male *E. w. haldemani* range from 47 to 51 mm in length; those of *E. w. wahlbergi* range from 52 to 56 mm; Andersen, 1912). There is considerable overlap in characters and it is possible that *E. w. haldemani* is not distinct from *E. w. wahlbergi* (Bergmans, 1988; Hayman and Hill, 1971). Intermediates have been found over a large part of the range of the species (particularly in eastern Africa) and size differences actually may represent clinal variation (Bergmans, 1979).

DIAGNOSIS. *Epomophorus* is distinguished from other members of the Pteropodinae by the presence of white epaulettes of fur in males; no white nose and eye patches; three upper cheekteeth; six prominent palatal ridges, one or two being post dental, which are no different from interdental ridges. The post-dental palate is strongly concave posteriorly (Hayman and Hill, 1971).

In the field, *E. wahlbergi* (Fig. 1) closely resembles *E. gambianus crypturus*. The two can be distinguished by post-dental palatal ridges; *E. g. crypturus* has two palatal ridges behind the last molar, whereas *E. wahlbergi* has only one (Smithers, 1983). The presence of one post-dental palatal ridge distinguishes *E. wahlbergi* from all other *Epomophorus*.

GENERAL CHARACTERS. *Epomophorus wahlbergi* is buff to brown in color with distinctive white tufts at the front and back bases of the ears. Yellowish individuals are females, whereas the darkest animals are males. Hair tufts at the ear bases are white in the darker animals and sometimes yellow in the light-brown individuals (Wickler and Seibt, 1976).

Ranges of measurements (in g or mm; males and females, respectively) for external characters are: body mass, 60–124, 54–125; length of forearm, 72–95, 68–88; wingspan, 510–600, 456–540; length of ear, 22–26, 21–25; length of tibia, 33–40, 28–37; length of hind foot (including claw), 21–26, 18–24 (Bergmans, 1988; Happold et al., 1987). Apart from the size difference, there are two other differences between sexes: males possess a small, central-pharyngeal sac, and adult males have shoulder pouches and erectable epaulette-like hair tufts (Andersen, 1912).

Ranges of measurements (in mm; males and females, respectively) for cranial characters are: greatest length of skull, 44–57, 41–49; condylobasal length, 44–57, 41–49; rostrum length, 19–23, 16–20; zygomatic width, 25–29, 23–27; length between first canine and first molar, 16–19, 14–17 (Fig. 2; Bergmans, 1988).

DISTRIBUTION. Epomophorine (epauletted) bats are found only in Africa (Wickler and Seibt, 1976). *E. wahlbergi* occurs in eastern and southeastern Africa (Fig. 3). The species ranges from Somalia and Uganda to South Africa and Angola and along the southern edges of the Congo basin forests at least to Gabon (Bergmans, 1988), and it has been reported from southwestern Cameroon (Aellen, 1952).

FORM AND FUNCTION. The lungs of *E. wahlbergi* are relatively large (lung volume per unit body weight is 0.043 cm^3/g). They have an extensive alveolar surface area (surface area of tissue barrier per unit of body mass is 138 cm^2/g), a thin blood-gas barrier (0.267–0.349 μm), and a high capacity for diffusing per unit of body mass (0.02 ml O_2 min^{-1} mm Hg^{-1} g^{-1}; Maina, 1982; Maina et al., 1982). Although the overall appearance and structure of the lung is similar to that of a non-volant mammal, these adaptations allow the lung to provide the large amount of oxygen necessary for flight (Maina, 1985). The left lung of *E. wahlbergi* is unlobed and the right lung has two incompletely separated lobes and an accessory lobe. To accommodate their large lungs, the thoracic cavity is large and the abdominal cavity is compressed towards the narrow pelvic

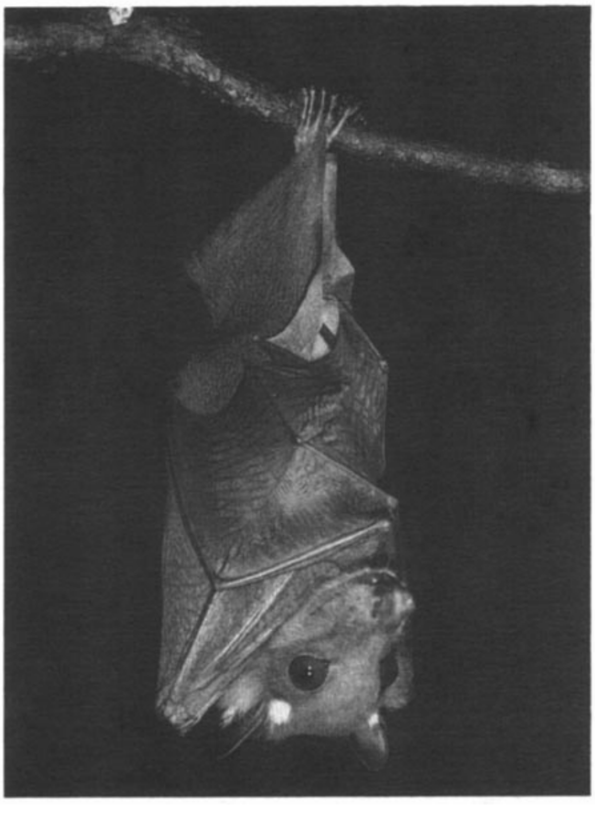

FIG. 1. *Epomophorus wahlbergi* photographed in Zimbabwe. Photograph courtesy of M. B. Fenton.

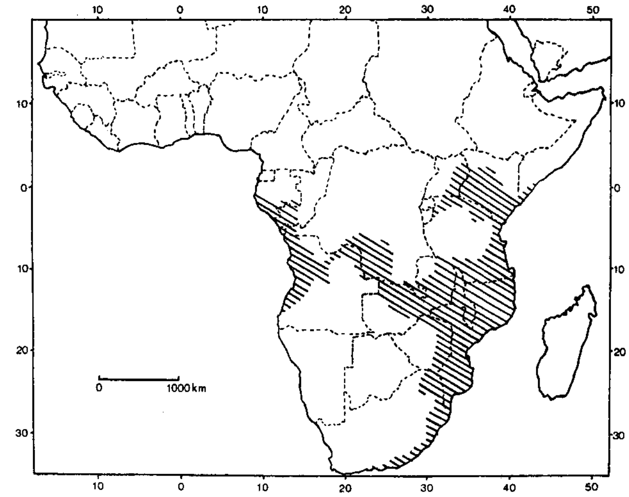

FIG. 3. The distribution of *Epomophorus wahlbergi* in Africa (modified from Bergmans, 1988).

inlet. The gastrointestinal tract is correspondingly small. Other lung structure also is similar to that of non-volant mammals with a conducting zone of bronchi, bronchioles, pulmonary arteries, and veins, an intermediate zone of alveolar ducts, and a respiratory zone of alveoli and capillaries (Maina, 1985).

ONTOGENY AND REPRODUCTION. *Epomophorus wahlbergi* has a seasonally polyestrous reproductive cycle with two birth periods per year (Anciaux de Faveaux, 1972, 1983). In Kenya (Andersen, 1912; O'Shea and Vaughan, 1980) and the Congo (Bergmans, 1979), the first birth period occurs in February and March, and the second from October to December. Varying parturition dates may reflect differently timed reproductive cycles in different parts of the range (Bergmans, 1979). One young and occasionally two are born (Anciaux de Faveaux, 1972).

In Kenya, the first lactation period of *E. wahlbergi* coincides with the peak of fruit availability during the rainy season, but the second lactation period occurs 6 months later during the dry season. It has been speculated that pteropodids (including *E. wahlbergi*) are capable of timing one lactation period to ensure a maximal supply of food, but are unable to optimally time the second because of a relatively rigid 5–6 month gestation period (Thomas and Marshall, 1984).

Individuals may be full-grown at the age of about 15 months. Females can take part in the second reproduction cycle after their own birth and males in the third. Females may be ahead of males in reaching sexual maturity; shoulder tufts in males seem to develop only after the bats have reached adult size (Bergmans, 1979).

At birth, the teeth of *E. wahlbergi* are lightly enamelled, small, and sharp. The dental formula of a neonate is i2/2, c1/1, m1/1, total 16. During weeks 2 and 3 of life, the second milk teeth premolars appear in the upper and lower jaws giving a total of 20 teeth. The adult dental formula is i2/2, c1/1, p2/3, m1/2, total 28. The permanent teeth are heavily enamelled. Premolars and molars are conspicuously cusped. The age at which all permanent teeth are present is 81–150 days; mean, 106 days (Sowler, 1980).

ECOLOGY. *Epomophorus wahlbergi* is a savanna, woodland, and forest-margin species not found at altitudes >2,000 m (Kingdon, 1974). The species occurs in areas with a mean annual rainfall of 700 mm and in drier areas of river valleys containing evergreen forests with a minimum annual rainfall of 250 mm (Smithers, 1983).

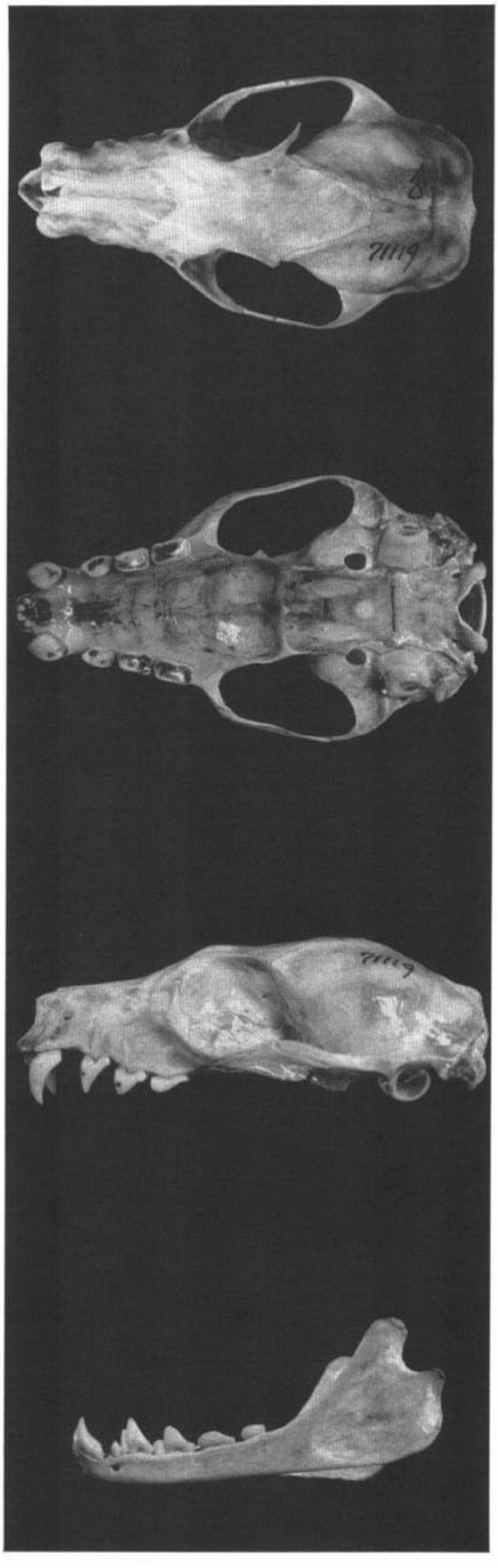

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FIG. 2. Dorsal, ventral and lateral views of the cranium, and lateral view of the mandible of a male *Epomophorus wahlbergi* (Royal Ontario Museum 71119 from Central Province, Kenya). Greatest length of the skull is 45.2 mm. Photographs courtesy of G. Temple.

The diet of *E. wahlbergi* consists mainly of figs such as *Ficus sycomorus*. It also eats the fruits of *Diospyrus* and *Psidium guajava* (Pienaar et al., 1980; Wickler and Seibt, 1976). *E. wahlbergi* also eats the leaves of two species of *Balanites*. The leaves of this plant contain two steroidal components, diosgenin and yamogenin (Wickler and Seibt, 1976). The species visits flowers of *Adansonia* in Kenya, acting as a pollination agent (Kock, 1972). Remnants of beetles and other insects have been found in the stomach contents of a few individuals, suggesting that *E. wahlbergi* is partially insectivorous (Pienaar et al., 1980, 1987). Fruit is carried from the source to a perch some distance away where the juice is eaten and the skin and seeds are spat out. Food is not carried back to the day roost (Fenton et al., 1985; Wickler and Seibt, 1976).

In daylight hours, *E. wahlbergi* roosts in groups of 3–100 individuals. Wickler and Seibt (1976) reported that the species roosts in the open and does not occur in caves. However, Fenton et al. (1985) found some animals roosting in dense-riverine forest and others in shelter caves. Kingdon (1974) stated that groups of *E. wahlbergi* move around according to the regional ripening of fruits and do not remain linked to a roost for long periods of time. Conversely, Wickler and Seibt (1976) suggested that *E. wahlbergi* has long-term site attachment to a given roost in a suitable area. Fenton et al. (1985) radiotracked *E. wahlbergi* roosting in trees with dense canopies in Kruger National Park, South Africa. All of the *E. wahlbergi* tracked switched day roosts, but there was no evidence of the bats selecting roosts that were close to the food supply. Switching of day roosts may reduce the risk of predation. At dusk, females usually made longer moves (up to 4 km) between their day roosts and feeding areas, while males tended to make shorter moves (<500 m) to feeding areas; males made longer moves later in the night.

Epomophorus wahlbergi sometimes associates with *E. labiatus*, roosting in separate groups, but in the same tree. At night, the two species will feed simultaneously from the same tree (Kingdon, 1974). *E. wahlbergi* also associates with *E. gambianus* (Smithers, 1983).

A malarian parasite (*Hepatocystis*) infects *E. wahlbergi* (and other African fruit bats). Exoerythrocytic schizonts (immature parasites) are found in the liver of infected individuals (Garnham, 1950). A virus isolated from the brain of *E. wahlbergi* is indistinguishable from that of rabies by fluorescent-antibody tests. The virus, called Lagos bat virus because it was first isolated from *Eidolon helvum* on Lagos Island, Nigeria, causes a fatal rabies-like disease in these Megachiroptera (Meredith and Standing, 1981).

BEHAVIOR. As in most Megachiroptera, flight in *E. wahlbergi* is mainly used for travelling from roosts to feeding areas. The wings of *E. wahlbergi* are relatively broad and flight is fairly slow. The animals rarely rise above the canopy, and during flight, individuals sometimes bang into obstacles and conspecifics. Take-off in the evenings usually is preceded by intensive 0.5 h-grooming sessions (Wickler and Seibt, 1976). Flight occurs throughout the night, but after approximately 2000 h, flight declines to almost one-half of peak level (Fenton et al., 1985).

Little social interaction has been witnessed in *E. wahlbergi*. Group cohesion is seen only during roosting time. The only other type of social interaction that has been observed is mother-young relationships (Fenton et al., 1985; Wickler and Seibt, 1976).

Males of the closely related genera *Epomops*, *Epomophorus*, *Micropteropus*, and *Hypsignathus* produce loud frog-like calls. Male *E. wahlbergi* begin calling after leaving the day roost. Usually, a calling male hangs from a branch at least 2–3 m above the ground. Calling usually occurs from 15 min to 1 h before a male moves to another tree. While calling, the normally concealed epaulettes can be everted and displayed. Skin muscles control this tuft erection. Males call an average of 75 times/min and occasionally the rate is increased to 100–120 calls/min (Wickler and Seibt, 1976). Periods of accelerated calling are brief (<60 s in length) and relatively rare (Fenton et al., 1985). Calls contain a few relatively pure frequencies with a slight click at the beginning. The fundamental frequency is at approximately 1,750 Hz and three more frequencies occur at 3,500, 5,200, and 7,000 Hz. In Kenya, males call mainly during the dry season. Calling appears to space males out at about 50-m intervals. In other epomophorines, calling attracts females, and the behavior also may serve this purpose in *E. wahlbergi* (Wickler and Seibt, 1976).

GENETICS. *Epomophorus wahlbergi* has a diploid number of 36 chromosomes and a fundamental number of 68 (Dulic and Mutere, 1973; Peterson and Nagorsen, 1975). The non-differentially stained karyotype is identical to that of *E. gambianus* with six metacentrics, eight submetacentrics, and four subtelocentrics. The X chromosome appears to be submetacentric and the Y chromosome acrocentric (Dulic and Mutere, 1973).

REMARKS. References to species of *Epomophorus* in this account follow Bergmans (1988).

Andersen (1912) described the range of *E. w. haldemani* as "essentially western (Cameroons to Benguela), but extends through the Congo Valley east to British and northern German East Africa" and that of *E. w. wahlbergi* as "southern British East Africa to eastern Cape Colony." Bergmans (1988) noted that the two subspecific ranges given by Andersen cross each other. Bergmans concluded that the geographical variation in size within *E. wahlbergi* is clinal and subspecific divisions on the basis of size differences are untenable.

LITERATURE CITED

AELLEN, V. 1952. Contribution à l'étude des chiroptères du Cameroun. Mémoires de la Société Neuchâteloise des Sciences Naturelles, 8:1–121.

ANCIAUX DE FAVEAUX, M. 1972. Répartition biogéographique et cycles annuels des chiroptères d'Afrique centrale. Ph.D. dissert., l'Université de Paris, France, 429 pp.

———. 1983. Les cycles annuels de reproduction chez les chiroptères phytophiles au Shaba (S.E. Zaire) et au Rwanda. Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques, 237:27–34.

ANDERSEN, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. I. Megachiroptera. Trustees of the British Museum, London, 854 pp.

BERGMANS, W. 1979. Taxonomy and zoogeography of the fruit bats of the People's Republic of Congo, with notes on their reproductive biology (Mammalia, Megachiroptera). Bijdragen Tot De Dierkunde, 48:161–186.

———. 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 1. General introduction; materials and methods; results: the genus *Epomophorus* Bennett, 1836. Beaufortia, 38:75–146.

BOULAY, M. C., AND C. B. ROBBINS. 1989. Epomophorus gambianus. Mammalian Species, 344:1–5.

DULIC, B., AND F. A. MUTERE. 1973. Les chromosomes de trois espèces des mégachiroptères (Mammalia, Chiroptera) d'Afrique orientale. Caryologia, 26:389–396.

FENTON, M. B., R. M. BRIGHAM, A. M. MILLS, AND I. L. RAUTENBACH. 1985. The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. Journal of Mammalogy, 66:461–468.

GARNHAM, P. C. C. 1950. Exoerythrocytic schizogony in bat malaria. Nature, 166:155.

HALLOWELL, E. 1846. Description of a new species of bat from western Africa. Proceedings of the Academy of Natural Sciences of Philadelphia, 3:52–53.

HAPPOLD, D. C. D., M. HAPPOLD, AND J. E. HILL. 1987. The bats of Malawi. Mammalia, 51:337–414.

HAYMAN, R. W., AND J. E. HILL. 1971. Order Chiroptera. Pp. 1–73, *in* The mammals of Africa: an identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.

KINGDON, J. 1974. East African mammals: an atlas of evolution in Africa. Insectivores and bats. Academic Press, New York, 2A:1–341.

KOCK, D. 1972. Fruit bats and flowers. East Africa Natural History Society Bulletin, 7:123–126.

MAINA, J. M. 1982. The morphometric pulmonary diffusing capacity of a bat *Epomophorus wahlbergi*. The Journal of Physiology, 325:36P–37P.

———. 1985. A scanning and transmission electron microscope study of the bat lung. Journal of Zoology (London), 205:19–27.

MAINA, J. M., A. S. KING, AND D. Z. KING. 1982. A morphometric analysis of the lung of a species of bat. Respiration Physiology, 50:1–11.

MATSCHIE, P. 1899. Die Fledermäuse des Berliner Museums für Naturkunde. I. Megachiroptera. Reimer, Berlin, 102 pp.

MEREDITH, C. D., AND E. STANDING. 1981. Lagos bat virus in South Africa. The Lancet, 1:832–833.

O'SHEA, T. J., AND T. A. VAUGHAN. 1980. Ecological observations of an East African bat community (Kenya). Mammalia, 44: 485–496.

PETERS, W. C. H. 1868. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1867:865–872.

PETERSON, R. L., AND D. W. NAGORSEN. 1975. Chromosomes of fifteen species of bats (Chiroptera) from Kenya and Rhodesia. Royal Ontario Museum, Life Sciences Occasional Papers, 27: 1–14.

PIENAAR, U., I. L. RAUTENBACH, AND G. DE GRAAF. 1980. The small mammals of the Kruger National Park. National Parks Board of Trustees, Pretoria, 149 pp.

PIENAAR, U., S. C. J. JOUBERT, A. HALL-MARTIN, G. DE GRAAF, AND I. L. RAUTENBACH. 1987. Field guide to the mammals of the Kruger National Park. C. Struik, Cape Town, 176 pp.

SMITHERS, R. N. H. 1983. The mammals of the southern African subregion. University of Pretoria, Transvaal, 736 pp.

SOWLER, S. G. 1980. Tooth eruption in known age specimens of *Epomophorus wahlbergi*. South African Journal of Wildlife Research, 10:112–117.

SUNDEVALL. 1846. Nya Mammalia från Sydafrika. Öfversigt af Kongliga Svenska Vetenskaps-akademiens Förhandlingar, Stockholm, 3:118–119.

THOMAS, D. W., AND A. G. MARSHALL. 1984. Reproduction and growth in three species of West African fruit bats. Journal of Zoology (London), 202:265–281.

WICKLER, W., AND U. SEIBT. 1976. Field studies on the African fruit bat *Epomophorus wahlbergi* (Sundevall), with special reference to male calling. Zeitschrift für Tierpsychololologie, 40: 345–376.

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